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Paleozoic Perspectives: A Paleontological Tribute to G. Arthur Cooper

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Foreword

This collection of papers was solicited from colleagues and students of G. Arthur Cooper as a *Festchrift* in recognition of his profound influence on the study of brachiopods and their biostratigraphic application to geologic problems, especially in the Paleozoic Era.

Dr. Cooper initiated a period of growth in both the research staff and the National Collections of Fossils that guided the Smithsonian Institution to its present position of leadership in paleontological research. His own superb studies of fossil and living brachiopods are unsurpassed in breadth and paleontological significance. Mainly through his efforts, the Smithsonian has acquired an outstanding reference collection of invertebrate fossils that is the envy of the scientific community.

It is a pleasure to add my own heartfelt appreciation for Cooper's contributions to the science of paleontology and to the Smithsonian Institution.

Porter M. Kier, Chairman
Department of Paleobiology,
United States National Museum
of Natural History,
Smithsonian Institution

G Arthur Cooper

An Appreciation of G. Arthur Cooper

G. Arthur Cooper, geologist and curator, is an old-fashioned scientist. I mean "old-fashioned" in the very best sense of the word, but perhaps "traditional" is the more appropriate word. One dictionary defines a traditionalist as "one who passes on an accumulated store of knowledge to his successors." This definition sums up much of Cooper's career. In one way or another, he has devoted his life to the accumulation of geological and paleontological knowledge and to passing this remarkable store of information on to his colleagues. Some of this has been accomplished through a magnificent series of publications. But much of it has been on a less formal basis—through joint field experiences, discussions, talks at meetings, and the brachiopod seminars at the United States National Museum.

Although he was never formally a teacher, there is scarcely a researcher in brachiopods in the western world who has not acquired much of his lore from Cooper. On at least three occasions during the 1950s Coop conducted a series of seminars on brachiopodology, each of which was attended by six to eight persons. At these informal sessions he unselfishly passed on to these young people much of his accumulated knowledge on the collection, preparation, and interpretation of brachiopods and their stratigraphic significance. He has taught more paleontologists more about fossils than many academicians at the universities.

While a certain amount of his knowledge was acquired from his predecessors, a large part of Cooper's contribution to geology is of his own making. His taxonomic studies represent a quantum jump beyond those of earlier workers. Further, his biostratigraphic methods and facies studies were pioneering efforts that only now are being understood and applied by a younger generation.

G. A. Cooper was born 9 February 1902, at College Point, New York, and he has retained a flavor of that part of New York ever since. Who hasn't detected the Brooklynese creeping into his speech now and then? And he is an avid baseball fan to this day.

An early urge to collect and identify things was satisfied with mineral collecting. His love for minerals remains, and his support of the development of the Smithsonian Institution's mineral and gem collection reflects this continuing interest.

Fossils became a passion with Coop during his undergraduate days at Colgate. The great wealth of geologic material in the Hamilton beds near the college attracted his attention early, and he spent much of his spare time poking about the quarry on the Colgate campus and in the creeks and glens nearby. This familiarity with Hamilton rocks and fossils led inevitably to the classic treatment of Hamilton stratigraphy that was Cooper's thesis at Yale. His meticulous detail regarding the physical stratigraphy and biostratigraphy of these Middle Devonian beds has not been approached in any later work. The recent New York State Correlation Chart accepts *in toto* the concepts of that epoch as developed by Cooper nearly 40 years ago.

Field work and fossil collecting remain a large part of Coop's life even today. Nearly every year has found him in the field, measuring, observing, collecting, interpreting—always adding to his own subjective "feel" for the geology and augmenting the collections of the United States National Museum.

During the first ten years of his work at the Smithsonian, Cooper wrote short summaries of his field experiences yearly in the Smithsonian's "Explorations and Field Work" series, an interesting publication that expired after 1940, doubtless a victim of the war years. His first paper was aptly titled "Dry-Dredging in East-Central New York." During these ten years Cooper was collecting in New York, the Gaspé, the Appalachians, the Midwest, Michigan and Ontario, Nevada, New Mexico, Utah and, inevitably, western Texas. During the past 20 years he has revisited these areas time and again with many associates.

The first results of etching for silicified fossils were reported in 1940. Of this trip, Cooper wrote: "Two weeks were spent in the Glass Mountains searching for blocks suitable for etching. Many were obtained, and a fine collection of hitherto rare species is confidently anticipated when the limestone lumps are finally decalcified." His wildest expectations have been exceeded a hundred-fold. After many revisits to the Glass Mountains, the Permian brachiopod collection has been augmented by tens of thousands of specimens, and I understand that Coop confidently looks forward to one last trip to pick up a few rare species in the spring of 1970. The residents of Marathon are so accustomed to these "last trips" to western Texas that they greet him each year with "Well, Dr. Cooper, it's good to see you back again for the last time!"

Cooper went to Yale where he received his doctor's degree in 1929. Here he came under the influence of two great brachiopod workers, Charles Schuchert and Carl Dunbar. Thus, he is a direct intellectual descendant of the first great American brachiopodologist, James Hall. This experience turned him from fossil molluscs, his first love at Colgate, to brachiopods, and we are all the beneficiaries of this good fortune. The breadth of his brachiopod research is unequaled by any other paleontologist, past or present. He knows, intimately, brachiopods through their entire geologic range, and he has published definitive monographs on many taxonomic groups—from orthoids to productoids and rhynchonelloids to terebratuloids.

He is a remarkable collector and an unexcelled preparer of these beasts. I will never forget the magnificent demonstration of needlework that he gave at one of his seminars. Taking a terebratuloid with a chalky filling, he skillfully and quickly removed a part of the shell, excavated the interior, and laid bare the loop that was within. It looked remarkably easy until the rest of us tried our hand at it. This care and precision crops out in all his work. He is the curator *par excellence.* Always on the lookout for ways to increase the collections of the museum, he takes advantage of every opportunity to add new material. Each field trip is an experience in the fine art of fossil collecting.

No chance is lost, both going to and returning from a major project area, to enrich the museum's collections. I remember, especially, a trip to New Mexico, when our main goal was to collect Upper Devonian brachiopods; but there were one or two places where we just *had* to stop to get a few rare shells. And before we were finished we had made fine collections of Upper Ordovician from central New Mexico, of Pennsylvanian and Permian from various parts of western Texas, of Mississippian from Lake Valley, New Mexico, of Upper Pennsylvanian and Cretaceous from north-central Texas, and of Middle Ordovician from the Arbuckles.

The broader implications of Cooper's research, however, are never obscured by the immediate collecting, sorting, labeling, and curating aspects of his daily work. The Devonian correlation chart, published by the GSA in 1942, is largely a result of his efforts. His concepts of facies, zonation, and stages went into the chart, and it is only a matter of time before all geologists realize the true significance of this contribution. Characteristically, Cooper is busily revising that chart—in his spare time at home so as not to interfere with his "regular" work.

The Chazyan brachiopod monograph of 1956 also incorporates large amounts of stratigraphic information, much of which was developed by Cooper, and his nonrelative Byron Cooper, in the central Appalachians. It will be another decade before all these data are assimilated into the working geologic backgrounds of even the more knowledgeable stratigraphers and generalists. Probably no one else in North America knows as much as G. Arthur Cooper about the geology of three great Paleozoic Systems—the Ordovician, the Devonian, and the Permian.

His paleoecological interpretations of the Middle Devonian of the eastern and central United States, in the Geological Society of America's Paleoecology Memoir are models of cautious extrapolations into the distant past, and they have not been surpassed in clarity and insight into ancient geography and fossil environments.

Comprehensive studies of large groups of brachiopods regularly have received a large part of Cooper's attention. The first of these was the orthoid and pentameroid book that he wrote with Professor Schuchert. There followed studies of Cambrian and Ordovician shells (with Ulrich), the Tully fauna (with Stewart Williams) the productoids (with Miss Muir-Wood) and the magnificent Chazyan brachiopod biostratigraphic study. And, as is well known, Cooper is now completing his West Texas Permian monograph (with R. E. Grant), a publication that will be unparalleled in the history of brachiopod research. Thousands of photographs will illustrate this magnificent taxonomic work. Its publication will be the crowning event of an illustrious paleontologic career.

A major classification of brachiopods, first put forth in the brachiopod chapter of the Shimer and Shrock book *Index Fossils,* is reflected in all of Cooper's taxonomic work and is used today by practically all brachiopod students. It is characteristic that Cooper never intended this to be a formal classification—merely a working hypothesis by which to test continuing systematic research.

Cooper is not just a collector, classifier, monographer, and stratigrapher. He is a curator of unmatched skill at the Smithsonian. He has worked assiduously for more than 35 years to build what is undoubtedly the greatest reference collection of brachiopods in the world. But his interests do not stop there. He is keenly appreciative of all invertebrate fossils. His own research has led him to studies of pelecypods, echinoderms, and trilobites; and he is nearly as thrilled at finding new and beautiful corals or bryozoans as he is at describing new brachiopod genera.

To have shared the experience of a field collecting expedition with Cooper is to have been very fortunate indeed. His enthusiasm and quiet good humor are infectious. He is at ease with all sorts of people: scientists, ranchers, laborers, teachers, oilmen, and spinster amateur collectors. No geologist who has been closely associated with him doubts for one moment that here, indeed, is a great and good man.

This recitation of what Cooper has been doing in the last 40 years barely scratches the surface of the man himself. As head curator of geology and chairman of paleobiology at the United States National Museum, he quiety distinguished himself as an administrator of scientific research. I am certain that he would be the last person to agree with this evaluation, but, after observing for a number of years the developing careers and scientific contributions of the people he gathered around him in the Museum, I can attribute much of the success of this paleontological venture only to

Cooper's administrative skill. He is a kind, generous, thoughtful man who, as he waged the paper-work campaigns over the years, kept uppermost in his mind the best interests of his staff, paleontology in general, and the Smithsonian in particular.

Nevertheless, his personal interests do not center solely on paleontology and geology. He is an avid student of history, having read widely about early American history, the Civil War, the opening of the West, and explorations in all parts of the globe. His interests range through the whole field of natural history. Many are aware of his long-standing love affair with the National Zoological Park. He and his wife are regular visitors there, and they follow the fortunes of the various animals almost as carefully as do the keepers themselves. He is also an afficionado of flowering plants and can rapturize over the stunning displays of blooming cacti in the southwestern United States. His photographic skill has caught much of this fascination with natural wonders wherever he has traveled. Of course, the most constant objects of his lenses are his brachiopods. Where else would one see a man, at this advanced stage in a distinguished research career, patiently taking hundreds of pictures a day to illustrate a taxonomic paper?

Many honors have come Cooper's way during the course of his career at the Smithsonian. He received, in 1953, an honorary doctor of science degree from Colgate, his alma mater; he is a fellow of the Geological Society of America; and is a past-president of the Paleontological Society, the Geological Society of Washington, and the Paleontological Society of Washington. In 1958 he received one of the National Academy's highest honors, the Mary Clark Thompson medal, and in 1964 he became the second recipient of the Paleontological Society medal in recognition for his outstanding contributions to paleontology.

All the contributors to this book have been brushed by the genius of this man. Each of us has gone to Cooper to learn of brachiopods and stratigraphy and has come away a much richer and wiser scientist. My own life has been the fuller for having known G. Arthur Cooper—geologist, paleontologist, curator, natural philosopher, and friend.

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The Publications of G. Arthur Cooper

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GENERAL TOPICS

Byron N. Cooper

Roles of Fossils in Appalachian Stratigraphy

ABSTRACT

Fossils play a dominant role in unravelling the Paleozoic stratigraphy of the Appalachians. The stratigrapher and mapping geologist should acquire a good working knowledge of the general sequence of fossil assemblages and should work in association with competent paleontologists. Teamwork of this kind can lead to the solution of the many difficult problems related to migrating lithofacies and biofacies, recurrent common rock types and faunas, environmental influences on both lithologies and faunas, correlations of all kinds, and structural interpretations.

The doubtful panaceas of guide fossils, key rock types, and faith in any single kind of fossil should be avoided if meaningful geologic results are to be obtained. Dominant themes of this analysis include algae and echinoderms as rock-builders, recurring faunas, the failure of the guide fossil concept, and the difficulties in relying solely on lithologic criteria for mapping purposes. Comprehensive systematic monographs of all groups of invertebrate fossils are considered indispensable tools in furthering the knowledge of the geology of the Appalachians.

Fossil faunas in Appalachian sedimentary formations serve a variety of scientific purposes, some of which are fully appreciated solely by the systematic paleobiologist, others of which are best appreciated by the seasoned field geologist. It is the purpose of this paper to record some personal observations about fossils that are useful aids in recognizing and mapping Appalachian sedimentary formations. Generic and specific identities are not of critical importance in these remarks and will be mentioned only where necessary. Some things noted are cited as mere curiosities or enigmas.

Many of the details enumerated were passed along to me by two great field teachers—Charles Butts and G. Arthur Cooper. Others have been gathered during the course of 35 field seasons in the Appalachians. All are offered in the hope that they may be useful to other stratigraphers working in the Appalachians.

One of the truly inspiring personal experiences I have had was an extended field trip in 1945 down the Appalachians with Carl O. Dunbar, Percy Morris, G. A. Cooper, Dr. Wang of the Geological Survey of China, and Raymond S. Edmundson with whom I was associated for many enjoyable field seasons. I gained enormous respect for the value of fossils by watching Dr. Dunbar examine the fossiliferous rocks from Virginia to Alabama and, largely from his knowledge of the evaluation of shell structures in brachiopods and other fossil groups, methodically and calmly zero-in on relative ages of the beds, often without even mentioning names of the fossils. I witnessed a master stratigrapher and paleontologist at work. I recall particularly his observations atop Draper Mountain in Pulaski County, Virginia.

For years I had taken geologists up Draper Mountain on old U.S. Route 11 and tested their awareness of a curiosity—all the rocks on Draper Mountain along the highway are overturned. To an Appalachian geologist unfamiliar with Draper Mountain, the ride up the mountain could fail to convey the message of the rocks. The southeast-dipping Millboro could be mistaken for Martinsburg, the "overlying" red beds could pass for Juniata, and the overturned Clinch atop the mountain could be taken as part of the normal succession. I used to keep a confidential box score of how visitors responded to Draper Mountain; many of them who could not or did not read the rocks judged the

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section as normal, but not Dr. Dunbar. On getting out of the car on top of Draper Mountain he nosed around the beautiful exposure and remarked, "What a museum piece these exposures are! There's inverted forest bedding in that layer, overturned fracture cleavage in that little shale bed, and, look, did you ever see so many *Arthrophycus* peering at you wrong side up!" Those brief observations of a master stratigrapher and paleontologist in unfamiliar country summed up the evidence of deformation structures, sedimentary structures, and of the fossils, which pointed to inversion of the section. He had not missed a thing. I realized a little better the resources a stratigrapher has at his disposal after seeing an "old pro" react so quickly and competently to what he saw.

Scolithus in Lower Paleozoic Rocks

Some fossils are so abundant as to determine the lithology of many Appalachian stratigraphic zones. The oldest organic remains in the Appalachian Paleozoics that literally give the rock its peculiar appearance are the so-called *Scolithus* tubes in the Erwin or Antietam Formations. Perhaps the best display of *Scolithus* in the Appalachians is in a slightly feldspathic orthoquartzite zone about 80 feet thick, exposed on the broad crest of a southwest-plunging anticline along historic Jordan (pronounced "Jerdan") Road between Buena Vista, Rockbridge County, and the Blue Ridge Parkway. The *Scolithus* are straight tubular structures in which the sand filling is commonly very micaceous and, characteristically, pale green (see Plate 1). The alignment of the *Scolithus* in the Erwin beds along Jordan Road is so perfect, the tubes so abundant, and the spacing so close that the rock has fracture cleavage (see Plate 2). The cleavage mullions obviously are the result of the *Scolithus* but, alas, despite their abundance we do not really know what organism made the tubular markings and casts. These markings are elsewhere commonly segregated in definite zones, as they are along Jordan Road. When "*Scolithus*-bearing sandstone" is mentioned in the geologic literature, the special rock type evident along Jordan Road is generally what the stratigrapher is trying to describe (see Plate 3). Abundance is the contributor to the peculiar appearance of the rocks. *Scolithus* is a very common fossil found in beds as old as Unicoi but not tremendously abundant at that level except in a fairly pure-sand lithofacies. The occurrences in the Erwin and its equivalents to the north (Antietam and Potsdam) and south (Weisner) are especially noteworthy, and *Scolithus* in true abundance is a valid indication of medial to upper Erwin beds.

Algae as Rock Builders

The role of algae as a prime lithologic determinant perhaps has been the least appreciated of all lithologic phenomena in Appalachian rocks. The characteristic "ribbon-banded" algal-matte limestones are widely distributed in the lower part of the Paleozoic section beginning with the Patterson Limestone Member of the Shady Formation and extending up to the early Trentonian Witten Limestone. The algal masses in the Patterson limestones show the greatest range in size and configuration of any in the entire Appalachian succession. The commonest forms of algal growths are "tufted pancake" or "pizza"-types with strange little digitate, inosculate projections. The "pancakes" are blue-gray limestone, especially bluish in tint only because they are interleaved with equally irregular interstitial fillings of buff-yellow to reddish brown dolomite or dolomitic siltstone. The smaller algae in the Patterson carbonates range downward from about ten centimeters in diameter to virtually "eyeball" size, and they are almost—but never quite—spherical in shape. The smaller the algae, the better structure lamination they show. Some of the Patterson algal beds are chevron-flexed or tufted and provide a very distinctive lithology. Not uncommonly, this variety is associated with coarse recrystalline dolomites, some of which have acicular and geopetal structures. Nests of coarse white to pink dolomite are especially common.

The lower and middle Patterson algal limestones are especially noteworthy for two features which probably are better illustrated in Wythe County, Virginia (in the Patterson-Foster Falls-Austinville-Ivanhoe-Cripple Creek-Speedwell sector), than anywhere else. Coarse "eyeball" algal masses with crystalline quartz centers are especialy noteworthy. Probably the most fascinating feature of layered, petaloid algal growths is the structures that resulted from partial desiccation of algal plates or matte during periods of low tide (see Plates 4, 5c). Exposure probably caused the algal plates to contract and to cup upward into saucer-like shapes. Waters evaporating in these natural petri dishes produced radiating or culstered nests of anhydrite crystals which were later converted to dolomite—probably

PLATE 1.—Close-up of *Scolithus* structures in quartzite, showing influence of the tubes on the lithology; in west foothills of Blue Ridge Mountains, three miles east of Grottoes and 13.5 miles southwest of Elkton, Rockingham County, Virginia. (Photo by W. D. Lowry.)

during an early return of water cover. These curious dolomite pseudomorphs after anhydrite are commonly prismatic in habit, but many of the crystals show flared, fibrous extensions at one or both ends (see Plate 5A). The crystal clusters, not at all rare, range through at least 100 feet of beds, most of which are partially dolomitized algal-matte limestones (see Plate 5B).

In some of the Patterson algal-matte limestones there are, also, curiously zoned oolites with conspicuous zonation of radiating fibers of calcite and external rinds of iron-rich dolomite or poorly crystalline silica. Some of the oolites show coalescence into linear chains, and there is a suggestion that these structures may be of algal origin.

Some of the Patterson algal-matte limestones are completely dolomitized without loss of original structures. The dolomite identity of the altered limestone is easy to recognize on weathered surfaces, but one needs the acid bottle to distinguish limestone from dolomite on fresh surfaces.

The algal-matte limestones with tufted pancake to tubiferous algae are common in the Rome Formation and in lower, equivalent parts of the Conasauga Formation. At this level the algal-matte limestones have irregular copper-red to burnt-sienna platelets of dolomite—evidently an especially iron-rich type of dolomite.

In the southern Appalachians the Rutledge Limestone, Rogersville Shale, and Maryville Limestone contain probably the thickest development of algal-matte limestones. These beds are so similar in lithology that an algal limestone in the Rutledge cannot be distinguished from one in the Maryville. Unlike dolomitized algal limestones in the Patterson member of the Shady, the algal limestones in the Rutledge and Maryville commonly are dolomitized to blue-gray dolomites of even grain and structureless appearance that show absolutely no residual algal masses of any kind. Such dolomites, composing the Honaker Dolomite, are about as homogeneous as any in the Paleozoic column.

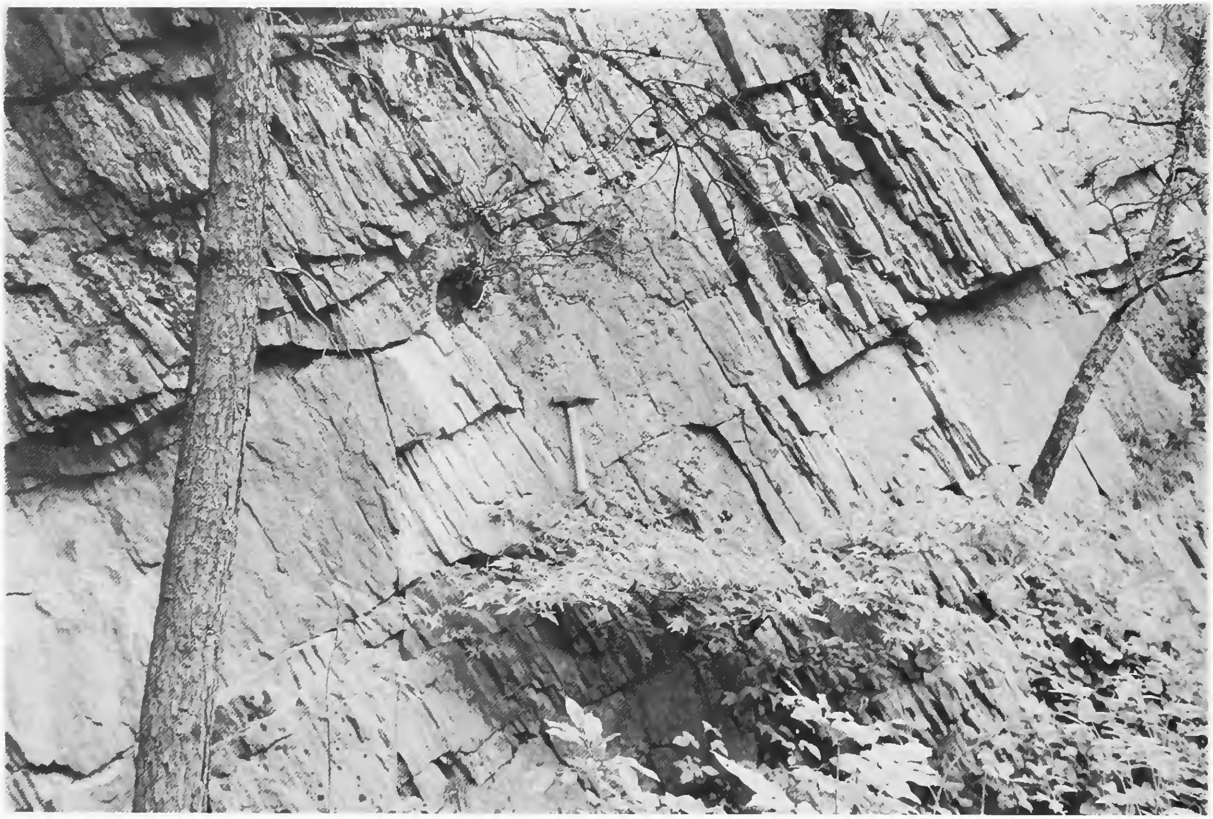

PLATE 2.—Fracture cleavage in Erwin (or Antietam) quartzites, controlled by abundance of *Scolithus* tubes; from same locality as strata shown in Plate 1. (Photo by W. D. Lowry.)

Good algal-matte limestones of Maryville type commonly contain considerable magnesia or dolomite (up to 20 percent magnesia calculated as $MgCO_3$). The blue-gray algal mattes and buff-yellow dolomitic interstitial fillings form a color contrast that is very distinctive. There are hundreds of feet of algal-matte limestone in the Maryville Limestone just south of Sunbright or Hortons Summit on U.S. Route 23 in Scott County, Virginia. The nodular polyp-like tuberosities on the algal plates are distinctive.

The lower Rutledge Limestone directly overlying the Rome along U.S. Route 25E between Thorn Hill and Evans Ferry in Tennessee shows somewhat nodular or conspicuously dimpled algal mattes, and the interstitial dolomite is a little more yellowish. Such rock is quarried for marble just northeast of U.S. Route 25E. When cut into slabs on the bias to bedding, the blocks accentuate the thickness of the alternate golden yellow and blue-black algal mattes to yield a kind of marble closely resembling the famous Belgian Gold marbles of commerce.

Locally, the Rogersville Shale between the Rutledge and Maryville Limestones contains thin zones of algal matte-limestone, as does the Nolichucky Shale that overlies the Maryville in Scott, Russell, and Tazewell Counties, Virginia, and in Sullivan and Hawkins Counties, Tennessee. Such algal-matte limestones generally have dolomite fillings with the copper-red characteristics of the Rome algal-matte limestones.

Throughout much of eastern Tennessee and the adjacent counties of Virginia, and locally as far northeast as New River, the upper part of the Nolichucky Formation is a distinctive magnesian, ribbon-banded, algal-matte limestone possessing somewhat thicker algal mattes and thicker interstitial zones of dolomite—each ranging from five-tenths centimeter to two centimeters in thickness. The chevron structure or "pleat-

PLATE 3.—"Hob-nail" bedding surface of *Scolithus*-bearing quartzite showing effect of tubes on the lithology; Erwin Formation, west foothills of Blue Ridge Mountains on Hellgate Creek, four miles east-southeast of Natural Bridge, Rockbridge County, Virginia. (Photo by W. D. Lowry.)

ing" of the algal limestone mattes at this stratigraphic level is a common characteristic. These beds are now widely identified as the Maynardville Limestone or Maynardville Limestone Member of the Nolichucky Formation. Generally, but especially in the Copper Ridge outcrop belt, the basal beds of the overlying Copper Ridge Dolomite are laminated carbonates of similar type but they are (almost, if not completely) dolomitized algal-matte limestones.

In southeastern belts of the central and southern folded Appalachians, the Elbrook Formation (equivalent to the Rutledge-Rogersville-Maryville-Honaker-Nolichucky succession) possesses three especially interesting kinds of algae. One type is characteristically displayed in nodular tufts about the size of a man's thumb, and these give a distinctive, nodiform surface to limestone layers. The best exposure of this kind of algal biostrome occurs east of Wytheville, Virginia, in a deep rail cut just southwest of the bridge of the eastbound lane of U.S. Route 11. Similar nodular algal beds occur along Route 81 about three miles northeast of Lexington, Virginia.

Far down in the Elbrook is a widespread persistent zone of large-diameter (up to 45 centimeters), plate-shaped algal colonies that grow upward convexly, are finely laminated, and are commonly 7.5 to 15.0 centimeters thick. These invariably are dolomitized algae that weather a fawn-buff to yellowish gray. Probably the finest exhibit of these algae is in the southwest wall of the Blue Ridge Stone Corporation quarry near the boundary line of Botetourt and Bedford Counties, just north of U.S. Route 460 in Virginia. To my knowledge, these broad plates are found only in the Elbrook.

Algal-matte limestones of the distinctive Maryville type also abound in the Elbrook, and doubtless the close similarity of these formations comes from the fact that much of the Elbrook is of Maryville age.

PLATE 4.—Algal-matte limestone in Patterson Member of Shady Formation (Lower Cambrian), 1.7 miles east of Foster Falls Station, on Foster Falls Farm of Neuhoff Packing Company, Wythe County, Virginia. Light areas are dolomite.

Among the formations hardest to distinguish are the Elbrook and Conococheague of the Upper Cambrian. I doubt whether the two actually have a discrete boundary. The Conococheague algal limestones are commonly algal-mattes with flexed or chevron-shaped plates, generally from three to eight centimeters thick, and with the intervening layers not as yellow or as uniformly dolomitic as in the older Cambrian formations. The beds or ledges generally are much thicker than those in the Elbrook.

Some of the algal matte limestones of the Copper Ridge are composed of large discoid, reniform to subspherical *Cryptozoon* masses. They also are prominent in the Conococheague between Verona and Harrisonburg, Virginia, particularly in the vicinity of the Bergtown Klippe of the Pulaski-Staunton fault block.

Cauliflower-shaped to spherical algal colonies commonly called *Crytozoon* occur as limestone masses and as siliceous or completely silicified masses which weather out of the Conococheague or equivalent Copper Ridge Dolomite of the southern Appalachians. These masses occur also in the Beekmantown limestones and dolomites, and in cherts in the equivalent Longview, Kingsport, Mascot successions of eastern Tennessee and adjacent areas in Virginia. The difficulty with the algal chert masses is that they creep away from their parent ledges and move downhill where they mingle with other cherts; therefore, they have little value as stratigraphic markers in mapping.

Copper Ridge algae commonly form nodiform to large subspherical colonies up to 60 centimeters in diameter with the structure preserved in alternate black and gray chert laminae. The larger colonies, when broken open, show incomplete silicification with curved zonal vacuities lined with drusy euhedral quartz crystals. The banded gray-black structures are fairly diagnostic of the Copper Ridge dolomites. Silicification of the algal masses may be due more to weathering than to a penecontemporaneous action, but the time of silicification is open to question.

The Longview Limestone—a persistent zone of partially dolomitized micrite with fossil gastropods but little else in way of invertebrate fossils—contains characteristic small algal microlaminated bodies that grew around abandoned gastropod shells. These irregular, billowy, tufted masses of algal limestone are scattered through the limestone layers, and in some places they determine the lithology because they are so numerous. A similar algal occurrence in the Appalachian Paleozoic beds is in the much younger Hillsdale (St. Louis) Limestone.

The Middle Ordovician limestones contain some algae of *Solenopora* type; these are especially prominent in the Wassum Limestone of the Wilderness Stage in Wassum Valley, four miles northwest of Marion, Smyth County, Virginia, and also are exposed along State Route 16 on the northwest slope of Walker Mountain south of Chatham Hill in the same county. These pinkish encrinal limestones or calcarenites preserve the algae as large distinct intraclasts in a matrix of bioclastic spar calcite. The margins of the algal masses suggest they were of a doughy consistency when broken up and transported.

The old familiar algal-matte limestones of Maryville type make their highest stratigraphic appearance in the slabby dove-gray limestones of the upper Witten; and along with the fucoid markings of *Camarocladia* and *Buthotrephis* they form a distinctive facies that has been identified from the northern Shenandoah Valley southwestward far into eastern Tennessee. In southwest Virginia these Maryville-type algal-matte limestones contain dolomitic partings and also fillings of *Camarocladia* tubes that weather buff-yellow. In my opinion, this is the most definitive lithozone in the Paleozoic succession of the southern Appalachians.

The next higher stratigraphic zone in which algae appear in any abundance is in the Hillsdale Limestone, the approximate correlative of the well-known St. Louis Limestone. Little is known about the nature of these algal masses. They are invariably very irregular in shape, possess sharp outlines, and appear to be intraclasts derived from more localized indigenous growths of algae. Despite the experience of examining many exposures of these beds over a strike length of 100 miles or more, I do not recall ever having seen even a suggestion of a fossil algal colony in place. The peculiar appearance of bluish gray algal micrite masses in the characteristically black Hillsdale Limestone is a lithologic quality worth noting because it is one of the more useful criteria for recognizing St. Louis age beds in the field. The familiar *Lithostrotionella* colonial coralla—both the *"mammilare,"* free-standing corallites and the *"castlenaui,"* basaltiform corallites of the compact variety—are not as common in the Appalachian Hillsdale Limestone as they are in the cratonic, sheet limestones with extensive *Lithostrotionella* biostromes found in the Middle Mississippi Valley.

Some of the limestones in the lower portions of the Chester and upper part of the Meramec series in western outcrop belts of Alabama, Tennessee, Virginia, and West Virginia contain similar intraclasts of algal limestone; this suggests a persistence of a widespread paleoecological condition wherein masses of biogenic micrite induced by algal growths existed in the same general environment in which black, pyritic, petroliferous lime mud was accumulating. Possibly, the algae grew on little mounds rising above the redox threshold in shallower waters.

The highest occurrence of algal masses I have seen are clasts in the locally conglomeratic Princeton Formation of late Chesterian age. These masses are always the single kind of limestone clast to survive dissolution and, therefore, present the familiar blue-gray color which shines through the dead, iron-stained appearance of weathered "wormeaten" surfaces of Princeton conglomerates.

Worm Burrows, Markings, and Trails

Fossil worms, preserved as pseudomorphic casts of burrows or as trails of ordered setae impressions, do not make much of an impression on the Appalachian field geologist, although trails of *Pteridichnites biseriatus* in the monotonous, thick sand-shale successions of the Brallier Formation (Portage age) are so abundant and widely distributed as to be a sort of identification label for beds of Portage type. But the Portage rock hardly needs fossil labels because its general lithology is so distinctive.

Worm markings—chiefly pseudomorphic fillings of segmented impressions or burrows—occur on the undersides of Tuscarora or Clinch sandstone ledges at so many places in the Appalachians that one can be assured of finding them if only he looks for them. These markings, widely known as *Arthrophycus*—both *A. harlani* and *A. allegheniensis*—are so abundant in places as to be a lithologic determinant. To find the undersides of projecting ledges plastered over with

Arthrophycus raises the question of how the things were formed. The worms evidently frequented muds, not sands. When the tides ebbed, the mud began to shrink and dry out, and this induced the worm to really flex its segmented body and to thresh around so that its free part flapped crazily here and there around the vise of drying mud that held the rest of the worm captive. Thus, after the mud had dried thoroughly the mud surface around a worm hole had a mass of markings. Each worm that eventually died for lack of water had made segmented, linear impressions that converge toward the hole where the trapped part of the worm was evidently held. Hence the "turkey track" type of impression.

Arthrophycus has a special value that I have found useful in mapping. The normal mode of occurrence is on the underside of sand beds. When the sand layer was deposited, loose sand was washed into the burrows and the segmented, groove-like impressions in the sand became firmly cemented and welded into orthoquartzite. The Clinch and Tuscarora, especially south of the James River in Virginia, in many places are involved in faulting and overturning of successions of beds. *Arthrophycus* provides the readiest cue as to whether the beds are right-side up or upside down. Without doubt the best display of *Arthrophycus* in inverted successions of ledgemaking sandstone is on Draper Mountain in Pulaski County, Virginia, in the cut made by old U.S. Route 11. As previously indicated, the casts of worm burrows are a part of a three-fold display of lithologic features that testify to the inverted position of the beds. In the same cuts, one ledge of the Clinch shows upside-down foreset bedding and an adjacent shale interbed shows fracture cleavage that likewise is indicative of inverted beds (B. N. Cooper, 1961, pl. 28A). Thus, the familiar though enigmatic *Arthrophycus* doubles as a primary sedimentary feature that helps the stratigrapher determine when the beds are in normal succession or overturned.

Echinoderms in Carbonate Strata

Perhaps the most significant contribution by invertebrates to the lithology of Appalachian sedimentary formations is made by echinoderms—particularly cystids, crinoids, blastoids, paleoasteroids, and edrioasteroids—in producing the texture of so many Appalachian limestones. Cystids, crinoids, and blastoid calyx and stem plates are secreted as crystallographic units which, to some extent, are knit together. When the animal dies, the skeleton may, with the decay of soft parts, yield an aggregate of loose plates or a fused monolithic structure which shows plate outlines but which will break either along plate boundaries or across them. Stem and pinnule plates are fragile and brittle and seldom survive much transportation and abrasion. This is especially true of the stem plates of cystids, which have an inordinately large lumen compared to crinoids.

Except for extremely rare biocoenoses of crinoids, cystids, and blastoids, such as the rare Crawfordsville, Indiana, crinoid beds, echinoderms occur overwhelmingly as cleavage fragments of biogenic spar calcite. Rocks composed of cleavage fragments of encrinal origin have a peculiar, coarse granularity characteristic of calcarenites or biosparites. Echinoderms in the Appalachian section make their first appearance as cystid-like tests in early Acadian rocks. In the southern Appalachians, the Maryville Limestone is probably the oldest Cambrian unit known to contain echinodermal remains. Unlike most of the younger biosparites or calcarenites, those in the Maryville are invariably dark-colored and are almost invariably oolitic. They are well exposed in the classic Thorn Hill, Tennessee, section but are best displayed in natural exposures about three miles southwest of Speers Ferry bridge over Clinch River on U.S. Routes 23 and 58 and about 600 feet north of the riverbank. Considerably comminuted trilobite "hash" occurs in the same beds. These oolitic biosparites are forerunners of the great masses of encrinal and cystoidal debris that were to be deposited in the Appalachian geosyncline beginning in Champlainian time (Middle Ordovician). The grain of an Appalachian Middle Ordovician calcarenite results in a distinctive and unmistakable roughness of the surface, produced by closely spaced, projecting corners of cleavage rhombohedra. Such rocks, however, are not indicative of any specific stratigraphic level but occur at many different levels, as Keith (1895, text) so clearly described in Tennessee. A personal experience illustrates how important it is to appreciate the feel of a calcarenite.

In 1944, I was asked to give a United States Geological Survey ground-water geologist a tour of western Virginia to help him become familiar with the stratigraphic section. At that time, the Pulaski fault was interpreted to cross U.S. Route 11 about 1.5 miles northeast of Buffalo Creek where Mid-Ordovician limestones supposedly were resting on Martinsburg shales (Butts, 1933). At that time the exposures were fresh

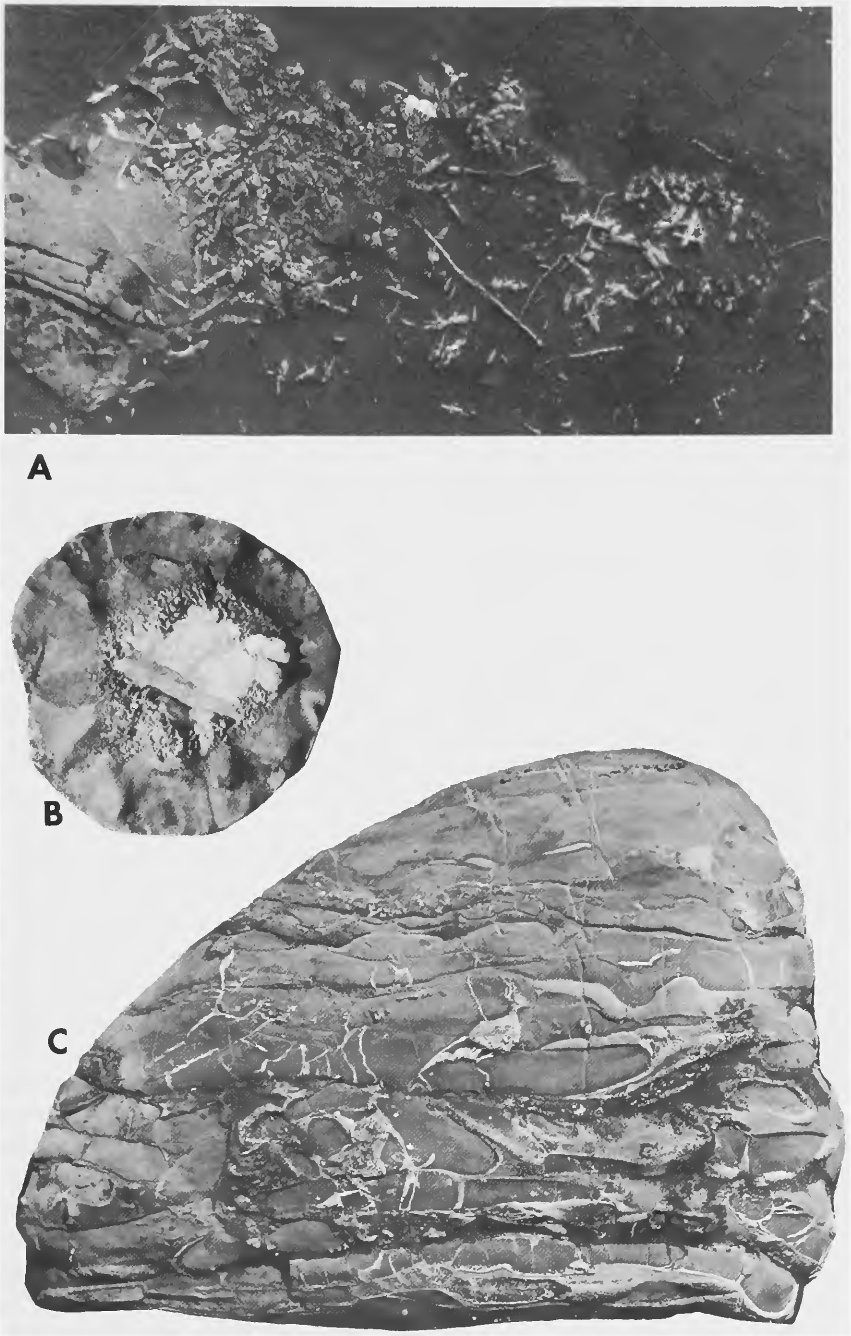

Plate 5.—Features of algal-matte limestones. a, Nests of dolomite crystals pseudomorphic after anhydrite, from Patterson Member of Shady Formation, Ward Creek section, northwest of Cripple Creek, Wythe County, Virginia. b, Algal-matte limestone cup or "petri dish" containing coarsely crystalline dolomite probably pseudomorphic after anhydrite, with center core of quartz crystals; from same locality as above. c, Hand-specimen of typical algal-matte limestone (natural scale), from Patterson Member of Shady Formation, 1.25 miles east of Huddle, Wythe County, Virginia.

and worthy of photographing. While my colleague set up his camera for a photograph of the supposed fault contact, I casually rested the palm of my hand against the rocks on the northwest side of the cut. The familiar feel of a calcarenite led me to look at it closely. The presence of orthid brachiopods and shreds of bryozoans confirmed my "Braille" impression. The rock was a calcarenite commonly found beneath the Liberty Hall black limestone-black shale lithofacies of the Edinburg Formation, so I began to suspect that the supposed Martinsburg actually might be Liberty Hall shaly limestone. This was quickly confirmed by finding graptolites in the black shale near the boundary with the calcarenite on the opposite side of the road. These discoveries led to curiosity about the dolomites under the Middle Ordovician limestone that also are fully exposed along the highway. Eventually we found the *Ceratopea* and *Lecanospira* faunules of the upper and middle parts of the Beekmantown beds in normal sequence under the Champlainian rocks, and the fault about to be photographed "disappeared." Downgrade to the southwest, just northeast of Buffalo Creek near old Buffalo Mills, I found the real Pulaski fault where the lower Beekmantown had been overridden by the Elbrook Formation and where a good development of Max Meadows crush conglomerate characteristic of the Pulaski fault zone separated the Beekmantown from the Elbrook. Indeed, the whole train of discoveries had been triggered by the recognition of the significance of the calcarenite, merely by feeling the rock.

Middle Ordovician calcarenites are very commonly pinkish-tinged because of the very characteristic color of the crinoid and cystoid debris of which the rocks are composed. Although these echinodermal groups in the form of abraded fragments are overwhelmingly predominant as rockmakers and are distinctive lithologic determinants, other fossil fragments also abound, including intraclasts of *Solenopora* algae, bryozoans of many types, brachiopods (especially tumid triplesids such as *Oxoplecia*), and triangular, strongly plicate *Oligorhynchia.*

One especially significant biosparite occurs at the very base of the Middle Ordovician Tumbez Limestone. It is often red or pink and is loaded with detrital chert clasts like its dolomite counterpart, the Blackford Formation. Almost invariably the biosparite is loaded with myriads of *Rostricellula,* a strongly plicate, tumid rhynchonellid that withstood rolling very well without dismemberment of the valves. The elegant little shells occur by the millions in pink encrinal limestones in the Clinch Mountain belt of outcrop from western Russell County, Virginia, southwestward all the way to the southwest end of the outcrop belt near Chesney, Union County, Tennessee.

Rocks so full of fossils as are these beds owe their color, coarse texture, characteristic cross-bedding, and stylolite markings to the abundance of organic remains. Such rocks, which as Ulrich (1911) indicated years ago aggregate nearly 700 feet of section in the Luttrell-Chesney district of East Tennessee, constitute a rock type commonly called Tennessee pink or red marble (Holston marble) which is very abundant in Tennessee and in southern Virginia.

How does one explain the many hundreds of feet of encrinal calcarenite whose pink to red colors come from the mass effect of pink or red calcite-spar fragments of crinoids and cystoids? Where were the crinoid and cystoid beds from which billions of tons of encrinal fragments could be derived by wave and current action and be transported as spar calite sands to form this dominant lithofacies of Ordovician limestone? What curious combination of marine sedimentary processes could continue to yield vast tonnages of spar calcite by recurrent disruption of enormous, growing areas for crinoids and cystoids sufficient to furnish hundreds of feet of nearly pure calcitic sediment? The enigma is further heightened by the fact that no one has yet reported a token occurrence of lush-growing crinoids or cystoids that could supply the sediment. That waves and currents swept the abraded echinodermal debris across the sea floor to its final resting place is indicated by the abundant development of bold foreset bedding in many of these calcarenites, particularly in those utilized as polished marble slabs. These echinodermal calcarenites are obviously a lithofacies that is repeated in the Ordovician Appalachian section of Virginia and Tennessee from the base of the Champlainian (as typified by the calcarenites at the base of the Lenoir Limestone at Friendsville, Tennessee) nearly all the way to the top of the Wilderness Stage.

A facies variant of the typictal Holston marble lithofacies is represented by the Effna Limestone on the Saltville fault block in Virginia and Tennessee. This unusual limestone is developed sporadically in the lower beds of the Porterfield Stage. The Effna is a series of isolated biohermal mounds of nearly white limestone that are laced together by gray to pinkish calcarenites. Some of the mounds and associated calcarenite sandbanks interfinger with black graptolitic shales as in Porterfield Quarry of Olin Mathieson Chemical

Corporation in Rich Valley, Smyth County, Virginia. The main reef body consists of limestones of algal origin but which are rich in bryozoans, octacorals, brachiopods, and trilobites and are mixed with pockets and stringers of calcarenite.

The bedded parts of the Effna form bold ledges, and the unbedded reefy masses, literally mounds of fossils of many kinds, form huge clints. A curious thing about the Effna reefy bodies is the inordinately low magnesia content—in many places less than 0.60 percent calculated as $MgCO_3$. Most of the fossils probably are bryozoans, and these animals always secrete shells with from 3.5 to 8 percent (or even more) of magnesia calculated as $MgCO_3$. How is magnesium selectively removed in such rocks?

Coarse calcarenites make a strong appearance in the Helderbergian of the Appalachians. In the northern Appalachians the encrinal calcarenite is the Becraft Limestone, which is loaded with round crinoid columnals. In the Central Appalachians much of the coarse limestone that occurs in the Helderberg is in the so-called Coeymans Limestone, which looks nothing like the Coeymans on Becraft Mountain but resembles the New York Becraft. The Central Appalachian Coeymans is locally a pink marble made up of a distinctive thick type of columnal with interlocking milled or ridged faces. This kind of rock is so like the Mid-Ordovician Tennessee marbles that it is uncanny. Yet close examination readily shows a difference, the Mid-Ordovician pink calcarenites are loaded with cystoid columnals whereas the Devonian pink marbles contain essentially no cystoid debris.

In the Clifton Forge district of western Virginia there is an aberrant pink calcarenite that occurs in the Keyser Limestone, which otherwise is mainly biostromal coralline limestone. The occurrence of two "Coeymans Marble" zones is not uncommon. What makes the crinoid stem plates pink? This question has never been answered, but the durability of the pink color is attested by slabs of Craigsville marble that were hewn out of a small quarry near old Craigsville on the C & O Railway. These slabs were hauled out by wagon through Buffalo Gap west of Staunton, Augusta County, to the Tinkling Springs Church cemetery west of Waynesboro, where some of them have reposed for 225 years without losing the delicate pinkish color of the Craigsville marble (a local variant of the Coeymans Limestone).

Lush crinoid beds are unknown in the Central and Southern Appalachians, but cystoids are locally plentiful in the late Silurian Keyser Limestone in Maryland. The origin of the Devonian encrinal calcarenites is as puzzling as that of the Middle Ordovician calcarenites of Holston-marble type.

Strata composed largely of crinoidal remains abound also in the Mississippian limestone lithofacies from Pennsylvania to Alabama. The Mississippian calcarenites are readily distinguished by the abundance of unbroken discrete stem and calyx plates, which are distributed through a finer grained matrix. Such calcarenites grade rather abruptly into oolitic limestone in which spar calcite is plentifully mixed. Mississippian calcarenites in the Appalachian region seldom are as coarse-grained as their Ordovician counterparts, except for the unbroken stem segments which are the hallmark of the younger calcarenites. The abundance of crinoidal calcarenite in the Appalachian Mississippian raises mystifying questions about the paleoecology.

The various calcarenites in the Appalachian section can generally be distinguished by using a combination of lithologic and fossil characteristics. The Mississippian calcarenites and the oldest ones in the Acadian limestones are variably oolitic, but oolites are essentially absent in the Ordovician, Devonian, and Late Silurian calcarenites. Ordovician calcarenites can be distinguished from Devonian or Late Silurian ones because the first-named are predominantly cystoidal, whereas cystoidal calcarenites are rare in the Silurian and Devonian. The latter are coarser and not uncommonly contain large spar-calcite intraclasts of fused columnal plates up to 2.5 centimeters in diameter. The Mississippian calcarenites are generally impure, clayey, and more erratic in thickness. The Tennessee marbles of commerce, so lavishly used in the National Gallery of Art in Washington, are composed entirely of fossil fragments, all somewhat recrystallized without loss of structural detail, fused into a coarsely crystalline mass devoid of porosity.

Brachiopods as Lithic Components

Brachiopods are surprisingly abundant rock makers. Waves and currents have segregated brachiopods in many places to form limestones of peculiar and highly distinctive lithologies. In many of these beds the particular fossils are sufficiently abundant to be the overwhelmingly predominant lithologic determinant.

The oldest Appalachian limestones to be literally composed of brachiopods are the *Rostricellula* biosparites of basal Lenoir or equivalent Tumbez Limestone or basal New Market limestone of the Shenandoah Valley of Virginia, and the lowermost Row Park limestones of Maryland and Pennsylvania. These rather erratically distributed beds were deposited as discontinuous concentrations of easily rolled shells which ultimately came to rest on deeper recesses of the post-Canadian surface of unconformity. The irregularities on this surface, including undercut projecting ledges, sink holes, and deep cut channels, account for some amazing occurrences of this Marmorian faunule sometimes found far down in sequestered dissolution cavities or clefts down in the Knox dolomites. At Eagle Rock, Botetourt County, Virginia, the *Rostricellula* brachiopods flushed into a narrow, current-cut, V-shaped cleft in the surface of unconformity developed in the Knox. The channel filling of *Rostricellula* brachiopods crops out as an inverted wedge of brachiopod pudding stone that projects upward into overturned, older Knox dolomites.

The Elway limestones of the basal Ashby Stage contain one of the more profuse displays of *Dinorthis* known, with *D. holdeni* the oldest known species. One large slab in the collections of Virginia Polytechnic Institute contains about 6,000 shells exposed on one surface. Some are silicified in blue-gray limestone, but many occur in black chert. All the shells are of about the same size and shape and degree of resupinacy. But on U.S. Route 25W south of Clinton, Tennessee, the cherty Elway has yielded thousands of free silicified shells of *Dinorthis* that can be sorted into various sizes and shapes and degrees of resupinacy presaging many of the species of *Dinorthis* that range as high as the Richmondian.

Dinorthis holdeni in company with other Elway fossils occurs in a wide range of limestone lithologies: pink Holston-type calcarenites at Chesney, Union County, Tennessee; cherty micrites in Elk Garden, Russell County, Virginia; and in black fine-grained limestones containing abundant lenses of black chalcedonic chert. The typical occurrence is in chert blocks that have been bleached and somewhat devitrified.

Although brachiopods are abundant throughout the Middle Ordovician, the *Sowerbyella*-limestones at the base of the Martinsburg Formation are the only other abundantly brachiopodiferous limestones in the Middle Ordovician formations. Any experienced Appalachian field geologist can be handed a piece of this *Sowerbyella*-bearing limestone and will identify it immediately because of the special look that the fossils give to the limestone. The slabs are packed with brachiopods—particularly *Sowerbyella, Zygospira,* and strophomenids—and profuse bryozoans that include *Hallopora, Rhinidictya,* and *Prasopora.* The fossil shells are embedded in a matrix of spar calcite, finely ground shell debris, and quartz silt. The limestones are slabby and irregularly bedded. Individual layers of shelly limestone are interbedded with black pyritic shales which weather greenish gray to brownish buff. The brachiopodiferous slabs of lower Martinsburg, or "Trenton" limestone, are commonly strewn over foothills at the base of obsequent slopes of typical Appalachian hogback ridges upheld by the basal Silurian Tuscarora or Clinch Sandstone. One can recognize them without even picking up the slabs. The curved, crisp, thin valves of *Sowerbyella* can be recognized either plastered over bedding surfaces or exposed on surfaces normal to bedding where the shells show as thin profiles. Finally, the luster of the shells imparts a silky appearance to the beds that is very distinctive.

The high Martinsburg from northern Virginia to Alabama and Georgia is represented by or contains limestone beds packed with tumid *Orthorhynchula* shells, many of which are filled with white calcite. The concentrations of these shells and their coarse ribbing is so distinctive as to impart a definite appearance to the rock as a whole. The rock in which the shells occur is very impure, and is composed largely of a silt matrix. The weathered limestones, full of holes where shells have been dissolved out, yield a pulp that is readily identifiable. Not uncommonly the leached rock will show whitish thread-like coatings of hydroapatite, evidently derived from myriads of *Lingula* brachiopods which have been partially dissolved by percolating waters that later evaporated to leave the whitish residues.

Silurian and Devonian Limestones

Of all the calcarenitic or highly fossiliferous limestones, the ones most difficult to distinguish in the field are the Cayugan and Helderbergian limestones. The Coeymans calcarenites unfortunately are mimicked by local coarse calcarenites in the Late Silurian Keyser Limestone. The true Coeymans has characteristic brachiopods, but in the calcite-spar matrix of the calcarenites they are impossible to extract without decorticating the shells so that they are useless for identification. The pinkish calcarenites in the Keyser tend to be adulterated with quartz sand, but to some extent this is also true of the Coeymans itself. The true Coeymans of the Clifton Forge, Virginia, district is easily the coarsest grained limestone in the Paleozoic succession.

Keyser limestones are blue-gray limestones that contain black chert and thus resemble, superficially, many of the Middle Ordovician limestones such as the Lincolnshire Limestone. But if one puts the lens on the Keyser limestones some clue of Cayugan age among the fossils can be detected very quickly. For example, *Cladopora* corals, or favositids, stropheodontids, or lirate to finely plicate spiriferids generally can be identified. The Keyser contains irregular biohermal bodies of very fossiliferous limestone permeated by coarse calcarenite. Such masses have a distinctively massive appearance but show ropy projections of chert and silicified shells. The experienced eye can recognize these biohermal beds, which are not duplicated in the Licking Creek Limestone or in the Coeymans Limestone. The main difficulty with the Devonian limestones is their lack of good exposure or evident continuity of exposures, and their soil cover is more often thick than thin.

Fossils in Devonian and Younger Clastic Strata

One might think that the fossiliferous Oriskany, so full of molds of large fossil shells, would be easy to recognize, but that is not so unless it is the only sandstone in the Devonian part of the section of Cayugan and Helderberg limestones. Generally, there are other sandstones—for example, those in the base of the Keyser Formation (generally but not everywhere indicated by a predominantly foreset-bedding structure), the Healing Springs Sandstone of New Scotland age, and the arenaceous zones in the Becraft which weather much like the Oriskany and pass southward into a sandstone known as the Rocky Gap Formation. The stratigrapher working in these beds will do well to depend on sequence to distinguish these sandstones. Of course, this is another way of saying that the lithologies themselves are not distinct.

In the great mass of Devonian clastics, fossils contribute notably to the recognition of only a few zones. The Needmore Formation (Butts, 1933, 1942), olive-drab shales of "Onondaga" affinities just above the Oriskany, is a unique lithology commonly characterized by almost unbelievably abundant molds of all the diminutive members of the Onondaga-Schoharie fauna—*Tentaculites, Leptostrophia, Ambocoelia.* Generally, the eye-catcher of the Needmore is a combination of two things: the lumpiness or lack of fissility and the curious surfaces formed by myriads of *Amphigenia* brachiopods which are so strongly curved that molds of the shells look like pebbles or granules.

The Millboro black shales contrast in color with the gray-green Needmore, but the former lacks any obvious implantation of fossils on lithologic characteristics of the rock.

The great thickness of rocks of Portage lithofacies, which in the Southern Appalachians extends upward from the upper biofacies zone of the Millboro Formation—Butt's (1942) Naples division—all the way up to the Maccrady red beds of Warsaw (Mississippian) age, at first glance or even after considerable study, appear to be essentially unfossiliferous. They are characterized by a monotonous repetition of rusty-weathering sandstones and drab shales, and their only noteworthy attribute is their great thickness. A very close examination will indicate some distinctive lithofacies and biofacies, but none of these are reliable stratigraphic markers. Much of the tremendously thick Brallier Formation is virtually devoid of fossils, but in the lower 300 to 500 feet of the formation there are crumbly, limy beds very commonly packed with brachiopods of the so-called Ithaca biofacies. The assemblage is dominated by brachiopods and clams, generally including *Rhipidomella, Spirifer mesastrialis,* athyrids showing interiors, *Chonetes, Leptodesma, Grammysia,* and *Paleoneilo.* One can learn to spot these beds after examining them and collecting fossils from them, but just what is distinctive about them is elusive.

A stratigrapher learns how to spot beds of different ages but, like the untrained musician who plays by an instinctive ear, he may find it very difficult to convey to others how he recognizes certain parts of the section. The inadequacy of language in description is illustrated by the following incident. Thirty-four years ago, I was driving with Dr. Charles Butts, dean of Appalachian geologists in his time and (luckily for me) my mentor, during a heavy rainstorm over Brushy Mountain along U.S. Routes 52 and 21 in Bland County, Virginia. The car windows were no more than translucent from condensate moisture. Suddenly, Dr. Butts exclaimed: "Stop on the shoulder! We will go back and collect some *Productella* shells and goniatities out of the Braillier; I just saw them back a little ways." It was hard to believe, but my doubts that he could see so much were wiped away when we walked only about 150 feet back up the road and I saw some soft, crumbly, rusty-weathering, lumpy rocks with just the fossils he said he had seen out of the corner of his eye. When I pressed him why or how he knew what he had seen, he said, "You cannot always put into words what you can see." Perhaps someone else, having a stronger emotional tie with these beds than I, can do justice in pinpointing what I am incapable of describing as distinctive about the the "Ithaca beds" and Naples beds in the Brallier Formation.

The upper part of the Portage lithofacies from James River southward—even down into Tennessee—contains a zone that is characterized by vast quantities of *Spirifer disjunctus, Productella, Camarotoechia,* and *Chonetes* brachiopods and great quantities of *Melocrinus* stem plates that are distinguished by strongly radial striations on the flat sides of the "buttons." No one has any trouble spotting this zone from a distance of 10 to 50 feet—so long as the assemblage contains plenty of thick *Spirifer* shells. If the road cut is fresh, the calcite of the shell glistens in the sun and outlines what could only be *Spirifer*; if the exposure is weathered, the *Spirifers* have dissolved away, leaving a peculiarly shaped cleft or indentation in the rock. Where these fossils are very abundant, both fresh and weathered surfaces have a look all their own. Not infrequently exposures of the *Spirifer disjunctus* beds contain some red-colored beds, probably signifying an admixture of in-washed Catskill red material. The *Spirifer disjunctus* biofacies in the Portage lithofacies is very calcareous—so strongly so that some of the rock could be called an impure limestone without stretching the imagination. Commonly, the fossils in this zone occur in relatively thick beds of sandstone-siltstone which aid in the eye-catching qualities of the fossils or their impressions.

But a little higher in the sequence, the *Spirifers* lessen in abundance and essentially drop out of the faunules—leaving *Camarotoechia, Productella, Chonetes,* and crinoid buttons. This is an equivocal, deceiving, frustrating assemblage that has but one redeeming feature—abundance of fossils. These beds are easy to spot, but almost always they occur as loose slabs of rock not uncommonly weathered and coated with a light-gray, case-hardened exterior. These fossils, forming the same kind of sandstone, cover quite a stratigraphic interval, and if one follows this zone upward he will in due course see the Mississippian spiriferids *Pseudosyrinx* and *Syringothyris*. Accompanying these fossils, besides *Productella, Chonetes,* and *Camarotoechia,* are Burlington-Keokuk brachiopods, notably *Tetracamera*. Thus, this confounding biofacies, which ranges down to the level of the Chemung—which Chadwick (1935) evaluated as just a "brachiopodiferous facies of the Portage"—surely ranges as high as the Mississippian Price Formation and its Tennessee counterpart, the upper part of the Grainger Formation.

What impressed me most about this troublesome group of distinctive fossiliferous beds of the same general lithology is that the mythical systemic boundary between the Devonian and Mississippian cannot be spotted. But this is not a rare phenomenon. Most systemic "boundaries" in the Appalachian section are figments of the imagination (Cooper, 1960). Many a vicious controversy among former geological friends is recorded in geological literature in the polemics of where to place these "boundaries"—many abetted principally by paleontologists.

The Price-Fort Payne-New Providence faunules of Burlington-Keokuk age are favored by one lithozone that aids in locating the biozone with *Pseudosyrinx* and its associates. This faunule is always found very close to a distinctive glauconitic siltstone.

The Mississippian Greenbrier limestones above the Hillsdale, which are of Ste. Genevieve and Gasper ages, are distinctive because of the prominent display of crinoid and blastoid remains, the former generally as isolated plates, the latter commonly as whole calyces. The Ste. Genevieve beds, which Wells (1950) has renamed the Denmar Limestone, are either calcilutites or calcarenites. The fine-grained beds are sparsely fossiliferous, but the calcarenites commonly are loaded with crinoid columnals among which the distinctive stems of *Platycrinites "huntsvillae"* are most conspicuous. The stem plates of that crinoid are elliptical in shape and have a spinose periphery. In the stem, each element is offset slightly to produce a flattened, ribbon-like spiral that must have had greater flexibility than most crinoid stems. In good light, these stem plates, which are only about 0.5 centimeter in maximum diameter, can be spotted ten feet away from the outcrop. Higher Mississippian limestones that have been widely called "Gasper" contain wing plates of two or three genera of crinoids of which *Talarocrinus* and *Pterotocrinus* are most easily recognized, and they are truly abundant. Mississippian crinoids clearly were great rockmakers. Most of the limestones of Gasper age are also characterized by rather common blastoids, of moderate size, that were rolled around by waves and currents without appreciable abrasion damage to the monolithic calyx, which was about as resistant to break-up as a hard pebble of rock. The impress of crinoids and blastoids on the Mississippian Greenbrier limestones is best conveyed by the 1,000 feet or more of limestones exposed along the lower slopes of Stony Ridge along State Route 16 southeast of Bishop, Tazewell County, Virginia (B. N. Cooper, 1945).

Fossils also contribute in a remarkable way to the peculiar, rusty-weathering calcareous shales of the basal part of the Bluefield Formation. The finest section to see the features is opposite the junction of West Virginia Route 12 and U.S. Route 460 just north of the rail underpass at the northeastern limit of Bluefield, West Virginia. The crisp, delicate markings made by thin fragile fossil shells contribute a diagnostic feature of these beds. Most of the fossils in this zone were evidently indigenous and little disturbed by deposition of muds around the shells as they accumulated. Bold markings on such beds are made by the screw-spiralled stolons of *Archimedes.* In just the right light the profusion of *Archimedes* shows up very prominently 10 to 25 feet away.

But for one or two exceptions, the lower Bluefield brachiopod and bryozoan limestones mark the highest level in the Appalachian Paleozoic sequence where fossils literally make rocks. This zone also is just below the tremendous thickness of predominantly clastic rocks of the red-green-black Mauch Chunk lithofacies or magnafacies which persists up to the base of the Pennsylvanian Lee Formation. In medial and upper portions of the Bluefield Formation in the great Hurricane Ridge syncline (B. N. Cooper, 1961, 1964; Thomas, 1966) and also in the calcareous portions of the Hinton Formation and even higher Bluestone Formation, the impress of fossils is less evident. Nevertheless, it should be mentioned that the abraded, broken, disoriented character of the invertebrate fossils in the Bluefield-Hinton-Bluestone successions—aggregating nearly 5,000 feet in both the Hurricane Ridge and Greendale synclines—does point to one general conclusion. The fossils clearly are part of a great accumulation of what Weeks (1952) aptly described as "dump deposits," and in their beaten, bruised, broken, and corraded condition they constitute the most clear-cut examples of transported thanatocoenoses in the entire Appalachian column.

Two markedly fossiliferous zones above the basal Bluefield *Archimedes* beds are valuable as key beds for mapping purposes and stratigraphic reference. One is a rather persistent zone of calcareous mudstone bearing whole or fragmented giant pentremites (*Pentremites mccalleyi,* the largest known Appalachian pentremite, rivaling in size *P. obesus* of the Mississippi Valley region). These fossils make a puddingstone rock zone of very distinctive appearance of up to four feet or so in thickness. They are almost unbelievably abundant in this one zone, but they have a considerably greater stratigraphic range through beds in which they occur as more or less isolated mavericks.

The upper of the two high Mississippian lithologic zones composed primarily by fossils is the Avis Limestone Member of the Hinton Formation. Near its top it has a thin argillaceous limestone in which the complete shells of an elliptical *Composita* abound to such an extent as to outweigh the matrix in many places. This is a widespread thin zone capable of yielding more pounds of whole fossils per cubic foot than any other division of the Paleozoic of the Appalachians, yet the still lowly estate of Appalachian Paleozoic invertebrate paleontology is attested by the fact that these *Composita* shells have never been described specifically.

Appalachian Stratigraphy without Fossils

For nearly 50 years prior to the early 1940s Appalachian stratigraphy was plagued by serious misconceptions which would not have existed had the invertebrate faunas been studied. The confusion of the Middle Ordovician Bays Formation with the Juniata-Clinch as described by Rodgers (1953, pp. 78, 97) is an example. Among the Ordovician limestone formations, one rock type was singled out by Ulrich (1911) as a lithologically distinctive zone which he named the Mosheim Limestone. Two other zones of the same kind of limestone, separated by a few hundred feet of beds and neither the same as the Tennessee Mosheim, were confused with the Mosheim in southwestern Virginia. This duplication of the Mosheim lithology (first described by Cooper and Prouty, 1944) was a source of much confusion. About six different stratigraphic zones of Holston-type limestone, another distinctive lithofacies, occur in Tennessee. The lowest occurrence in the basal Marmorian is directly on top of the Knox Dolomite of Canadian age. The highest occurrences are in the Wilderness Stage in Virginia and Tennessee. All of the different Holston marbles could be easily distinguished if the enclosing rocks maintained some semblance of lithologic continuity from belt to belt, but the entire succession containing marble beds ranges greatly in lithology from place to place. The stratigraphic positions of all the marble lentils could be worked out if the fossils in the individual marble beds were studied in detail. Conodont studies may prove helpful in solving problems with the marble zones.

It is regrettable to me that the term Chickamauga was revived and used so widely by Rodgers in Tennessee. Rodgers's lettered zones of the Chickamauga can be related to a number of Virginia formations that have an established faunal basis for their recognition, whereas the lettered zones do not. The only reliable and consistent way to work stratigraphic successions is to use all the information that the rock supplies. Assumption of unique nature of some limestone lithologies was a serious retardant in Appalachian stratigraphy that could have been avoided had fossils been used in conjunction with the lithologic characteristics.

Perhaps the part of the section that best illustrates the deceptive quality of lithology criteria alone is along U.S. Route 25E south of Evans Ferry bridge over an inlet of Norris Reservoir. There are three prominent zones of buff-weathering cobbly limestone—all of which have been confused with the so-called Ottosee Limestone of Ulrich (1911). The lowermost zone of this cobbly buff-weathering limestone, the lower part of the Lincolnshire Limestone of Ashby age, contains the Lincolnshire brachiopod fauna. The middle zone of cobbly limestone along U.S. Route 25E in the Evans Ferry section contains abundant Porterfield fossils that are easily distinguishable from those of the Ashby Stage. The third cobbly zone of "Ottosee" type is the Wardell Limestone of the Wilderness Stage. Fossils in the Wardell are markedly different from those in either the middle or lower zones of cobbly limestone commonly called Ottosee. Knowledge of the fossils is essential to consistent stratigraphic identification of recurrent zones of the same lithofacies.

Discreditation of Guide Fossils

The question might be asked: "What is the value of any individual fossil in the recognition of any stratigraphic unit in the Appalachian Valley?" One would have to respond by saying that no single index fossil has stood the test of time. A number of individual fossils were misused in the past for identification of certain ages of beds, with rather disastrous results. Among such fossils were *Lecanospira,* the depressed spired gastropod once thought to be confined to the Longview Limestone; various species of *Tetradium,* some of which are but growth stages of others; the enigmatic *Cryptophragmus; Cyrtospirifer disjunctus;* and many others. All of these were touted to be "dependable guides." The only way to use fossils meaningfully in stratigraphic work is to make full use of the various elements of the fauna or faunule that are found and identified. There is safety in using numbers of genera and species in stratigraphy. The facts regarding the wide stratigraphic range of the fossil *Cryptophragmus antiquatus,* long supposed to be a valid guide to beds of Lowville age, exemplify the danger of relying on a single kind of fossil for stratigraphic work (Cooper and Cooper, 1946, pp. 58, 59). The last Appalachian Paleozoic guide fossil to fall from grace was the genus *Lithostrotionella,* which was long respected as a valid guide to the Appalachian Hillsdale Limestone, or its equivalents, commonly identified as St. Louis Limestone by Butts (1927, 1942). This distinctive coral is now known to range outside the St. Louis Limestone or Hillsdale Limestone; it has been found in the Little Valley Limestone in the Greendale syncline.

Value of Maverick Fossils

The fact that fossils make up so much bulk of strata and actually determine the physical appearance of so much rock is the best reason for the stratigrapher to seek help from or to join up with a good, experienced paleontologist and thereby learn what a great help fossils can be. One kind of fossil that has special value in stratigraphic work is the maverick organism that became separated from its paleoecological habitat and was buried and preserved in a lithofacies environment, and in the midst of other buried organisms, foreign to its natural habitat. The maverick fossil has special value in contributing information indicating the essential contemporaneity of different sediments containing relatively different fossil assemblages.

In the Appalachians, some faunal assemblages are little known outside a given lithofacies. For example, the Normanskill graptolite fauna seldom is observed in rocks other than black shales. When G. A. Cooper and I were working on the Middle Ordovician of the Shenandoah Valley, the problem of the relation of the Normanskill graptolite fauna, in the rocks long called

Athens black shale by Butts and others, to the fauna of the rocks formerly called Chambersburg Limestone was finally resolved in two ways. First, detailed collecting showed clearly that the trilobites and at least some of the brachiopods occurred both in the beds identified as Athens and in those to the north called Chambersburg. This did not convince everyone of the equivalency of the two formations. Detailed collecting in the so-called Athens platy black limestones and graptolitic shales at Lacey Spring in Rockingham County, Virginia, led to the discovery of one of the most characteristic Chambersburg fossils, *Christiania lamellosa.* Extensive collections of fossils from the Chambersburg farther north in Shenandoah County, Virginia, led to the discovery of Normanskill graptolites in token quantities in Chambersburg limestones. Doubtless the graptolites and the characteristic Chambersburg brachiopod, *Christiania lamellosa,* were strays and were atypical of the rocks in which they were found. But the token occurrences of the two in both the Athens and Chambersburg beds provided additional information needed to clinch the correlation. The possibility of finding maverick fossils in foreign lithofacies is sufficient reason to look for them, but diligent collecting may be necessary to round up even a few such fossils. Stray fossils are most apt to be found in the border fringes of two adjacent but relatively distinct lithofacies, and that is where the search for them is most likely to be fruitful. The maverick fossil may also be turned up in the etching of limestones. Rare fossils that cannot expectably be broken out of rock may be dissolved out and freed for study. Thus, all the material recovered from etching must be combed over to see if a "one-in-a-million" fossil find can be made.

Recurring Faunules

Recurring faunules have all too often put the paleontologists on the defensive in answering the question: "If fossils are any good for stratigraphic work, how can they be depended on if they recur?" Recurring faunules should be expected if faunas evolve gradually and if the depositional environment exercises a strong control over the dispersion of a given faunal assemblage. The key to the understanding of recurrences lies in faunal associations. For example, in the Edinburg Limestone of the Shenandoah Valley the distinctive cystoid *Echinosphaerites* occurs in two relatively widely separated zones, one at the base of the Edinburg and the other several hundred feet higher in the overlying Oranda Formation, which is the approximate equivalent of the Trentonian Salona Formation of Pennsylvania. The lower occurrence is the main one; the Oranda occurrence is the anomalous one. The recurrence of *Echinosphaerites* is in an association of brachiopods, trilobites, and bryozoans that are very different from the associated fossils in the lower part of the Edinburg Formation (Cooper and Cooper, 1946, pp. 35–113). In the geographic area of the recurrences of *Echinosphaerites,* the phasing out of the Edinburg fauna and phasing in of the Oranda fauna expectably would be consummated gradually, with some favored organisms managing to survive longer than other members of the earlier fauna. *Echinosphaerites,* which probably had a drifting habit, could have survived a bit longer in some secluded place and then could have broken out of captivity and spread over the area a second time before being eliminated. Lack of similarity of the associated fossils is indication of a different age for the two occurrences, and the occurrences of *Echinosphaerites* are subordinate in importance to the preponderant weight of faunal evidence indicated by dissimilar nature of the sets of fossils associated with the two occurrences of *Echinosphaerites.*

In the area immediately north of Strasburg, Virginia, near the junction of U.S. Route 11 and State Highway 81, the Edinburg slabby limestones contain thin intercalations of shaly material bearing anomalous occurrences of lower Martinsburg brachiopods and bryozoans that are normally found higher in the section in a faunule commonly referred to as the *Sinuites* Beds. The anomalous occurrences of Martinsburg fossils in the subjacent Edinburg is understandable if one appreciates the fact that, on the east side of the Massanutten syncline, the base of the Martinsburg lithofacies drops way down in the section and supplants much of the limestone constituting the Edinburg Formation. The different faunas of the Edinburg and Martinsburg are largely facies-controlled.

The occurrence of members of the lower Martinsburg faunule in the Porterfield Stage in the Edinburg Formation is a clear indication that the characteristic Trentonian assemblage actually came into existence during Porterfield time but thrived only within the environmental limits in which Martinsburg clastics were being deposited. Narrow enclaves of shale in the Edinburg Limestone north of Strasburg are logically interpreted as the result of significant shifts in the boundary between the Edinburg lithofacies and the

Martisburg lithofacies during the time when the Martinsburg fauna was making its debut principally—though not entirely—within an area lying to the east of the environment in which the Edinburg Limestone was accumulating. The overlapping of fossil faunas of essentially different ages should be expected as a normal phenomenon; it should not be taken as an indication that fossils do not mean anything.

Multiple occurrences of the same faunule in thin intercalations within beds containing different fossils are no less to be expetced than interfingering of facies, and both phenomena point to shifting boundaries of partially contemporary lithofacies. In making such interpretations a much more sophisticated view of depositional conditions is necessary to comprehend the paleoecological conditions which so often are sensitive to bathymetric changes, such as could result from tidal fluctuations. If we look at the Appalachian succession, we can see that sharp changes in fossils are essentially everywhere controlled by depositional environments of enclosing sediments. If depositional environments change suddenly, faunal changes will be just as sudden; if the depositional boundaries shift slowly over a period of time, facies intertonguing and repetition of separate biofacies can be expected.

Some Concluding Observations

The Paleozoic faunal succession in the Appalachian region is distinctive enough in a general way so that, if one appreciates the evolutionary development of even one or two groups of invertebrates and knows when shell features were introduced and how long they survived, the most elemental paleontological information can save the stratigrapher from making serious mistakes in mapping and correlation.

Paleontology does have its weaknesses insofar as stratigraphy is concerned. Fossils just simply do not show up as often as the stratigrapher needs them, which is all the time and everywhere. The hapless stratigrapher who follows on the heels of an avid collector more often than not finds little left but unidentifiable scraps. Furthermore, many important sections are based upon road cuts, which are notoriously poor for fossil collecting. As the cuts gradually weather, the fossils may begin to show themselves, but by that time the exposures are not as complete and original boundaries of lithologic units may be lost.

The transient inadequacies of fossils can be overcome largely by using all the lithologic features as well as all the fossils that are available. In my opinion, neither fossils nor lithology alone can be a basis for sound stratigraphy, but together they can provide a sound answer. The local geologic mapper has a great advantage over the stratigraphic intruder sent out by his major professor to make a regional study of the beds by sampling them every 20 to 30 miles. The local mapper sees virtually *all* the exposures where remnant caches of fossils provided by weathering have escaped the less trained eye. The "road-runner" geologist seldom will see these natural caches.

The greatest recent breakthrough in paleontology was undoubtedly the technique of etching fossils, first used with tremendous success in the United States by G. A. Cooper. The probable causes for selective silicification of fossils in a given rock are not very well understood—not even the time of silicification. But etching has yielded fossil assemblages surpassing any that might have derived by natural forces of weathering.

Etching has made it possible to resample the same locality for more fossils as long as there is any rock left to collect. Etching of fossils has produced biologically significant numbers of fossils from a single locality for the first time. With large numbers of specimens of a given fossil, the paleontologist can pick and choose the best specimens for illustration and description; he can determine the range in size and the characters of young, mature, and merontic tests; and, most important of all, he can obtain both interior and exterior morphologic features. With this background of information at his disposal, the stratigrapher can make more use of his scraps of fossils or his good single specimens. The paleontology of all megascopic fossils is tremendously useful— that is, what there is of it. But the truth is that, in the Appalachians, except for the brachiopods and trilobites, the groups of abundant fossils in the Paleozoic rocks—ostracodes, bryozoans, algae, graptolites, cystids, crinoids, blastoids—are yet to be monographed in modern systematic detail. Even whole groups of brachiopods and trilobites await study. It is hoped that more work can be stimulated in this classic region, where sparsity of substantive data on fossils has so long handicapped stratigraphy.

A new way of collecting and describing fossils has come to the fore during the past five years, but its usefulness to the mapping stratigrapher is extremely limited, if not completely lacking. Systematic grab or channel sampling of well-exposed stratigraphic sections in 5-, 10-, or 20-foot intervals, measuring the sections, and returning to home base for time-consuming digestion of the rock in chloracetic and/or formic acid will yield conodonts in considerable numbers. Conodont paleontology, looked on by many as the panacea of regional stratigraphy, will, without doubt, prove to be less than that. The pragmatic value of conodont paleontology is still to be proven. I would be disinclined to view conodonts as of much use to the field stratigrapher who must make his stratigraphic decisions in the field as he goes about his business of mapping and of geologic interpretation. The value of fossil remains whose biological relationships are yet so poorly known that a military classification for them still prevails cannot have the scientific value of etched megafossils from the same rocks.

Conodont paleontology has two great attractions. First, it is relatively quick and one can cover a great deal of section in little field time by systematic sampling. Second, there is no denying that teeth from a mobile, cosmopolitan swimmer can be far more widely distributed than the sessile, semisedentary, or passively moved members among invertebrates could possibly be. But they will not and cannot provide the last word on biostratigraphic correlations. The last word will await all the systematic paleontology that has to be done, and which the stratigrapher continues to need.

In the fast tempo of today's scientific work, the tendency will be for the paleontologist to work on the fossil groups that will provide him with material for the greatest number of papers. It is hoped that some paleontologists will elect the harder and more time-consuming groups of megafossils for detailed study even though their study and monographing will require more preparatory time, more acid, more photography, more plates, and better descriptions to supplement the illustrations. The future progress of stratigraphy will be controlled by the amount of good paleontology that is available for the stratigrapher to use.

The common interests of stratigraphy and paleontology are rooted in paleoecology, and if we are to make progress in unravelling details of ancient environments both the rocks and their contained fossils must be studied exhaustively. Many of the problems in stratigraphy, and also in paleontology, are far too profound to be fully comprehended by one person. Continuing associations of stratigraphic mappers and competent paleontologists alone can provide the answers to many current geologic problems.

The status of our knowledge of Appalachian invertebrate fossils is far from satisfactory. The first and only truly exhaustive and comprehensive monograph dealing with an important group of Paleozoic fossils is G. A. Cooper's (1956) "Chazyan and Related Brachiopods," which sets a standard of excellence far above that of any other paleontologic monograph on a group of Paleozoic fossils. If treatises of similar nature and quality were available on Appalachian Paleozoic gastropods, cephalopods, pelecypods, bryozoans, corals, ostracodes, trilobites, and other fossil groups it would be possible to quicken the painfully slow advance of Appalachian Paleozoic stratigraphy and to accomplish work of considerably higher quality than that now being produced.

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Michael R. House

The Goniatite Wrinkle-Layer

ABSTRACT

The wrinkle-layer, a finely striate or ridged structure on the surface of certain goniatite shells, is probably related to some feature of the extended nacreous layer—the ostracum, as broadly interpreted—in the cephalopod animal. Dorsal and ventral structures are demonstrated for some genera in the Anarcestaceae and Pharciceratacea; only the dorsal wrinkle-layer is known from the Cheiloceratacea and, probably, the Goniatitaceae; restriction to an irregularly patterned structure is found in the Clymeniina. All groups with wrinkle-layer structure are composed of smooth, nonribbed forms.

Keyserling, in his classic report on an expedition to the Pechora region in 1843, drew attention to the occurrence of finely striate or ridged structures upon the surface of some goniatite shells. He aptly compared them with human fingerprints (Keyserling, 1846, p. 274). Subsequently, structures of this type have been described on many Paleozoic ammonoids, and several terms have been applied to them. The best known of such terms is the wrinkle-layer, or Runzelschicht; others include Ritzstreifen, épidermides, couche ridée, stries creuse, and hypostracum. Various analogies have been drawn between these structures and those found in the living *Nautilus.*

In recent years confusion has grown concerning the use and interpretation of many of the terms. This is due partly to the lack of good illustrations of the structures and partly to the difficulty in their interpretation. Perhaps these difficulties explain the omission of all such terms from a glossary of "Morphological Terms Applied to the Ammonoidea" (Arkell et al., in R. C. Moore, 1957, p. L2). The time is clearly ripe for a description and illustration of these structures. Furthermore, a review of the occurrence of wrinkle-layer structures among the early ammonoids reveals differences in pattern and arrangement which appear to be of taxonomic importance; also, some of the analogies which have been drawn with the living *Nautilus* prove difficult to substantiate while others appear more likely. Hence, with some brevity, these matters are discussed here in the hope that more detailed studies and records of them will be made in the future. Because some of the best known examples are Devonian, such occurrences are discussed more fully than later ones.

Historical Review

The significant literature on the subject is about a century old. Guido Sandberger (1851), in his neglected paper "Organisation der Goniatiten" has given the best illustrations of the structures in Devonian goniatites. The terms Runzelschicht and Ritzstreifen were proposed in 1850 by Guido Sandberger and his brother Fridolin. They applied the former term to the structures found on the dorsal side of the goniatite body chamber, as described in *Beloceras,* and others which had been noted as early as 1842 by A. d'Archiac and M. E. de Verneuil. The Sandbergers considered the Runzelschicht to be homologous with the black-layer of *Nautilus.* The term Ritzstreifen, or Einritzung, was applied to the structures seen on internal molds showing the flanks and ventral parts of the whorl, as common in *Gyroceratites;* they thought this analagous with the fine striations seen on the inside of the ventral portions of the shell of *Nautilus* (Sandberger and Sandberger, 1850, pp. 11, 12). Later, Barrande (1867, p. 23) expressed the opinion that the two structures were but two styles of preservation of the same feature, but he used the terms couche ridée and stries creuse for them. This anomaly he later rationalized (Barrande,

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1877, p. 1189), and used the term épidermides for both. Suess (1870, p. 10) confirmed Barrande's view on the identity of the Runzelschicht and Ritzstreifen but argued that both represented an incomplete nacreous layer.

It is curious, therefore, that Foord and Crick (1897, p. xx), who established the anglicized versions, considered the wrinkle-layer to be the equivalent of "the 'black layer' near the aperture of *Nautilus* . . the Runzelschicht of G. & F. Sandberger and the *couche ridée* of Barrande." They used the term epidermids for "the Ritzstreifen of G. & F. Sandberger and the *stries creuses* or *épidermides* of Barrande" and regarded them as "reproducing the surface of the mantle." Few detailed records of the structures in the older goniatites have been made subsequently; it happens that the structure most commonly found in post-Devonian ammonoids is of the Runzelschicht type, and it is this that has been referred to as the wrinkle-layer. Miller, Furnish, and Schindewolf (in R. C. Moore, 1957, p. L12) refer to the structure as the hypostracum, implying that it is distinct from and below the ostracum. Ruzhencev (in Orlov, 1962, p. 247), however, expresses the view that wrinkle-layer represents the wrinkled inner surface of the ostracum and that the hypostracum is distinct from it.

Review of the Occurrence of Wrinkle-Layer Structures

Barrande's conclusion that the Runzelschicht and Ritzstreifen are but two expressions of the same structure is confirmed in the present work. Not all goniatites show both, or either, however. Particularly well-preserved specimens showing both are instructive. Specimens of *Manticoceras sinuosum* (Hall) preserved as barytic replacements found in the Cashauqua Shale of New York (Plate 1: figures 1, 2) often show the full development. These show that in the body chamber the wrinkle-layer may extend over both the ventral and dorsal parts of the internal surface and that the structure is continuous over these areas (Figure 1). In the dorsal part, the layer overlies the previous whorl and may be referred to as the dorsal wrinkle-layer. In the ventral parts, the layer forms the innermost layer usually preserved, and this may be referred to as the ventral wrinkle-layer. The terms as used here are, for practical purposes, the same as the Runzelschicht and Ritzstreifen, respectively, of the Sandberger brothers. In a large number of genera, however, only the dorsal wrinkle-layer is known, and it is conjectural whether a ventral structure was ever developed. It seems preferable to keep some reference to position of development in the terminology, notwithstanding. The term wrinkle-layer is preferred to the term hypostracum because there still is uncertainty whether the implied homology is the correct one, but this is discussed below.

For convenience, the following systematic review conforms to the classification for Palaeozoic ammonoids as given in the treatise edited by R. C. Moore (1957).

ANARCESTACEAE.—So far, examples of the wrinkle-layer have not been described from those most primitive Lower Devonian goniatites which, as Erben has so elegantly shown, form the origin of the Ammonoidea. The later Emsian and Eifelian genus *Gyroceratites,* however, shows well the ventral wrinkle-layer on pyritic internal molds from the Wissenbacher Schiefer (Plate 1: figure 4; also Sandberger 1851, pl. 3, figs. 23, 25; Erben, 1953, pp. 190, 191). These layers form incised grooves on the mold. The genus shows no impressed area, and it is uncertain whether these structures continue on to the dorsal part of the whorl; they are best developed in the body chamber.

The dorsal wrinkle-layer has been noted in one specimen of *Agoniatites oxynotus* Wedekind; the layer is recrystallized and shows little radial pattern (Plate 2: figure 2), but the site is on the dorsum close to the aperture where the structure is frequently weakly and irregularly developed.

The structure which has been referred to as the wrinkle-layer in *Mimagoniatites fidelis* (Barrande, 1865, pl. 8, fig. 20) does not appear to be so; rather,

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PLATE 1: figures 1, 2.—*Manticoceras sinuosum* (Hall). Views of the wrinkle-layer on the inside of the umbilical wall, the flanks, and the dorsum of a specimen (in NYSM) preserved as a barytic shell replacement. From a concretionary nodule from near the top of the Cashaqua Shale, Shurtleff's Gully, Livonia, Livingstone County, New York, collected by Professor J. W. Wells. (Both views about × 6.)

Figure 3.—*Sudeticeras ordinatum* Moore. A topotype showing a structure in the shell of the outer whorl, which is pressed against the usual crenulate ornament of the preceding whorl; aperture to right. Specimen from the Viséan P_2 at Kinckley, Yorkshire; BM c74994 (× 15.)

Figure 4.—*Beloceras sagittarium* (G. & F. Sandberger). The dorsal wrinkle-layer (× 6) on a specimen (figured in Glenister, 1958, pl. 14, fig. 2) from the Frasnian of the Fitzroy Basin, Western Australia.

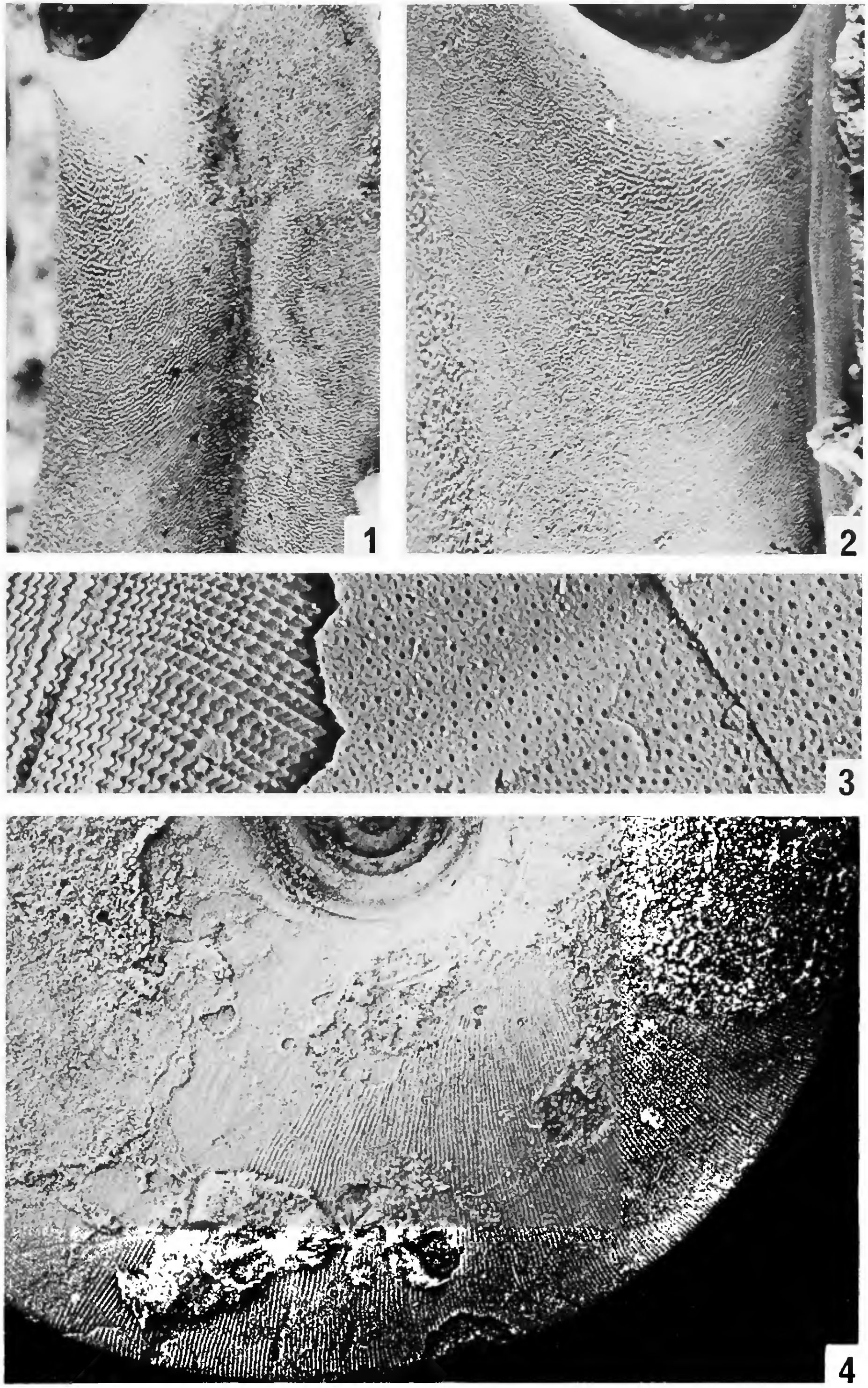

PLATE 1

it is reminiscent of the structure figured here under *Sudeticeras* (Plate 1: figure 3).

A feature that may be the ventral wrinkle-layer is illustrated for *Anarcestes praecursor* (Frech) by Barrande (1865, pl. 7, fig. 9), showing transverse and irregular striae crossing the outer flanks and venter.

Illustrations are available (Holzapfel 1895, pl. 6, fig. 6b) for the dorsal wrinkle-layer of *Maenioceras terebratum* (G. & F. Sandberger). A specimen figured here (Plate 2: figure 5) shows it developed through much of the body chamber, and it has been recorded, with a diameter of about 40 millimeters, as being slightly prosiradiate and continuing to the position of the base of the apertural lappet (House, 1962, p. 269, pl. 43, fig. 8).

PROLOBITACEAE.—The only representative known to show the wrinkle-layer is *Sobolewia,* and the writer has doubts that this is the correct taxonomic position. In *S. virginiana* House (Plate 2: figure 1) the dorsal wrinkle-layer has been observed for a quarter-whorl on the dorsal side of the apicad part of the body chamber. The course bears no relation to the course of the growth lines (the rule), and the lirae are firm and continuous, branching occasionally.

PHARCICERATACEAE.—Some comment has already been made on the contguity of the dorsal and ventral wrinkle-layer as shown in well-preserved specimens of *Manticoceras* (Figure 1; Plate 1: figures 1, 2). The ventral wrinkle-layer shows frequently on both the phragmocone and body chamber of pyritic molds; for example, on Büdesheim specimens. Illustrations have been given for several species (G. Sandberger, 1851, pl. 3, figs. 19, 21, 23, 24; Sandberger and Sandberger, 1850, pl. 7, fig. 9). The pattern ventrally takes the form of almost rectiradiate striae, but with a slight forward sweep in some specimens and with a slight backward sweep in others. At least one species group can be distinguished by the wrinkle-layer. The *M. affine* group is characterized by a much finer pattern than *M. cordatum* and its allies. *Ponticeras genundewa* (Clarke) from the Genundewa Limestone of New York occasionally shows the wrinkle-layer in pyritic forms (e.g., NYSM [1] 3645) as close-set, rather prorsiradiate striae on the lower flanks at diameters of less than 5.0 millimeters. Forms from the Cashaqua Shale barytized horizon that have been referred to *Probeloceras* by the writer show the dorsal wrinkle-layer particularly well (Figure 2B; Plate 2: figure 6) but no ventral structure has been observed. These specimens show that the layer terminates near the aperture. Keyserling (1844, pl. B, fig. 1) illustrated a similar structure in *Ponticeras*(?) *uchtense.* In *Timanites keyserlingi* (Miller) the dorsal wrinkle-layer striae have been described as "passing slightly backwards from the umbilicus" and continuing "in an irregular rectilinear course towards the venter, frequently bifurcating" (House and Pedder, 1963, p. 526, pl. 75, fig. 5).

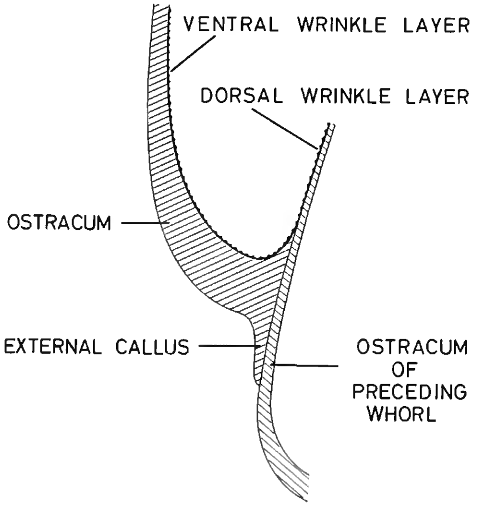

FIGURE 1.—The relationship between the dorsal and ventral wrinkle-layers, based on a specimen of *Manticoceras sinuosum* (Hall) from the Cashaqua Shale of New York (see Plate 1: figures 1, 2).

In the Pharciceratidae, G. Sandberger (1851, pl. 3, fig. 36) illustrated the structure of the dorsal wrinkle-layer in *Pharciceras lunulicosta.* In this specimen the the lirae pass across the flanks and are slightly prorsiradiate, the lirae numbering some 14 per millimeter, and without the spiral tendency close to the umbilical seam as shown, for example, in *Beloceras* and *Probeloceras.* The striae are coarser close to the seam, however.

Among the Beloceratidae, the structure in *Beloceras* is best known (d'Archiac and de Verneuil, 1842, pl. 26, figs. 7a, 8; G. Sandberger, 1851, pl. 3, fig. 35; Glenister, 1958, pl. 5, fig. 12, and pl. 14, fig. 2). The writer is indebted to Professor Glenister for supplying the negatives for the enlargements shown here (Plate 1: figure 4; Plate 3: figure 9). Only a dorsal wrinkle-layer has been observed and, again, it terminates at

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[1] New York State Museum, Albany. Other abbreviations used in this paper: BM, British Museum (Natural History); USNM, United States National Museum.

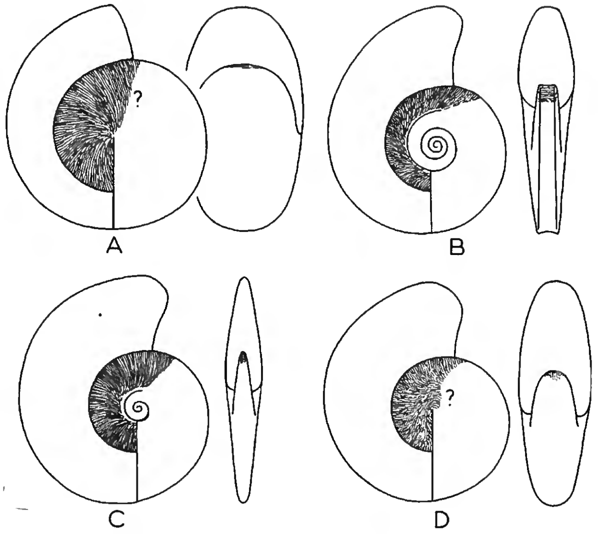

FIGURE 2.—The dorsal wrinkle-layer pattern in certain genera, based on specimens discussed in the text: A, *Sobolewia,* Givetian; B, *Probeloceras,* Frasnian; C, *Beloceras* Frasnian; D, *Tornoceras,* Middle and Upper Devonian.

the aperture. A diagrammatic representation is illustrated in Figure 2c.

CLYMENIINA.—Gümbel, in refiguring most of Münster's species, illustrated the dorsal wrinkle-layer in a number of genera, including *Cymaclymenia, Clymenia* and *?Cyrtocylmenia* sp. (Gümbel, 1863, pl. 15, fig. 6e); and in these the pattern is distinctly irregular. The figures for *Kosmoclymenia undulata* (Münster) illustrated by Gümbel (1863, pl. 17, fig. 1k) show an irregular transverse arrangement near the dorsal line associated with a raised band along the midline. This arrangement also has been observed by the writer in Devon specimens of *Cymaclymenia.* The ventral wrinkle-layer has not been described in this group, but it seems that the dorsal layer tends to be best developed close to the dorsal midline.

CHEILOCERATACEAE.—So far, only the dorsal wrinkle-layer has been met with in the Tornoceratidae, notwithstanding the large variety in the preserved specimens examined. The pattern is, however, remarkably distinctive, characterized by lirae which spiral backward from the umbilicus, become radial or slightly backwardly directed across the flanks, and are disrupted or vaguely spiral on the venter (of the preceding whorl). This pattern is illustrated diagrammatically in Figure 2D. The best illustrations are of *Tornoceras uniangulare obesum* from the Cashaqua Shale barytized fauna (House, 1965, pl. 8, fig. 72, and pl. 9, figs. 78, 79). Other illustrations have been given by Whidborne (1890, pl. 6, fig. 3a), Keyserling (1844, pl. A, fig. 5d), Sandberger and Sandberger (1852, pl. 10, fig. 14), and G. Sandberger (1853, pl. 3, fig. 37). In this genus also it can be demonstrated that the dorsal wrinkle-layer is not restricted to the body chamber. This is shown at least by *T. arcuatum* from the Squaw Bay Limestone of Michigan (House, 1965, pl. 8, fig. 7; it may be remarked that the writer never intended his recognition of specimens conforming to this species in the Tully Limestone to imply a correlation with that formation, the Squaw Bay would seem to be slightly younger, but older than the Genundewa). The same distinctive pattern is shown by *Parodiceras.* The only remaining genus of this family in which the wrinkle-layer has been described is *Pseudoclymenia,* which was illustrated by G. Sandberger (1853, pl. 8, fig. 4b) under the name *Clymenia pseudogoniatites.*

In the Cheiloceratidae the pattern seems the same as in *Tornoceras.* It has been recorded in *Cheiloceras* (House and Pedder, 1963, p. 530), but only the dorsal wrinkle-layer is known. If *Neoaganides* belongs in this family, then Miller and Furnish (1957, pl. 131, fig. 4) have illustrated another example.

GONIATITACEAE.—Knowledge of the wrinkle-layer in Carboniferous goniatites suffers from frequent mention but infrequent description. Some records are as follows: *Beyrichoceras* (de Koninck, 1880, pl. 49, fig. 10; Bisat, 1924, p. 83; 1934, p. 293; Gordon, 1957, p. 41); *Beyrichoceratoides* (Currie, 1954, p. 553); *Münsteroceras* (Gordon, 1957, p. 35); "*Pericyclus*" (Crick, 1899, p. 432, fig. 2; Foord 1901, p. 145); *Girtyoceras* (E. W. J. Moore, 1945, p. 414). Certain structures apparently connected with the ostracum are illustrated here in *Sudeticeras* (Plate 1: figure 3), but such structures are not comparable with the wrinkle-layer (and the same may be true of other records). Some of the finest illustrations of the dorsal wrinkle-layer occur in *Platygoniatites* described by Ruzhencev (1956; 1963; in Orlov, 1962, p. 247, figs. 2a,b); they show backwardly spiralling striae close to the umbilicus becoming more radial outwards, a course shown also in *Tornoceras.*

DIMORPHOCERATACEAE.—Ruzhencev (1956) has recorded a wrinkle-layer in *Delepinoceras* (which he would place in the Goniatitaceae).

PROLECANITACEAE.—There appears to be an occurrence reported by Foord (1903, p. 205, pl. 48, fig. 4a) in *Merocanites compressus* (Sowerby).

MEDLICOTTIACEAE.—A wrinkle-layer is noted by Gordon in ?*Pronorites,* but the structure on a figure of *Pronorites ludfordi* (Bisat, 1957, pl. 3, fig. 4) is a fingerprint. Miller and Furnish (1947, pp. 2, 44) have commented on the structure in *Artinskia* as follows: "fine lines which are not parallel to the growth lines; each forms a deep narrow rounded sinus with parallel sides on the ventral portion of the conch and a prominent rounded salient on the flanks."

Of the stratigraphically younger occurrences of wrinkle-layer structures, little can be reported. The Jurassic records have not been confirmed, and their general absence from ribbed ammonoids is perhaps significant. There are a number of Triassic records for which Mojsisovics (1893) is a primary source, although some of his attributions may be questioned. Two good examples showing a dorsal wrinkle-layer are illustrated here—*Arcestes* (*Proarcestes*) and *Owenites* (Plate 3: figures 1, 5–7). These suggest that a systematic survey might be profitable.

Generalizations

From the foregoing references and illustrations several general comments can be made. Firstly, the only groups in which both dorsal and ventral wrinkle-layers are authenticated are the Anarcestaceae and Pharcicerataceae; and in both of these groups the dorsal wrinkle-layer striae have a nearly radial or forwardly projecting course. Secondly, in these groups the structure is well enough known to demonstrate that certain species groups have distinctive styles of wrinkle-layer striae. Thirdly, in the Cheilocerataceae only the dorsal wrinkle-layer is known, and it contrasts with the preceding in that the striae are backwardly directed close to the umbilical seam, although they become more radial outward. Fourthly, the Clymeniina show a restriction of the structure, the dorsal midline is commonly associated with a raised band and the pattern is irregular. Fifthly, goniatitacean structures, whilst still poorly known, seem to agree with those of the Cheilocerataceae; that is, with their ancestors as generally interpreted. Sixthly, all groups showing the wrinkle-layer are smooth, nonribbed forms.

It has been demonstrated that the structure when complete continues to the aperture on the inside surface of the body chamber, but that the course of the striae bears no relation to that of the growth lines or form of the aperture. The structure is often found on the early whorls and phragmocone and is not a feature of maturity alone.

Interpretation

It is appropriate to discuss briefly the structures in the living *Nautilus* that might be homologous. More point is given to this when it is recalled that fossil nautiloids also show structures which have been described as the wrinkle-layer (for example, see Plate 2: figure 3). Six structures in *Nautilus* have been considered to be homologous with the wrinkle-layer:

(1) The black layer (G. Sandberger, 1851, pars).
(2) Reproduction of the surface of the mantle (Foord and Crick, 1897).
(3) Post annular lirae (G. Sandberger, 1851, pars).
(4) The ostracum (Ruzhencev, 1963; Teichert, in R. C., Moore, 1964, pp. K13, K15).
(5) Nacreous layer (Suess, 1870).
(6) Hypostracum (Miller and Furnish, in R. C. Moore, 1957, p. L12).

There is, among these recorded opinions, a nomenclatorical confusion, for, as Stenzel (in R. C. Moore, 1964, p. K77) has pointed out, in some usages

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PLATE 2: figure 1.—*Sobolewia virginiana* House. Dorsal wrinkle-layer on the posterior part of the body chamber (the last chamber is shown); aperture to right, umbilicus below. Specimen from the Millboro Shale (Bed 3 of Butts, 1940, p. 311) 0.4 mile due north of Hayter's Gap, Virginia; USNM 137650 (× 9).

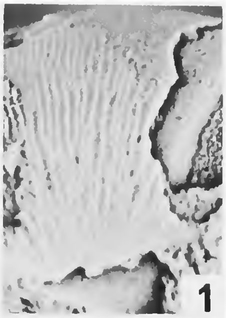
Figure 2.—*Agoniatites oxynotus* Wedekind. Dorsal wrinkle-layer on the posterior part of the body chamber; orad direction to left. Specimen from the Middle Devonian of Oberscheld, Germany; Berlin Museum c401 (× 4.6).

Figure 3.—*Vestinautilus* sp. The dorsal wrinkle-layer (below) and ventral wrinkle-layer (above) joining across the site of the umbilicial seam; orad direction to left. From the Lower Carboniferous of the Askeaton Limeworks, County Limerick, Eire. BM c74996; (× 1).

Figure 4.—*Gyroceratites gracilis* (Bronn). An internal mold of the body chamber showing the ventral wrinkle-layer; orad direction to left. From the Wissenbacher Schiefer, Dillenburg, Germany. BM c55963 (× 8).

Figure 5.—*Maenioceras terebratum* (G. & F. Sandberger). The dorsal wrinkle-layer in the posterior part of the body chamber; outer part of the body chamber, with growth lines, is shown above. From the Brilon Ironstone, Martenburg, Adorf, Germany. BM c74995 (× 4).

Figure 6.—*Probeloceras* aff. *lutheri* (Clarke). The dorsal wrinkle-layer in the body chamber (last septum is at top right). Specimen is a barytic replacement, probably from the upper part of the Cashaqua Shale near Honeoye Lake, New York; NYSM 4063 (× 9).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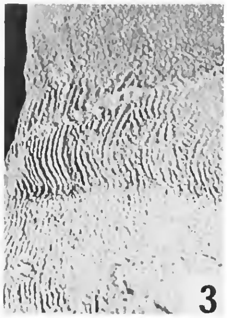
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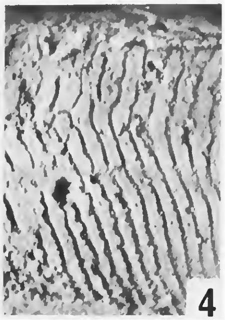
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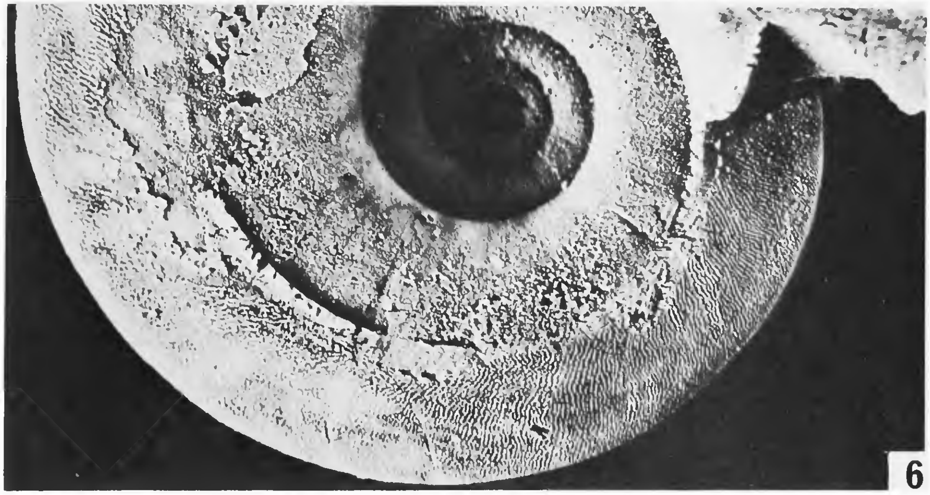
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PLATE 2


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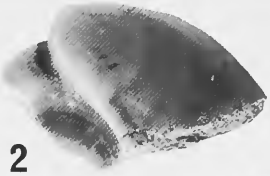
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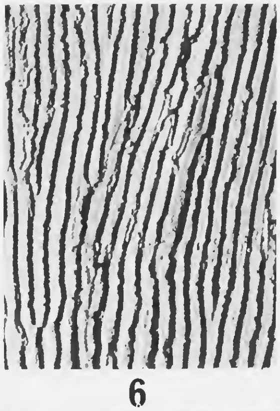
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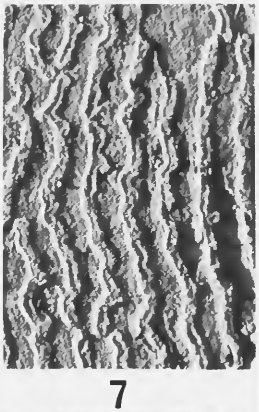
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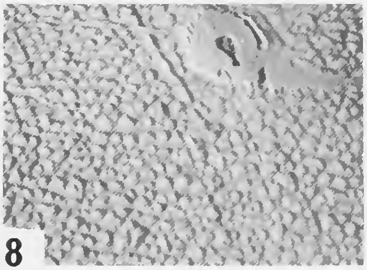
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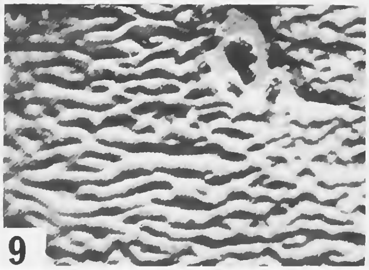
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PLATE 3

the ostracum can include both the nacreous layer and the hypostracum.

The analogy with the black layer has little to commend it, for, whilst it is a line of weakness in *Nautilus,* it has no linear structure, and there is no dominant development on the ventral surface. Also, Foord and Crick's interpretation is difficult to substantiate. Similarly, correspondence with postannular lirae is improbable in view of the restriction of that structure to the posterior part of the body chamber (and a posterior annular elevation has been described also in a number of ammonoids by Crick, 1898). This, then, leaves the ostracum in its broad interpretation. It is, of course, the dorsal nacreous layer which corresponds to the position of the dorsal wrinkle-layer. As is well-known, dissolution of *Nautilus* ostracum produces a wrinkled etched surface (Miller 1947, p. 20), as shown in Plate 3 (figures 8, 9). The dorsal nacreous layer is in continuation with the ventral nacreous layer—the inner part of the outer ostracum as used by Stenzel (in R. C. Moore, 1964, p. K78)—and, hence, continuation between a dorsal and a ventral wrinkle-layer could be expected.

But dissolution is not wholly satisfactory as it has been shown that the wrinkle-layer structures can be preserved in the phragmocone (where they might be less subject to dissolution), and the pyritic preservations would demand dissolution before the internal molds were formed.

It was considered that there might be a relation between the apertural "pallial line," inferred by the writer on another occasion to be close to the goniatite aperture (House, 1960). But there is little evidence to relate this to the course of the ventral wrinkle-layer striae. A chance find of a curious aperture at Büdesheim (Plate 3: figures 2–4), possibly of *Tornoceras* (it shows traces of growth lines with ventrolateral lappets), indicates how little it known of apertural conditions and emphasizes how uncertain any interpretations must remain. That the wrinkle-layer reflects in some way structures in some part of an extended nacreous layer, however, seems probable.

PLATE 3: figures 1, 7.—*Arcestes (Proarcestes) hauieli* (Welter). The dorsal wrinkle-layer. Specimen from the Triassic of Timor (figured in Welter, 1914, pl. 29, fig. 6); in Bonn Geologisch und Palaeontologisch Institut. (Figure 1, × 1; figure 7, × 10.)

Figures 2–4.—The aperture of a supposed goniatite (× 6) from the Frasnian of Büdesheim, Germany, collected by the writer from outcrops 400 meters south of the village church.

Figures 5, 6.—*Owenites egrediens* Welter. Specimen (figured in Welter, 1914, pl. 14, fig. 24) showing the dorsal wrinkle-layer; in Bonn Geologisch und Palaeontologisch Institut. (Figure 5, × 1; Figure 6, ×10.)

Figures 8, 9.—*Nautilus pompilius* Linné. Views (×4) of two stages in the dissolution of ostracum from the ventral part of the body chamber during etching in dilute hydrochloric acid.

Figure 10.—*Beloceras sagittarium* (G. & F. Sandberger). View (×7.5) showing the dorsal wrinkle-layer close to the aperture on a specimen (figured in Glenister, 1958, pl. 5, fig. 12) from the Frasnian of the Fitzroy Basin, Western Australia.

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Valdar Jaanusson

Evolution of the Brachiopod Hinge

ABSTRACT

In articulate brachiopods the hinge-teeth grow either by simple addition of shell material distally (deltidiodont hinge-teeth) or by means of a complex process of secretion distally and resorption proximally (cyrtomatodont hinge-teeth). It is shown that the mode of formation of the hinge-teeth influences the construction and function of the whole hinge mechanism as well as the growth of the posterior margin of the shell. During evolution of the hinge a minor and a major functional discontinuity had to be overcome. The minor functional threshold or instability was at the change from strophic to nonstrophic shells with deltidiodont dentition. The major threshold had to be passed when resorption in forming the hinge-teeth was introduced. Some evolutionary implications of the process of passing these functional thresholds are discussed.

The groups of articulate brachiopods with deltidiodont and with cyrtomatodont dentition correspond to Beecher's subdivisions Protremata and Telotremata, respectively. It is suggested that the use of these subdivisions should be reintroduced, for example, as subclasses of the Class Articulata.

In the past, little attention has been paid to the morphology, mode of growth, and mechanism of the articulating structures in articulate brachiopods. This is astonishing, because the general morphology and microstructure of the shell have been studied in considerable detail in this group.

The purpose of the present paper is to draw attention to the importance of the articulating mechanism in the function and construction of the articulate brachiopod shell. The observations included herein summarize some of the results on the functional morphology of the brachiopod shell which the writer has carried out during many years. An early version of the work was presented at the Symposium on Early Palaeozoic Invertebrates held in Warsaw in 1961. In this paper, attention is focused on dentition. Other components of the articulating mechanism and associated structures will be treated elsewhere.

For this study it was necessary to have access to a wide variety of articulate brachiopod groups with specimens showing internal morphological details. Although the paper is mainly based on material deposited in the Departments of Palaeozoology and Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, many additional specimens were examined in other collections. The opportunity, in 1959, to examine the world's largest collection of brachiopods—in the United States National Museum, Washington, D. C.—has been of great value, and the writer is greatly indebted to Dr. G. A. Cooper for his hospitality and generous help.

Dr. T. W. Amsden, Oklahoma Geological Survey, Dr. H. A. Lowenstam, California Institute of Technology, and Dr. A. Rõmusoks, Tartu University, kindly placed specimens pertinent to this study at the writer's disposal. Thanks also are due the officials of the Department of Invertebrate Zoology, Swedish Museum of Natural History; Zoological Museum, Uppsala University; and Laboratoire Arago, Banyuls-sur-Mer (through Dr. H. Mutvei, Stockholm) for material of modern brachiopods.

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All figured specimens, with the exception of the one shown on Plate 2: figure 10, belong to the Department of Palaeozoology, Swedish Museum of Natural History. For phototechnical reasons the ventral valves are consistently orientated with the ventral or posterior side up, and the dorsal valve with the dorsal or posterior side down. In order to facilitate comparison, this orientation of the valves is maintained also in the text figures.

The Hinge Structures

The main components of the hinge in articulate brachiopods normally are a pair of ventral hinge-teeth which accommodate into dorsal hinge-sockets and a pair of dorsal shell projections which, in certain groups, fit into a groove (crural fossette of Kozlowski, 1927) at the base of the hinge-teeth. The terminology used for the dorsal positive element of the hinge differs in various groups of articulate brachiopods (brachiophore, socket ridge, inner socket ridge). As this paper deals with articulate brachiopods in general, the use of different terms for the same structure is confusing. This difficulty has provisionally been solved here by the use of the descriptive term "dorsal hinge process." In some groups of articulate brachiopods with a hinge-line, the articulation becomes simplified secondarily by reduction of normal hinge structures; limitation of space prevents a further treatment of these modifications.

In addition to the main articulating devices there occur accessory hinge structures, the main function of which seems to be to direct the free valve edges when the shell closes. Such structures are not further treated in this paper.

Examination of articulated shells of modern brachiopods (rhynchonellaceans, terebratulaceans, terebratellaceans, and thecideaceans) reveals that the articulating structures serve four main functions. (1) They make possible a rotating movement of the valves relative to each other. In nonstrophic shells (Rudwick, 1959) they determine the position of the axis of rotation; in strophic shells the axis of rotation coincides with the hinge-line, and the construction of the articulating devices is such that this position of the axis of rotation is maintained at all degrees of opening or closing of the shell. (2) They prevent the transverse (lateral) and longitudinal movement of the valves relative to each other. (3) When the shell is being closed they direct the valves so that the free valve edges can fit snugly. (4) They limit the extent to which the shell can be opened. In an articulated shell it is not possible to move the valves sideways or backwards and forwards relative to each other without damaging some of the hinge structures. When the valves are forced apart beyond the limit allowed by the articulating devices, some of these structures break (Thomson 1927, p. 77).

These functions are integrated in the hinge mechanism, and all seem to be important to the animal; thus, an effective hinge mechanism would fulfill all these functions. When dealing with extinct groups, study of the functions of the articulating mechanism imposes problems because, as a rule, it is not possible to examine the hinge in action. In some cases simple models, constructed on the basis of serial sections, have been useful. In this paper the functions are discussed separately for each type of dentition.

Growth of the Hinge-Teeth

There are two main types of growth of the hinge-teeth. In one large group of articulate brachiopods the hinge-teeth grow as simple projections of the shell by addition of shell material distally (Figure 1; Plate 1: figures 1, 3, 5). The entire secreted hinge-tooth substance is fully preserved from the apex of the valve to the functional hinge-teeth. This kind of hinge-teeth is here termed the "deltidiodont type" (alluding to the often triangular, delta-like track of growth on the interarea). In the other group of articulate brachiopods the hinge-teeth either are knoblike (Figure 2A; Plate 2: figures 5, 7, 10), rising directly from the floor of the valve, or they are somewhat hook-shaped with a posteromedially protruding process (Figure 2B; Plate 2: figures 1, 8, 9).

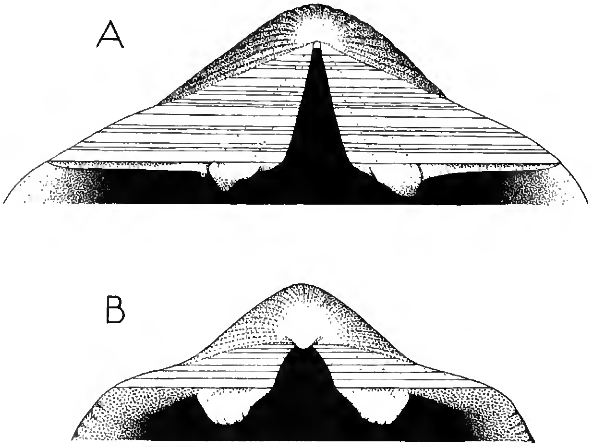

FIGURE 1.—Posterior part of ventral valves of strophic shells with deltidiodont hinge-teeth. A, *Hesperorthis davidsoni* (Verneuil); B, *Resserella elegantula* (Dalman).

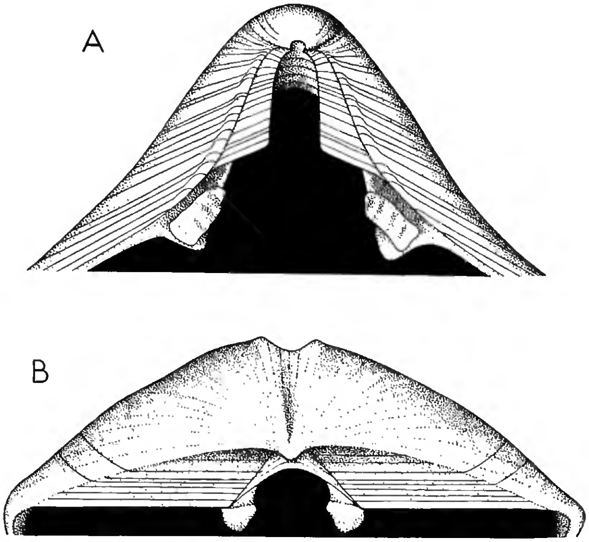

FIGURE 2.—Posterior part of ventral valves with cyrtomatodont hinge-teeth. A, *Hemithyris psittacea* (Gmelin), nonstrophic, with knoblike hinge-teeth; B, *Eospirifer radiatus* (Sowerby), strophic, with hook-shaped hinge-teeth.

Hinge-teeth of such shapes cannot possibly grow without a continuous resorption of the previously secreted tooth substance behind the protruding portion of the hinge-tooth. For this type of hinge-teeth the term "cyrtomatodont" (from the Greek word meaning "knob") is here proposed.

The deltidiodont hinge-teeth characterize (in the classification of Williams and Rowell, in Moore, 1965) all members of the orders Orthida, Strophomenida (except those groups in which the hinge-teeth have become secondarily reduced), and Pentamerida. Further exceptions are *Tropidoleptus, Perditocardinia,* and *Cadomella,* which have hinge-teeth of the cyrtomatodont type. In the writer's opinion, these three genera should be classified, respectively, with the Terebratulida, Rhynchonellida, and Spiriferida (see section on classification, below). In a few other genera of somewhat doubtful taxonomic position—such as *Enantiosphen* and *Thecospira*—the dentition is poorly known.

Among groups with deltidiodont hinge-teeth, only two known examples indicate the use of resorption during the growth of a shell structure. In *Dicoelosia* the hook-shaped dorsal hinge process obviously requires resorption for its growth (Wright, 1968), and there is some doubt whether or not some other advanced enteletaceans formed their dorsal hinge process in the same manner. In *Porambonites* the pedicle foramen became enlarged during the ontogenetic development, and, here again, resorption evidently was involved. Apart from these exceptions, brachiopods possessing deltidiodont hinge-teeth do not seem to have acquired the ability to use resorption for the construction of their shells. A few specimens exhibit a hook-shaped hinge-tooth (or similar features of other internal structures) which could not possibly grow and preserve this shape if resorption had not been involved. Such examples that are known to the writer, however, obviously belong to gerontic individuals which have ceased to grow, and most specimens of the same species do not show these features.

All members of the orders Rhynchonellida, Spiriferida, and Terebratulida and of the suborder Thecideidina possess cyrtomatodont hinge-teeth. In Spiriferida and Terebratulida resorption also is widely used for the construction of other shell structures, such as brachidia, loops, and pedicle foramina.

The extent of resorption during the growth of the cyrtomatodont hinge-teeth varies within wide limits. In most instances, previous growth stages of a hinge-tooth have been completely removed by resorption, and the hinge-tooth then has the shape of a knob which rises directly from the floor of the valve (Figure 2A; Plate 2: figures 5, 7, 10). In other cases only the shell material behind the posteromedially protruding portion of the hinge-teeth is resorbed, and the rest of the once-secreted hinge-tooth is preserved; the hinge-teeth then have a hooklike appearance (Figure 2B; Plate 2: figures 1, 8, 9). The hooklike hinge-tooth is associated with strophic shells such as those of the Spiriferacea (Figure 2B) and Thecideacea (Plate 2: figures 8, 9) but occasionally it also occurs in nonstrophic shells. It is interesting that very small shells of certain rhynchonellaceans possess hooklike hinge-teeth (Plate 2: figure 11) which, during the ontogenetic development, gradually change into knob-shaped hinge-teeth (Figure 2A). Gradations seem to exist between these two shapes of cyrtomatodont hinge-teeth and, thus, gradations in the degree of resorption used for producing hinge-teeth of this type.

Articulation in Strophic Shells with Deltidiodont Hinge-Teeth

In the Orthida, Strophomenida, and Porambonitacea (excluding Camerellidae, Parastrophinidae, and Brevicameridae, which in this paper are tentatively included in a separate superfamily, the Camerellacea) the hinge-teeth accommodate into dorsal hinge-sockets. As in articulate brachiopods in general, the hinge-sockets cannot be formed as simple pits in the floor of the valve as the thinness of the test sets a definite limit to the depth of such pits; consequently, the main part of the hinge-sockets has to be constructed as a kind of pouch upon the floor of the valve. In the brachiopods under consideration, the posterior shell wall is used as the posterior wall of the hinge-socket and the anteromedian wall of the socket is formed by the secreting of a ridge, plate, or boss upon the inner surface of the valve (the "brachiophore" of Schuchert and Cooper, 1932; the "socket ridge" of Williams, 1953; and the "dorsal hinge process," as in the present paper). In certain groups the posterolateral surface, corner, or edge of this process accommodates into a depression or groove ("fossette crurale" of Kozlowski, 1927) at the base of the hinge-teeth; other groups, such as clitambonitaceans, strophomenaceans, and triplesiaceans, lack crural fossette. In some plectambonitacean genera the crural fossette is so deep that the hinge-tooth appears to be bifid. Laterally the hinge-socket has no wall, and the reason for this is clear: if such a wall were present in the direction of growth of the hinge-socket it would have to be continuously resorbed and secreted during the growth of the hinge-teeth.

All brachiopods under consideration have a strophic shell, which means that they have a hinge-line (Rudwick, 1959). Continued existence of the hinge-line during the growth of the shell produces an interarea, at least ventrally. Contrary to the opinion of Rudwick (1959, p. 21), *Porambonites* has a well-defined hinge-line, although it is very narrow. In these shells the position of the axis of rotation was fixed along the hinge-line. During opening or closing of the shell the anterodorsal surface of the hinge-teeth glided upon the floor of the hinge-socket. The interlocking arrangement of the hinge-teeth and the dorsal hinge processes prevented lateral and longitudinal movements of the valves relative to each other and, during closing of the shell, directed the valves so that their edges would fit snugly. One of the main functions of this tight interlocking arrangement was to maintain the position of the axis of rotation exactly along the hinge-line at all degrees of opening or closing of the shell. In this kind of articulation it is difficult to find a mechanism which effectively controlled the maximum degree of opening of the shell; it is probable that, as in invertebrate brachiopods, this function has been exerted by the muscles.

Some few members of the group under consideration developed structures which could, and possibly did, control the maximum width of the gap between the valves. In *Dicoelosia* the shell could be opened until the unique, hook-shaped dorsal hinge process became pressed against the base of the hinge-teeth. In *Porambonites* the distance between the beaks of the valves is short, and a relatively narrow gap between the valves would bring the beaks into contact and thus prevent a further increase of the width of the gap.

Articulation in Nonstrophic Shells with Deltidiodont Hinge-Teeth

The pentameraceans and camerellaceans that I examined do not possess a hinge-line. It has been repeatedly stated, for example, that *Stricklandia* and *Costistricklandia* are provided with an interarea, at least on the ventral valve (Schuchert and Cooper, 1932; Rudwick, 1959; Amsden, in Moore, 1965; and others). In these genera, however, the plane areas on either side of the delthyrium or cardinalia could not have been formed by the growth of a hinge-line because the anterior margin of these areas is not straight (Plate 1: figures 1, 2). Moreover, in these brachiopods the plane areas on either side of the cardinalia cannot represent interareas if one considers the mechanics of articulation. The topographically anterior margin of these areas is situated in front of the main part of the hinge-notch and, thus, in front of the axis of rotation.

The following discussion is based on a study of the pentameraceans; however, the examination of a few well-preserved interiors of the camerellaceans indicates that all the important points mentioned apply also to the Camerellacea.

The small size of the hinge-teeth in the pentameraceans makes it difficult to study their shape with serial sections. In isolated ventral valves the hinge-teeth usually are partly or completely broken off, thus giving the impression that the posterior edges of the spondylium acted as articulating structures. The writer has mainly studied the hinge-teeth of pentameraceans in articulated shells either by removing parts of the dorsal valve around the hinge-teeth or by cleaning the interior of the shell.

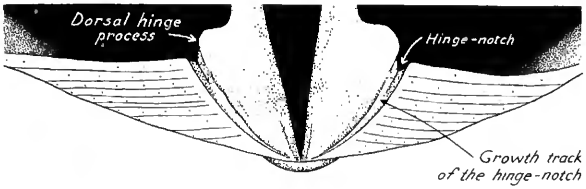

FIGURE 3.—*Costistricklandia lirata* (Sowerby). Posterior part of a dorsal valve in ventral view (cf. Plate 1: figure 2).

The hinge-teeth of the pentameraceans and camerellaceans are of the deltidiodont type, the whole ontogenetic development of a hinge-tooth being preserved along the delthyrial margin (Plate 1: figure 1). As a rule the hinge-teeth grow along a longitudinally strongly curved line which is reflected by the strong curvature of the beak of the ventral valve. As a result, the posterior side of a hinge-tooth is somewhat concave. The cross-section of a hinge-tooth is commonly more or less rounded in contrast to the often pronouncedly triangular shape in the brachiopods that possess deltidiodont hinge-teeth and a strophic shell.

The pentameraceans lack a normal hinge-socket (St. Joseph, 1935 p. 404). The posterior side of the hinge-teeth commonly accommodates into a notch at the lateral margin of the cardinalia, here termed the "hinge-notch" (Figure 3; Plate 1: figure 2). In the pentameraceans with hinge-notches the distal part of the hinge-teeth projects freely into the interior of the dorsal valve, and the anterior sides of the teeth are free and unprotected (Figure 4; Plate 2: figure 4). In some pentameraceans (e.g., *Sieberella,* Plate 2: figure 3) and many camerellaceans (e.g., *Anastrophia*) the hinge-teeth fit into a niche-like recess in the anterior wall of the cardinalia. The growth-track of a "hinge-niche" resembles a normal hinge-socket in strophic shells except that its longest axis is more anteriorly directed.

Anteromedially the hinge-notch or the hinge-niche is bounded by the lateral edge of what, in the pentameracean terminology, is called the "inner plate." This structure does not take part in the immediate construction of the hinge-notch or hinge-niche, and it is situated at a higher level ventrally. Its general position relative to a hinge-tooth is similar to that of the dorsal hinge process in strophic shells with deltidiodont hinge-teeth, and the same term can be used provisionally for this structure both in the camerellaceans and pentameraceans. The dorsal hinge process grew from the apex of the valve obliquely to the axis of rotation, and it assumes the same oblique position anteromedially in front of the hinge-teeth (Figure 3; Plate 1: figure 2). No trace of a depression or groove at the base of the hinge-teeth for the accommodation of the edge of this process has been observed in any camerellacean or pentameracean.

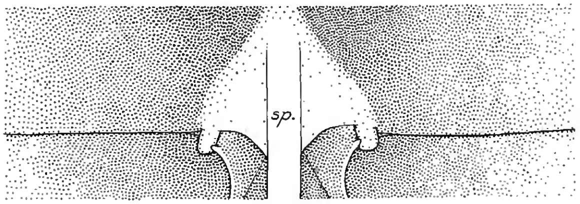

FIGURE 4.—*Gypidula galeata* (Dalman). The interior of an articulated shell showing the fitting of the hinge-teeth into hinge-notches (sp.=spondylium); after specimen Br. 2738.

There were no essential differences in the process of articulation whether the hinge-teeth accommodate into hinge-notches or hinge-niches. When the shell opened the posterior sides of the hinge-teeth were pressed against the posterior wall of the hinge-notch or the posteroventral edge of the hinge-niche, and the contact surface between these dorsal and ventral hinge structures obviously determined the position of the axis of rotation. The distal part of the hinge-teeth moved freely in anterior direction as there is no dorsal surface upon which it could have glided. The dorsal hinge processes are situated ventral to the apparent position of the axis of rotation and their role in the process of articulation is not quite clear. As these processes lie obliquely in front of the hinge-teeth, however, they prevented a longitudinal movement of the valves relative to each other.

In this articulating mechanism, too, there are no structures which effectively control the maximum degree of opening of the shell; however, these shells possess another mechanism which potentially could have served this function. It is difficult to ascertain whether this mechanism actually was used or the pivotal movement of the valves became arrested at an earlier stage by the action of the muscles.

In nonstrophic shells with cyrtomatodont hinge-teeth the diductor muscles are attached dorsally to the inner side of the incurved beak of the dorsal valve. The axis of rotation is situated fairly deep within the dorsal valve. When the shell opens, the force of the diductor muscles moves the beak of the dorsal valve into the ventral valve until the interaction between the ventral and dorsal articulating structures makes a further movement impossible. The movement takes place just at the dorsal margin of the delthyrium and deltidial

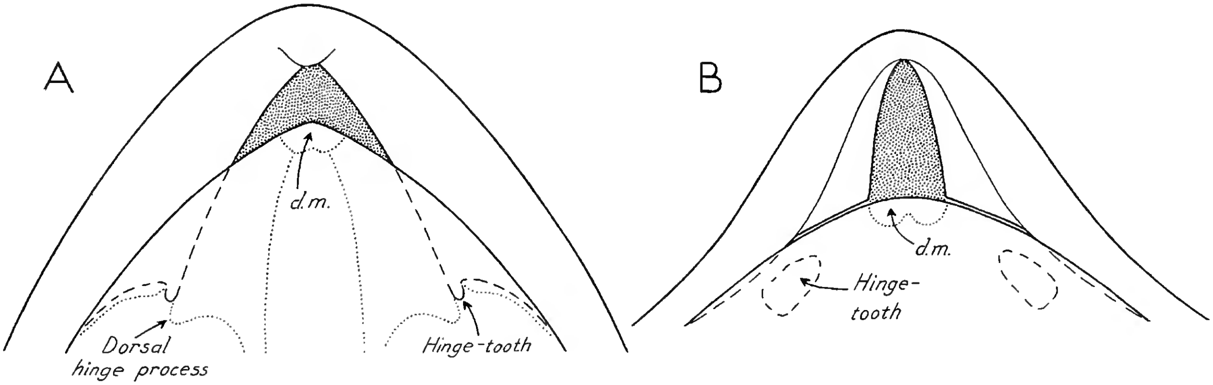

FIGURE 5.—The relationship between some hinge structures and the posterior margin of the dorsal valve in closed, articulated, nonstrophic shells. A, in shell with deltidiodont hinge-teeth (a pentameracean); B, in shell with cyrtomatodont hinge-teeth (a rhynchonellacean). Dashed lines, structures of the ventral valve; dotted lines, structures of the dorsal valve; d.m., area of insertion of the diductor muscles.

structures (Figure 5B) or, if these are lacking, at the posterior margin of the ventral valve.

In nonstrophic shells with deltidiodont hinge-teeth the diductor muscles also were attached to the beak of the dorsal valve, but on opening the shell only a restricted movement of the dorsal beak into the ventral valve was possible. In these brachiopods the delthyrial opening cannot possibly be wider than the distance between the hinge-teeth, provided that no resorption was involved. The hinge-teeth have to fit into the dorsal analogues of the hinge-sockets formed on the inner side of the dorsal valve (Figure 5A). As a result of these conditions the total width of the dorsal beak in the pentameraceans and camerellaceans is always larger than the distance between the hinge-teeth. When the shell opened, the beak of the dorsal valve could move until it became pressed against the delthyrial margins and the movement was arrested. In the pentameracean and camerellacean shells examined the amount of such movement allowed varies, but in several genera only a narrow gap could have been produced between the free edges of the valves.

Articulation in Shells with Cyrtomatodont Hinge-Teeth

The method of using resorption in the formation of the hinge-teeth opened a new way in the construction of the articulating structures. An effective mechanism could be constructed in the articulating devices for controlling the maximum width of the gap between the valves. Resorption of earlier ontogenetic stages of the hinge-teeth allows the delthyrial-deltidial region to become wider than in shells with deltidiodont hinge-teeth where the distance between the hinge-teeth sets a definite limit to the width of the delthyrium. Thus, when the shell opens, the beak of the dorsal valve can move into the ventral valve as described in the foregoing section. As a result, the contact between the beak of the dorsal valve and the delthyrial margins lost the potential function of controlling the maximum degree of opening of the shell, and this function was taken over by the articulating structures.

In nonstrophic shells with cyrtomatodont hinge-teeth the hinge-socket grows along a curved line following the curvature of the posterior margin of the dorsal valve. This is the case also with the homologues of the hinge-socket in the camerellaceans and pentameraceans. Due to the resorption of the hinge-teeth proximally, however, the resulting knob- or hook-shaped hinge-tooth can fit into a socket and perform a limited rotating movement relative to the hinge-socket. The anteroventral wall of the socket is formed by the dorsal hinge process (inner socket ridge) which has a thickened, rounded margin. As a result of the direction of growth, the hinge-sockets, the long axis of the hinge-teeth, and usually also the dorsal hinge process, are directed anteromedially and thus obliquely to the axis of rotation. When the shell opens, the convex posterior surface of the hinge-tooth performs a pivotal movement upon the floor of the socket until the truncated proximal end of the hinge-tooth is pressed against the bottom of the hinge-socket, and the inner margin of the hinge process becomes pressed against the base of the hinge-tooth. In some terebratulaceans the interaction between the dorsal and ventral hinge structures is more complicated but the general result is the same. A further opening of the shell then is impossible without breaking some of the articulating structures. This mechanism effectively controls the maximum degree of opening of the shell. The axis of rotation is not fixed in a certain position but makes a slight translative movement during the pivotal movement of the hinge-teeth.

Brachiopods with cyrtomatodont hinge-teeth and a strophic shell have the same principal construction of the hinge as those with a nonstrophic shell. A translation of the axis of rotation does not take place, however, and the position of the axis of rotation is fixed along the hinge-line. The hinge-sockets grow along a straight line (Figure 6A) as do the hinge-teeth. Compared with strophic shells which possess deltidiodont dentition, the growth of the hinge-socket is different. In shells of the former type the hinge-sockets grow by addition of shell within the socket; thus, their floor is continuously raised. In shells with cyrtomatodont hinge-teeth the growth proceeds in an anterolateral direction by continuously widening the hinge-socket. In this case no further shell is secreted upon the floor of the socket except secondarily at a later stage. As a result of this, in shells with a dorsal interarea the growth-track of the hinge-socket often remains open, forming a furrow from the beak of the valve to the functional hinge-socket (Figure 6A; Plate 2: figure 2).

Evolution of the Brachiopod Hinge

All Cambrian articulate brachiopods possess deltidiodont hinge-teeth and all the shells are strophic. The growth of the articulating structures is simple, and the animal obviously had not acquired the ability to use resorption for their construction. It is probable that the other types of dentition have evolved from the kind found in strophic shells with deltidiodont hinge-teeth.

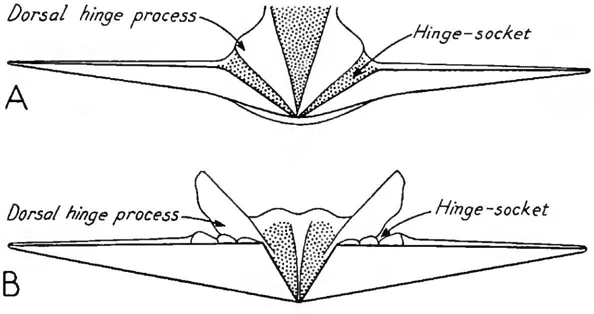

FIGURE 6.—Posterior parts of dorsal valves in shells with a dorsal interarea, showing the position of the hinge-socket relative on the notothyrial margin. A, in telotremate brachiopods (*Eospirifer*); B, in protremate brachiopods (*Hesperorthis*).

The ancestors of the camerellaceans and pentameraceans probably should be looked for among the porambonitaceans (Williams and Rowell in Moore, 1965). Early in the Ordovician there was a tendency among some lineages of the porambonitaceans to reduce the length of the hinge-line and thus form shells which are narrow posteriorly. One such group is the Lower Ordovician (Ontikan) Angusticardiniidae (placed among Orthida and Enteletacea by Williams and others (in Moore, 1965), but evidently belonging to the Porambonitacea, cf. Rubel, 1961). Schuchert and Cooper (1932, p. 84) suggested that *Angusticardinia* is the earliest rhynchonelliform shell which might, with more complete reduction of the interareas, have given rise to rhynchonellids. Unfortunately, in this family as well as in early camerellaceans the dentition is still poorly known.

The change from strophic to nonstrophic shells in brachiopods with deltidiodont dentition involved the loss of the anterior wall of the hinge-socket. Owing to the growth along a transversely curved line, the hinge-socket grew in anterolateral to anterior, instead of lateral, direction. As explained earlier, no wall could be formed in the direction of growth of the hinge-socket; otherwise this wall would have to be continuously resorbed and secreted during the growth of the shell. The lack of the anterior wall of the hinge-socket implies that no surface existed for the hinge-teeth to glide upon, and thus the distal surface of the hinge-teeth did not actively participate in the process of articulation. During the pivotal movement of the valves, the posterior side of the hinge-teeth became pressed against the margin of a hinge-notch or a hinge-niche by the action of the normal force.

The change also involved a decrease in the size of the hinge-teeth. In strophic shells a large contact area was needed between the hinge-teeth and hinge-sockets in connection with the function of keeping the position of the axis of rotation fixed along a long hinge-line. When the hinge-teeth became secondarily reduced, accessory structures such as the denticles in stropheodontids usually were developed for fulfilling the same function. Nonstrophic shells with deltidiodont dentition are narrow posteriorly and, since the distal surface of the hinge-teeth could not be used in the process of articulation, there was no need of forming large hinge-teeth. The small size of the hinge-teeth in the pentameraceans has led to the opinion that their dentition is of a degenerate nature and that in this group the articulation would have been of no use in maintaining the valves together, a function that must have devolved almost wholly on the muscles (St. Joseph, 1938, p. 247). There is no doubt, however, that in the pentameraceans the dentition was sufficiently strong to allow a pivotal movement of the valves and to prevent a lateral movement of them relative to each other. There is, of course, the question whether or not the normal force caused by the action of the diductor muscles was sufficiently strong for holding the hinge-teeth in place. If not, the presence of an additional muscle, with its line of action directed transversely to the long axis of the hinge-teeth and going through the axis of rotation, would have been necessary. The sole function of this additional muscle would have been to hold the hinge-teeth in their proper position by the action of the normal force during the pivotal movement of the valves. At the present state of our knowledge, however, this question is purely theoretical. Neither the necessity for nor the existence of such a muscle in the articulating mechanism of the pentameraceans has been proven.

The articulation in nonstrophic shells with deltidiodont dentition can easily be derived from that in strophic shells. There obviously is a functional instability involved at the transition to anteriorly open hinge-sockets, but in order to discuss this a more detailed knowledge is needed on the dentition of late porambonitaceans and early camerellaceans.

The use of resorption in forming hinge-teeth certainly marks one of the major steps in the evolution of articulate brachiopods. The first shells that made use of this invention appeared early in the Middle Ordovician; gradually, shells with cyrtomatodont dentition began to dominate among articulate brachiopods. All modern articulate brachiopods have cyrtomatodont hinge-teeth.

From the standpoint of mechanics, a hinge with cyrtomatodont hinge-teeth is a more elegant solution to the problem of articulation in the brachiopod shell than is a hinge with deltidiodont hinge-teeth. The axis of rotation could have been placed fairly deep inside the dorsal valve, and at the same time there could have been constructed a hinge which efficiently fulfilled all essential functions of the articulation. The former condition made it necessary to find a solution for attaching the diductor muscles dorsally so that the force of these muscles would attain the greatest possible moment when the shell opens (Jaanusson and Neuhaus, 1965).

There is an obvious functional discontinuity between the cyrtomatodont and deltidiodont dentition. The shells either possessed or lacked the ability to use resorption when forming the hinge-teeth, and no intermediary stages could have existed.

Cyrtomatodont hinge-teeth agree with the deltidiodont hinge-teeth as developed in the camerellaceans and pentameraceans in that, in the process of articulation, their morphologically posterior side is the functionally active surface and not, as in the deltidiodont hinge-teeth of strophic shells, the distal surface. In fact, in cyrtomatodont hinge-teeth, the morphologically distal surface does not participate in the process of articulation at all. This and other considerations strongly suggest that the cyrtomatodont dentition has been derived from the deltidiodont hinge-teeth in nonstrophic shells.

Most brachiopods with cyrtomatodont dentition have nonstrophic shells, but strophic shells are not uncommon and they characterize separate genera in some groups or all members in other groups. The cyrtomatodont dentition is easily adapted to both kinds of shells. The strophic condition of the shells with cyrtomatodont dentition obviously is secondary (Williams and Rowell, in Williams et al., 1965) and genera or groups with such shells probably have evolved from ancestors with nonstrophic shells and with the same type of dentition. A derivation of strophic shells with cyrtomatodont dentition from those with deltidiodont

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PLATE 1: figures 1, 2.—*Costistricklandia lirata* (Sowerby), Gotland, Visby, Norderstrand. Silurian, Lower Visby Marl. 1, Ventral valve in posterior view (×5) showing well-preserved deltidiodont hinge-teeth; Br. 102331. 2, Cardinal region of the dorsal valve, in ventral view (×5); Br. 102332.

Figures 3, 4.—*Hesperorthis davidsoni* (Verneuil), Gotland. Silurian, Lower Visby Marl. 3, Ventral valve in posterodorsal view (×5) showing deltidiodont hinge-teeth; Br. 44011, Västkinde. 4, Interior of the posterior part of a dorsal valve in posteroventral view (×6); Br. 102333, Visby, Norderstrand.

Figures 5, 6.—*Clitambonites squamatus* (Pahlen), Estonia, Kohtla. Middle Ordovician Kukruse Stage. 5, Ventral valve in posterior view (×4) showing deltidium and well-preserved deltidiodont hinge-teeth; Br. 102334. 6, Interior of the posterior part of a dorsal valve in posteroventral view (×4); Br. 102335.

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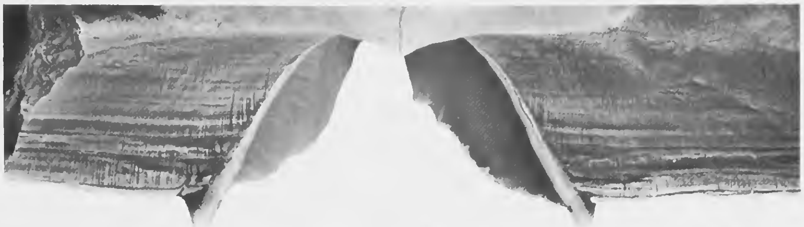

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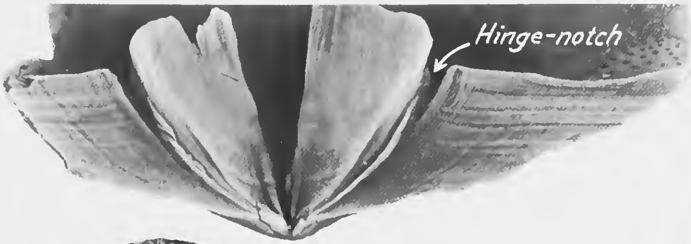

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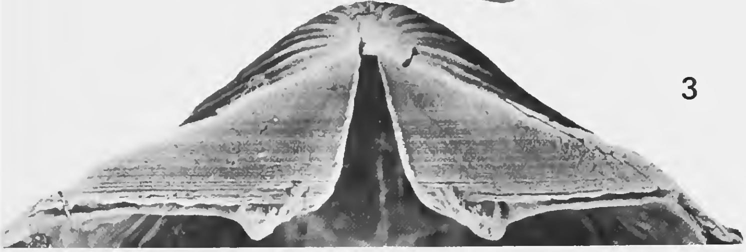

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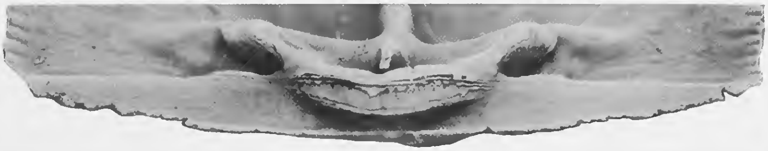

PLATE 1

dentition would have required a number of coordinated changes in the articulating mechanism, and this is considered unlikely.

In the evolution of the hinge in articulate brachiopods there are thus both minor and major functional discontinuities. Once a functional threshold had been passed and an advantageous construction created, the dentition remained remarkably constant during long periods of geological time. The dentition of the Ordovician rhynchonellaceans is practically identical with that of the modern representatives of the group, and in no important respect does it differ from the dentition of other groups with cyrtomatodont hinge-teeth. With the exception of reduction phenomena, the morphology of the hinge-teeth varies but slightly within the group that possesses deltidiodont hinge-teeth and strophic shells. This is one of the reasons why details of the hinge-teeth are almost completely ignored in descriptions of articulate brachiopods.

Study of the evolution of the brachiopod dentition gives results of great theoretical interest. It furnishes excellent examples of passing functional thresholds and the creation of new advantageous constructions which lead to an adaptive radiation of the groups with the new construction. Moreover, in this case there is the possibility for us to actually understand what happens when a functional threshold is passed during the evolution. This is possible because it is easy to analyze the function in terms of the mechanics involved; and the growth of the components that constitute the mechanism can be followed in often well-preserved and abundant fossil material. Much work remains to be done in following the changes of the dentition and analyzing the mechanism, especially in the groups which are assumed to be near the functional threshold. Some tentative conclusions can be made with the material at hand, however.

The functional thresholds under consideration are of such nature that, in order to fix the innovation in a population gene pool, individual brachiopods with and without the new construction had to co-exist in one population. This implies that there probably existed at least one population of brachiopods with deltidiodont dentition in which some individuals had a very short hinge-line and the others lacked this structure. Likewise, it is probable that a population or populations existed in which some individuals had acquired the ability to use resorption in forming hinge-teeth and that these individuals were able to cross-breed with others that lacked this ability. In other words, the populations under consideration were variable enough to include the morphological types of the shell and articulation on either side of the functional threshold.

The populations probably lived in an environment wherein the selection pressure against articulating mechanism was extremely low, because, in its early stages, the new construction of the dentition was not likely to have served its functions as well as did the old construction. In fact, a selective advantage in some other characters that were useful in the particular environment and were pleiotropically linked to the genes which carried the characters of the new construction possibly was needed in order to carry the new construction through the functionally unstable stage. In the process of passing the functional threshold the species probably had very small, thin shells. In small, light shells the forces acting upon the articulating devices are weak, and a certain laxity in the construction of the hinge mechanism is easier for such shells to endure than in large, heavy shells where strong forces are acting upon relatively massive articulating devices. All of the earliest representatives of brachiopods with cyrtomatodont dentition have very small shells.

Classification of the Articulate Brachiopods

The groups of articulates with deltidiodont and cyrtomatodont hinge-teeth correspond closely to Beecher's subdivisions Protremata and Telotremata, respectively. When defining these groups Beecher (1891) overemphasized the importance of the pedicle opening and the role of the pedicle in influencing the growth of the posterior part of the shell. The criteria used for distinguishing these groups in adult shells were based mainly on deltidial structures, and later work showed the general appearance of the deltidial structures to overlap in the two groups. Following criticism by Cooper (1944), the use of Beecher's classification was discontinued (cf. also Williams 1956, p. 259, and Williams and others in Moore 1965, p. H222).

The results reported in the present paper, however, strongly support Beecher's classification. In fact, characters also exist in the deltidial structures that contribute to defining these groups; however, the factors controlling the differences in the delthyrial-deltidial region are not connected with the pedicle but are influenced by the growth and function of parts of the articulating mechanism.

In shells with deltidiodont hinge-teeth the delthyrium cannot possibly be broader than the distance between the hinge-teeth, and in these shells the growth track of the hinge-teeth can be said to define the margins of the delthyrium (Figure 1; Plate 1: figures 1, 3, 5). The inner margin of the delthyrium and that of the hinge-teeth do not correspond exactly since in many protremates the convexity of the hinge-teeth causes their inner margins to protrude farther medially than the margin of the delthyrium as defined at the level of the interarea. If the hinge-teeth are bridged by a continuous or discontinuous shell cover (deltidial structures), the growth lines on the cover commonly are continuous with those of the shell lateral to the hinge-teeth (Plate 1: figure 5). In shells with deltidiodont hinge-teeth and a dorsal interarea the hinge-sockets invariably are situated lateral to the notothyrial margin (Figure 6B; Plate 1: figures 4, 6).

The definition of delthyrium as taken from shells with deltidiodont dentition has been applied to this structure in all articulate brachiopods (Williams, 1956, p. 257; Williams and others in Moore, 1965, p. H93). However, in brachiopods with a cyrtomatodont dentition and delthyrial-deltidial structures, the growth-track of the hinge-teeth invariably is situated medially to the delthyrial margin or to the lateral margin of the deltidial structures (Figure 2; Plate 2: figures 1, 5). In nonstrophic shells the reason for this is the closeness of the hinge-teeth to the posterior margin of the shell. During opening or closing of the shell the beak of the dorsal valve moves into the ventral valve along a line just in front of the deltidial structures and behind the hinge-teeth (Figure 5B). Because of this, when the posterior shell margin is secreted a discontinuity or a sharp flexure develops in the growth lines laterally or posterolaterally to the hinge-teeth (Figure 2A). This discontinuity or flexure in the growth lines sharply deliniates a triangular area on the posterior side of the ventral valve. If the hinge-teeth are situated farther anteriorly, so that they do not interfere with the growth of the posterior margin of the shell, the shell is secreted continuously and no triangular area is formed; this is the case with *Bouchardia* (Plate 2: figure 10).

In strophic shells with cyrtomatodont dentition the reason for the development of delthyrial-deltidial structures is somewhat different. Here the beak of the dorsal valve does not become tucked into the ventral valve. In these shells parts of the hinge-teeth normally project posteriorly beyond the hinge-line, causing a sharp flexure in the growth lines of the posterior margin of the ventral valve lateral to the main part of the hinge-teeth (Figure 2B; Plate 2: figure 1). Again, if the hinge-teeth are placed farther anteriorly, as is the case with the thecideaceans (Plate 2: figures 8, 9), no median triangular area is developed (cf. *Thecidellina*). If an area is developed (cf. *Lacazella*), the cause of its presence lies in the configuration of dorsal structures. In shells with a dorsal interarea, the notothyrial margin invariably is lateral to the hinge-sockets, and the lateral margin of the hinge-socket defines the notothryial margin (Figure 6A; Plate 2: figure 2). Thus the delthyrial-deltidial and notothyrial-chilidial structures are not strictly homologous in Protremata and Telotremata.

The phylogenetic results presented in this paper closely agree with those outlined for articulate brachiopods by Williams and Rowell (in Moore, 1965) but they are based on a quite different set of characters. The addition of characters of dentition to those discussed by Williams and Rowell brings certain points more clearly into focus and causes some changes in emphasis. Williams and Rowell (in Moore, 1965, p. H180) suggest a close affinity of the groups here included in the Telotremata, but since those authors failed to find exclusive characters by which this group could be defined they preferred not to express this affinity in the classification.

As outlined in preceding sections in this paper, the main event in the evolution of the articulate brachiopods was the change from the delitidiodont to cyrtomatodont dentition. At present there is no evidence in the Early Paleozoic which suggests that the functional threshold associated with this change was passed repeatedly in different phylogenetic lineages of articulate brachiopods.

On the basis of dentition and associated structures, the class Articulata can be divided into two main, well-defined subdivisions. There is no need to replace Beecher's names Protremata and Telotremata for these subdivisions despite the fact that Beecher distinguished these groups by the use of characters that subsequently have been found to be incorrect or poorly defined.

In the classification used by Williams and Rowell (in Moore, 1965) the subclass Telotremata would comprise the orders Rhynchonellida, Spiriferida, and Terebratulida and the suborder Thecideidina. In addition, the characters of the dentition reveal that certain genera—which, in the current classification are included in other orders—ought to be classified with the Telotremata.

The loop-bearing Devonian genus *Tropidoleptus* currently is considered to be a member of the Enteletacea (Williams and Wright, 1961; Wright, in Moore, 1965). The dentition of *Tropidoleptus* is of the cyrtomatodont type (Hall and Clarke, 1894, pl. 82, fig. 35; Williams and Wright, 1961, fig. 10f). Similarly, the hinge-sockets are like those in the other telotremates, and are bordered posteriorly by the chilidium (Williams and Wright, 1961, fig. 10a,b). In protremate genera that possess a chilidium the hinge-sockets invariably are situated lateral of the chilidium. In the writer's opinion the presence of a chilidium (or antygidium, if a distinction between these two structures is found to be advantageous) and the lack of a functional pedicle are weak arguments for placing *Tropidoleptus* with the protremates. The dentition and the presence of a loop strongly indicate that *Tropidoleptus* is a member of Telotremata.

The genus *Cadomella* was included in the separate superfamily Cadomellacea within the suborder Chonetidina by Muir-Wood (in Williams et al., 1965). Cowen and Rudwick (1966) described a spiral brachidium in *Cadomella* and transferred that genus to the Koninckinacea, which they included in Chonetidina. The dentition in this Lower Jurassic genus is clearly of the cyrtomatodont type (Muir-Wood, in Moore, 1965, fig. 295:2b), and the writer regards *Cadomella* as a late member of the order Spiriferida. The Koninckinidae were classified by Boucot and others (in Moore, 1965) with the Spiriferida, and, although the dentition in this family is still poorly known, there seems to be no serious reason to doubt the correctness of this classification.

The Mississippian genus *Perditocardinia* currently is included in the Enteletacea but it has no hinge-line and the hinge-teeth are of the cyrtomatodont type (Schuchert and Cooper 1932, pl. 19, figs. 14, 21). No crura, brachidium, or loop have ever been described in this genus but the absence of crura should be confirmed by serial sections. *Perditocardinia* might be a member of Rhynchonellida but only further studies could prove this.

The Devonian *Enantiosphen* and the Triassic *Thecospira* are two additional loop-bearing genera that currently are included in protremate orders (Pentamerida-Pentameracea and Strophomenida-Davidsoniacea, respectively). In both these genera the dentition is poorly known and the writer regards their taxonomic position as uncertain. Should it be proved that *Enantiosphen* and *Thecospira* possess hinge-teeth of the cyrtomatodont type, then the Subclass Protremata would not include any genera with a loop or a brachidium. Moreover, with the exception of the Triassic oldhaminidinid *Bactrynium,* the subclass would be confined to the Palaeozoic.

Another important step in the evolution of the dentition has taken place within the subclass Protremata. The writer is inclined to place greater emphasis on the differences between the protremate groups with strophic and nonstrophic shells than do Williams and Rowell (in Moore, 1965). In order, however, to determine the taxonomic rank of the differences between the group comprising Camerellacea and Pentameracea and the rest of the Protremata (the orders Orthida and Strophomenida, and the superfamily Porambonitacea

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PLATE 2: figures 1, 2.—*Megerlia truncata* (L.), Mediterranean, exact locality unknown. Recent. 1, Ventral valve in posterodorsal view (×6) showing interarea and hook-shaped cyrtomatodont hinge-teeth; Br.102341. 2, Dorsal valve in ventral view (×6) showing interarea and the lateral margin of the hinge-socket forming the notothyrial margin; Br.102342.

Figure 3.—*Sieberella roemeri* (Hall and Clarke). Tennessee. Silurian, Brownsport Formation. Articulated shell (Br.102336, ×4) with lateral part removed to show the fitting of a hinge-tooth in a hinge-niche (sp., spondylium).

Figure 4.—*Antirhynchonella linguifera* (Sowerby). Gotland, Stora Karlsö. Silurian, probably Slite Marl. Interior of an articulated shell (Br.3068, ×6) showing how the hinge-teeth fit into hinge-notches and that the distal part of the hinge-teeth project free into the cavity of the dorsal valve. The distal part of the spondylium (sp.) is broken off.

Figures 5–7.—*Terebratulina retusa* (L.). Sweden, Gullmar Fjord, Skår. Recent. 5, Posterior part of a ventral valve in dorsal view (×6); the cyrtomatodont hinge-teeth are complete and have been exposed in an articulated shell by carefully removing the hinge-structures of the dorsal valve with a needle; Br.102337. 6, Posterior part of a dorsal valve in ventral view (×6); Br.102338. 7, Posterolateral view (×6) of complete hinge-tooth in ventral valve (same specimen as shown in figure 5).

Figures 8, 9.—*Lacazella mediterranea* (Risso). Western Mediterranean, exact locality unknown. Recent. Ventral valve in dorsal and posterodorsal views (×15) to show the hook-shaped cyrtomatodont hinge-teeth; Br.102339.

Figure 10.—*Bouchardia* sp. Locality unknown (stated to be from Singapore). Recent. Eugenia Expedition. Ventral valve in dorsal view (×8) to show the anterior position of the hinge-teeth and the continuous posterior margin of the valve; Department of Invertebrate Zoology, Brachiopoda, Dry Collection No. 75.

Figure 11.—*Hemithyris psittacea* (Gmelin). White Sea, exact locality unknown. Posterior part of a very small (1.3 mm long) ventral valve in dorsal view (×40) to show the hook-shaped cyrtomatodont hinge-teeth; Br.102340.

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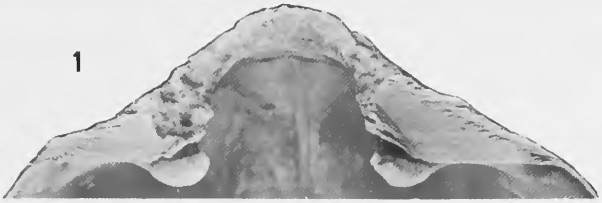

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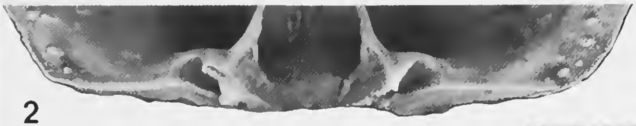

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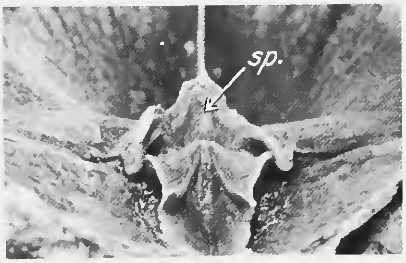

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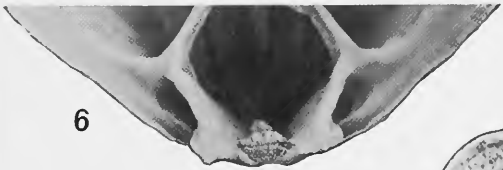

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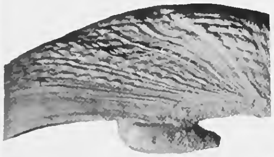

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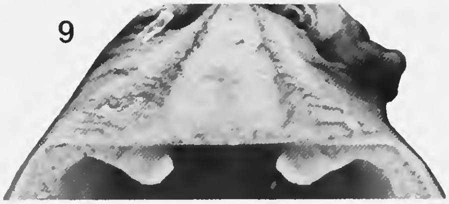

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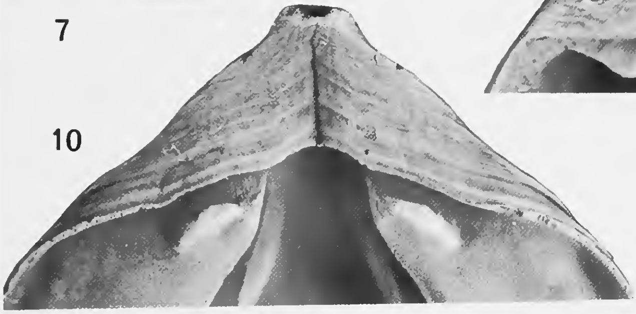

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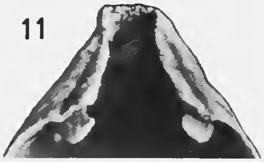

PLATE 2

with the exclusion of members with a nonstrophic shell), more information is needed about the dentition and the mechanism of articulation in early camerellaceans and late porambonitaceans.

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Alwyn Williams

Comments on the Growth of the Shell of Articulate Brachiopods

ABSTRACT

Growth of the shell of articulate brachiopods, which is controlled at the mantle margin of each valve by a "conveyor belt" of secreting cells proliferated from an intramarginal generative zone, involves two distinct types of surfaces. Isotopic surfaces separate different shell layers and represent regular changes in the secretory regime of migrating outer epithelial cells. Synchronous boundaries indicate contemporaneous surfaces of secretion, including superficial surfaces, such as the valve floors, and a fine banding—discernible in the microfabric of the calcareous shell—which probably represents daily deposition.

Ultrastructural studies of these surfaces show that disruptive forward movements of the mantle (transgressions) are less frequently recorded than retraction from the shell edge (regressions), which may be facilitated by the secretion of a protein membrane between the outer epithelium and the exoskeleton. Following regression, all cells resume shell deposition at that phase in the secretory regime where they left off. Partitions reducing the internal volume of pedicle valves in certain fossil species also were formed by mantle retraction, and their deposition must have been preceded by secretion of a proteinous seeding membrane.

The brachiopod phylum, dominated as it is by the richness and diversity of its past relics, has furnished many paleontologists with an unrivalled wealth of material for the exercise of their talents. Indeed, so profound and sustained has been the challenge posed by the fossil record that a disproportionate number of those paleontologists, who are freely acknowledged to be among the greatest students of the science, have attained this select rank by life-long researches on the phylum. Thomas Davidson and James Hall are obvious examples of such paleontologists of the last century; in such pedigree of scholarship, G. Arthur Cooper is their natural successor today.

The researches for which Dr. Cooper is universally acclaimed have ranged throughout Phanerozoic time, and his output of original work is remarkable for its quantity as well as quality. In fact, it is no small achievement to become familiar with the full measure of his systematic and morphological studies of the Brachiopoda, let alone his contributions to stratigraphic correlation. In both pursuits, the balance of his researches has been concerned with Paleozoic faunas, especially those of Ordovician age. But the impending publication of his account of the Permian brachiopods, the culmination of an intellectual drive that has been sustained for very many years now, will outstrip even his classic "Chazyan and Related Brachiopods" (1956) in the number, novelty, and morphological diversity of species studied. Nor should it be forgotten that, between the issues of his monographs beginning with those written in collaboration with C. Schuchert (1932) and E. O. Ulrich (1938), he has published a host of significant papers varying from a definitive survey of Cainozoic rhynchonellides (1959) to penetrating analyses of specialized Devonian articulates (1954, 1955).

Three invariable features of Dr. Cooper's work have always combined to set the seal of authority on his publications: the completeness of his collections, the acuteness of his observations, and the quality of his illustrations. These features reflect his constant concern with the variation of constituent species as well as the entirety of an assemblage, and they stem from his brilliant fieldwork and his unrivalled skill in the mechanical and chemical cleaning of embedded speci-

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mens. One need only see his superb illustrations of the fossils etched and dissected by him during the preparation of his monographs on Ordovician brachiopods (1956) and the Productoidea (with H. M. Muir-Wood, 1960) to have some indication of our indebtedness to him. For above all, he has made us aware of the importance of morphological detail; and by demonstrating the constancy of subtle differences in skeletal characters he has introduced new and wholly acceptable standards of precision into the notoriously opinionated world of systematic procedure.

In many respects, one of his earliest papers—a study, published in 1930, of a number of North American species of Ordovician brachiopods that had been masquerading under the name of *Pionodema*—was a prelude to the scale of reform that was about to be set into motion by his researches. He showed that if the microstructure of the shell, the disposition of the ventral muscle field, and the composition and morphology of the cardinalia are taken into account, a meaningless jumble of species could be segregated into three well-defined groups typified by *Pionodema, Doleroides*, and *Mimella*. At the same time, he drew attention to the remarkable degree of homeomorphy that existed between the punctate *Pionodema-Schizophoria* and the impunctate *Doleroides-Hebertella* lines, not only in many internal features but even in shell shape and the development of hollow ribs. This neat demonstration of the similarity between plectorthids and early enteletids is now recognized as a classic example of parallel evolution; and, like very many other discoveries of his that could have been quoted, is itself a lasting tribute to his palaeontological insight.

Diverse as Dr. Cooper's brachiopod studies are, they are necessarily concerned, as indeed are all palaeontological researches, with the morphological variation of the exoskeleton in time and space. Such variation, whether it be manifest during the development of the individual or the emergence and subsequent evolution of a species, is an expression of differential shell growth. It is, therefore, essential to be at least familiar with the processes of shell growth if one wishes to conduct a viable systematic study of a fossil assemblage, or to trace the origin and development of an exoskeletal feature. These processes are very complex, despite the fact that any increase in shell area is controlled at the mantle margins and is intimately related to the proliferation of cells from a pair of intramarginal generative zones. All macroscopic variation from slight modifications in the shape of the shell to complicated internal and external extensions of either valve are brought about by differential changes in rates of exoskeletal secretion that, in turn, are reflected by ultrastructural realinements in the shell fabric. Indeed, certain exoskeletal outgrowths involve such accelerations in secretion that they can be catered for only by the development of secondary generative zones which may be located anywhere on the mantle surface. Moreover, temporary checks or accelerations in secretion are not the only means of fashioning the exoskeleton. Under certain conditions, localized or widespread retreats of the mantle margin can take place, while resorption of the calcareous shell normally occurs simultaneously with secretion during the growth of internally disposed projections of the exoskeleton. Even shell repair is simply a distinctive phase of growth which has been promoted by abnormal environmental conditions. Except for the last, these several processes are briefly considered below. They are discussed mainly in the light of researches carried out on recent articulate brachiopods which afford the means of relating the exoskeletal ultrastructure to the morphology and secretory activities of the outer epithelial cell. This may not be palaeontology in the traditional sense, but the conclusions derived from such studies of living species are directly relevant to the interpretation of fossil fabrics which, in the majority of stocks, are known to have been stable since at least early Cambrian times (Williams, 1968c).

Material referred to in this paper was examined under an EM6B electron microscope and a Cambridge "Stereoscan" scanning electron microscope. Preparation of sections for the study of soft tissues involved the fixing of living specimens in glutaraldehyde followed by their decalcification in up to 10 percent EDTA (Ethylenediamenetetraacetic acid), postosmication and embedding in "Epon Araldite"; sections were cut with a Porter-Blum microtome and stained with aqueous uranyl acetate and lead citrate. Calcareous exoskeletons were prepared for electron miscroscopy by removing adherent tissue and periostracum with 1 percent aqueous solution of potassium hydroxide or detergents. Shell sections were polished, briefly etched with 1 percent EDTA, and replicated by cellulose acetate strips which, before being dissolved away, were shadowed with gold-palladium at 1-to-1 and coated with carbon to provide casts for examination. Shell surfaces were coated with gold-palladium before being viewed under the "Stereoscan."

I am indebted to Mr. Christopher Bang of Blomsterdalen, Norway, Dr. C. A. Fleming, F.R.S., of the Geological Survey of New Zealand, Dr. D. G. Jenkins of the University of Canterbury, and Dr. R. T. Paine of the University of Washington, all of whom so generously provided me with living specimens of species referred to in the text. I also thank Dr. Jean Graham and Dr. Katharine McClure, research assistants in the Department of Geology of the Queen's University, Belfast, for their help in the preparation of illustrations and some of the sections figured here.

Growth of the Articulate Exoskeleton

The growth of the brachiopod shell can be analyzed in two seemingly different ways. Fundamentally, it is a biochemical process controlled by the mantle lining the shell (Williams 1956, 1968a, 1968b). Alternatively, growth can be thought of as a microscopic modification of the exoskeleton (Rudwick, 1959). The former process is the "momentary" growth of Rudwick (1959, p. 2) and has to be considered as an expression of cellular activity. The latter is Rudwick's "cumulative" growth (1959, p. 2) and is best understood in terms of growth vectors summarizing three dimensional variations in the rate of growth.[1] As Westbroek (1967) has shown, differences between the two concepts are important. Yet, they are also readily reconcilable in that a single cell performs several distinct secretory operations in turn and thereby successively contributes to a consistently multilayered skeleton; whereas the mantle, in its entirety, is made up of cells—simultaneously engaged in every phase of the secretory regime—which deposit an assortment of materials on a contemporaneous growth surface. Hence, a brief review of the way in which cells secrete the exoskeleton and become incorporated into the mantle is a necessary introduction to any commentary on shell growth. In respect of both shell secretion and growth, the processes worked out for the rhynchonellide *Notosaria nigricans* (Sowerby) have been used as standards. Apart from the advantages of being readily available in all stages of growth, this species is impunctate, so the development of the exoskeleton is not complicated by the presence of caeca, while the strongly lamellose shell affords an opportunity to study the effects of periodic retraction of the mantle.

The Standard Secretory Régime

Marginal increase of the mantle lining a brachiopod valve is controlled by a generative zone located within a circumferential groove separating the outer and inner lobes of the mantle edge (Figure 1). The inner lobe is part of the ciliated inner epithelium and need not be considered further. The outer lobe is a fold composed of rotating secretory cells that acts like a "conveyor belt" to supply periostracum to a growing exoskeleton and rows of cells to an expanding outer epithelium. The core or axis of this conveyor belt, around which the cells released from the generative zone rotate, is composed of connective tissue. As each cell moves around this axis, its secretory surface initially faces inward and is part of the inner side of the outer mantle lobe. But when the secreting surface reaches the tip of the lobe, having been "moved along" by the steady proliferation of younger cells from the generative zone, it is rotated to face outward and becomes an integral part of the outer side of the mantle responsible for the secretion of the calcareous shell. In *Notosaria*, the secretory regime of every outer epithelial cell originating and migrating in this manner consists of six different operations which occur in the order (Plate 1: figure 1) described below.

At first, the secreting surface of a newly released cell, with its short prostrate microvilli, exudes a mucopolysaccharide. But as the cell approaches the tip of the outer lobe, the periostracum is quickly assembled under the protective mucopolysaccharide cover before the cell is rotated externally to the tip of the outer lobe. The first periostracal constituents to be secreted are protein rods, flattened distally and arranged in arrays in a 75-degree rhombic pattern. They are about 20nm thick and stand about 35nm above a triple-unit membrane which is deposited almost simultaneously with the rods. The membrane is about 140A thick and, once formed, is pushed away from the secreting surface of the cell by further exudation which gives rise to a var-

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[1] Shell growth is here understood to include any reduction or expansion of any part of the organic and mineral exoskeleton resulting from its incremental resorption or secretion, respectively, by mantle epithelium. Pauses in growth constituting a state of equilibrium between these two conditions probably are much rarer than is generally assumed from the frequency of "growth lines" on the brachiopod shell. Such indications of differences in growth rates are as likely to represent condensed mineral deposition, temporary reversions to organic secretion, or even resorption, as they do absolute breaks in biochemical activity of the mantle.

iable organic layer up to 1μm thick. The finely divided osmiophilic granules composing the layer suggest that it initially has a gel-like consistency. It is probably a form of mucoprotein because it is seen to be built up from the densely osmiophilic contents of secretion droplets of the cell, which are histochemically identifiable as mucoprotein. Apart from ellipsoidal mucin inclusions and commonly occurring, long fibrils lying more or less normal to the bounding surfaces, the completed layer invariably contains sporadically distributed vesicles of various sizes which are always bounded by a triple-unit membrane comparable in thickness with those forming the limiting surfaces of the periostracum. The vesicle coats are discards from the secreting cells, which have been trapped like bubbles in the solidifying mucoprotein before it is sealed off by an inner membrane. This membrane seems to be identical with the outer bounding one and is also associated with a distal constituent consisting of a mat of erect fibrils which extend into the mucoprotein layer for about 30nm and may be only morphologically different from the rods attached to the distal surfaces of the outer bounding membrane.

Secretion of the inner bounding membrane completes the deposition of the periostracum, although exudation of impersistent patches of protein as embedding cement for the first calcite nuclei may still take place. At this phase in the secretory regime the cell occupies the tip of the outer lobe, but as the secretory surface of the cell is further rotated to face outward it begins to deposit isolated calcite rhombs. With further secretion, these calcite seeds start amalgamating with one another and with the continuous front of the primary layer (Plate 1:figure 2). In this way the calcareous shell expands peripherally and the outer epithelium becomes separated from the periostracum which it has already secreted by an increasing thickness of primary shell. As deposition proceeds, the cells, now regularly arranged in alternate rows, leave traces of microvillous trails and periodic banding within the fabric of the thickening primary layer. However, when a row of cells comes to occupy a certain distance behind the tip of the outer mantle lobe through the addition of new cells at the tip, it starts secreting the calcareous-organic secondary shell. Each cell exudes a triple-unit membrane, along an arcuate anterior strip of its secret-

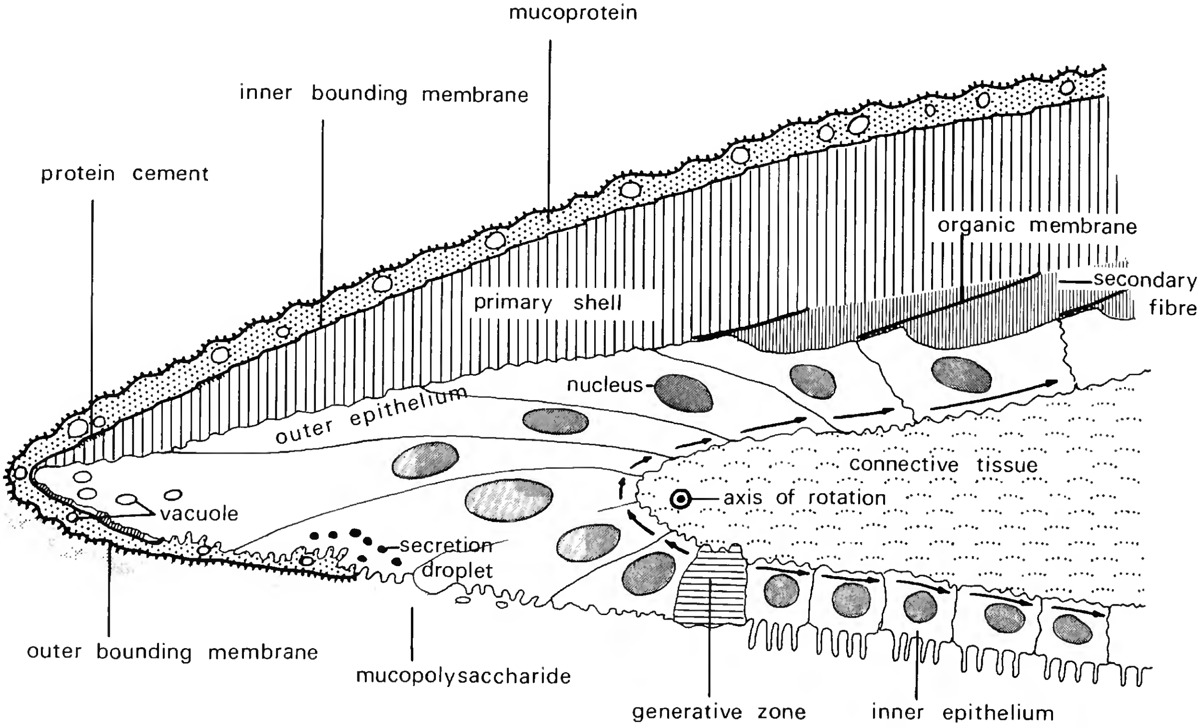


FIGURE 1.—Stylized longitudinal section of a valve edge of young *Notosaria* showing the relationship between the outer mantle lobe and the triple-layered exoskeleton of periostracum, primary and secondary shell.

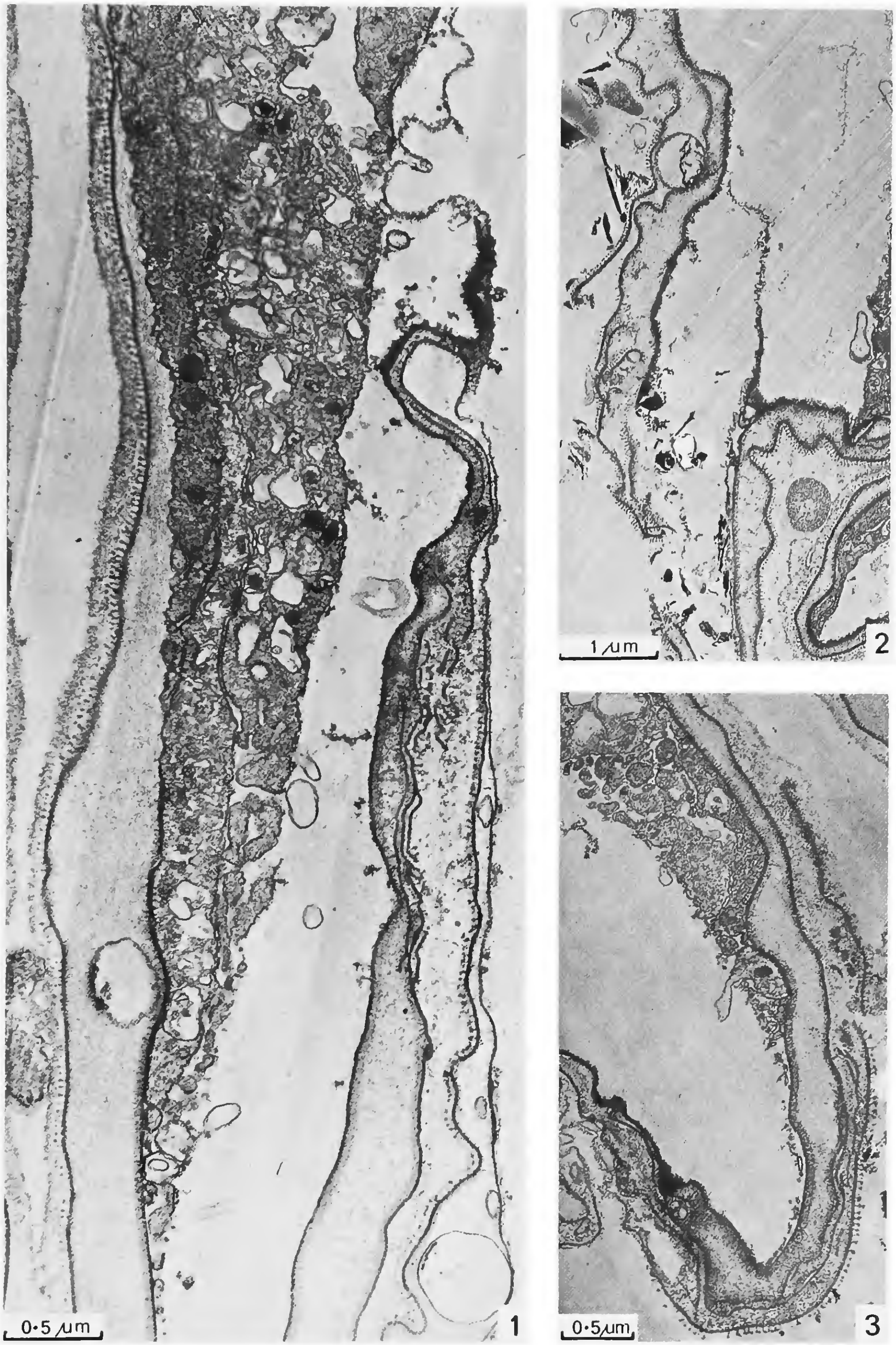


Plate 1.—Electron micrographs of parts of longitudinal sections of the outer mantle lobe of a young *Notosaria nigricans* (Sowerby) showing various features of the periostracum: 1, exuded mucoprotein and inner bounding membrane (to the left side of figure) and a regression (on the right) affecting these two layers; 2, a transgression within the periostracum (in top left quarter of the outer bounding membrane and mucopolysaccharide (in bottom right quarter of figure); 3, rhythmic layering causing a repetition of the outer bounding membrane and mucopolysaccharide (in bottom right quarter of figure).

ing cell surface. The membrane is comparable in thickness and possibly composition with those in the periostracum, and initially intervenes between the primary shell and the base of a calcite fiber being secreted by the posterior part of the cell surface, which is now more or less free of microvilli. But because the same operation is carried out in all adjacent cells, the membranes join up with one another to form a series of sheaths, each containing a long, thin, calcite fiber normally inclined at about 10 degrees to the primary shell (Plate 2: figures 3–5). Each fiber has a distinctive cross section reflecting the disposition of the concave secreting cell surface controlling its growth, and occurs within a characteristically stacked series, the regularity of which reflects the orderly arrangement of the cells relative to one another (Plate 2: figure 6). The secondary shell continues to grow so long as the cells remain functional, and in this respect it is quite unlike the periostracum or the primary shell, both of which have a more or less constant thickness for any given period in the growth of the individual.

Thus, any cell originating within the intramarginal generative zone of the mantle of *Notosaria* secretes six successive covers in the course of its functional life; mucopolysaccharide, outer bounding membrane, mucoprotein, inner bounding membrane, calcareous primary layer, and calcareous-organic secondary layer. The mucopolysaccharide layer may be a relict of the prototypic brachiopod exoskeleton (Williams, 1968d, p. 285), but it rarely persists beyond the tip of the outer mantle lobe, in living species at least, and can be ignored. The mucoprotein, with its inner and outer bounding membranes, is variably developed in other species of articulate brachiopods, but together the membranes make up the periostracum, which is always present, in some form or other, as a seeding sheet for the mineral shell. Hence, this layer, although lost during fossilization, plays an important part in the growth of the exoskeleton and the molding of its topographic detail. The primary and secondary layers are the most permanent constituents of the exoskeleton. Recognizable traces of their ultrastructure survive even in early Cambrian shells (Williams, 1968c) and show that the fabric of a primary cryptocrystalline layer and orthodoxly stacked secondary fibers, so characteristic of the terebratulides and rhynchonellides, was equally prevalent in extinct groups. Consequently, detailed studies of these layers in relationship to the outer epithelium will afford as valid a guide to the skeletal growth of extinct stocks as to that of living species. Indeed, even for groups like the strophomenides and thecideidines, in which the development of the primary-secondary layers greatly differs from that characteristic of other articulates, it is likely that the basic growth processes are the same.

In examining the relationships between the outer epithelial secretory surface and each of the three principal exoskeletal layers—periostracum, primary shell and secondary shell—it is essential to distinguish physically between momentary and cumulative growth. Westbroek (1967, pp. 20–24) has discussed fully the problems involved. He found it convenient to regard the outer epithelium underlying the shell as constituting a number of units, each consisting of a suite of cells performing the same secretory function and consequently giving rise to a homogeneous shell unit. These are his isotopic shell units, which are separated from each other by well-defined isotopic shell unit boundaries and are expressions of cumulative growth (Figures 1, 4). He also recognized that isotopic (shell unit) boundaries are quite different from surfaces of active shell deposition or resorption, i.e., momentary growth, which he termed the superficial shell unit boundaries. Unlike the former, the latter are contemporaneous as well as anisotopic and are more appropriately referred to as synchronous (shell unit) boundaries because they have proved to be as easily identifiable as isotopic boundaries throughout the exoskeletal fabric (Figure 4). The actual surface of deposition at the moment of death can then be referred to as the superficial synchronous boundary. The use of these terms with the meanings just given has helped to sort out the various aspects of growth described below. They also help to correlate processes of shell growth of the Brachiopoda and Bivalvia. The "matrix" of Lison (1949, p. 47) is really the commissural zone of the synchronous shell unit minus the outermost rim of calcite representing the *first* mineral secretion by cells that have only just been rotated into position. The rate of incorporating such cells into the main spread of the mantle lining the shell is considered by Carter (1967, p. 271) to be partly responsible for generating the actual curve of the external surface of a bivalve. Carter's conclusions were based on considerations of shell geometry, but they are in line with the idea that consistent biochemical changes in migrating cells generate similar isotopic surfaces in brachiopods. His views on brachiopod growth (Carter, 1967, p. 277) are less agreeable because he con-

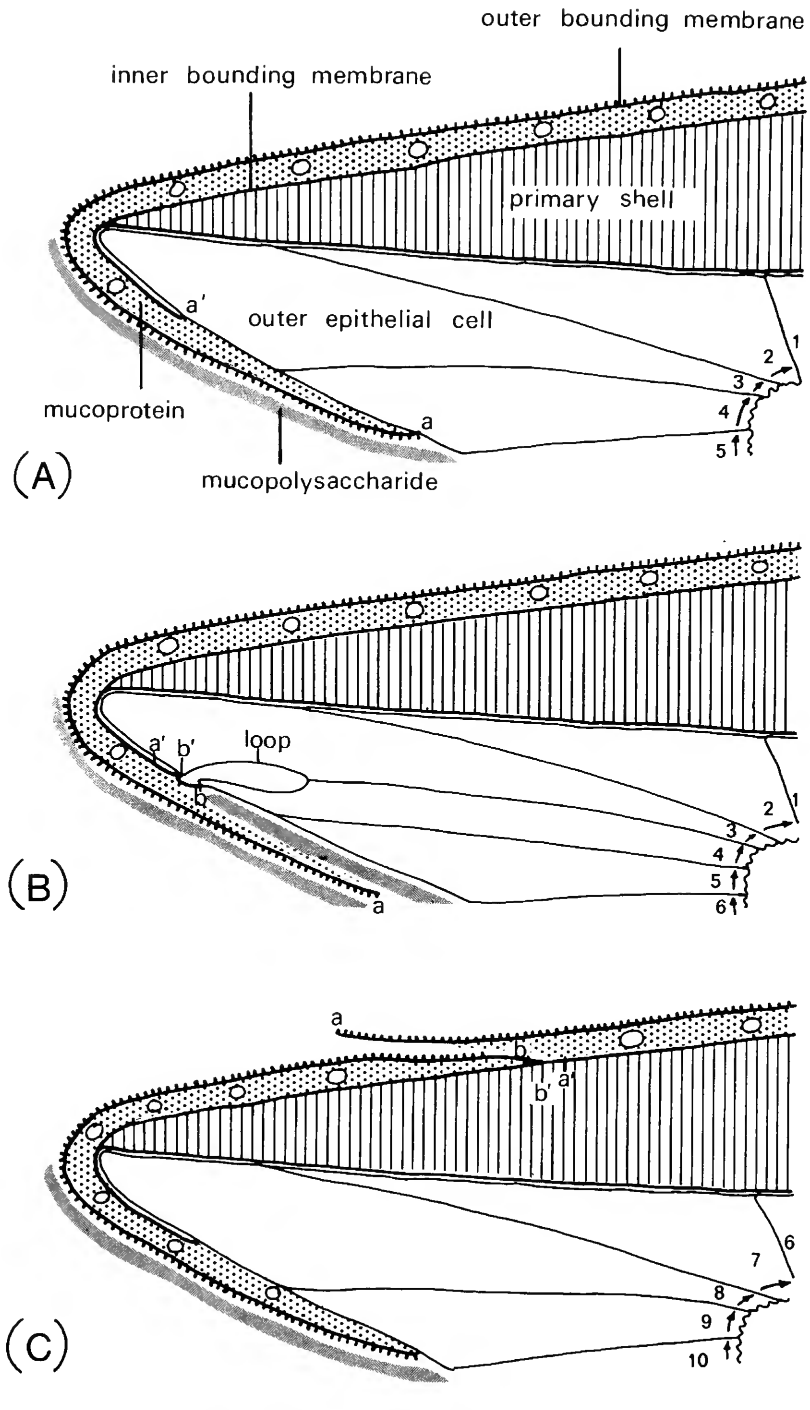
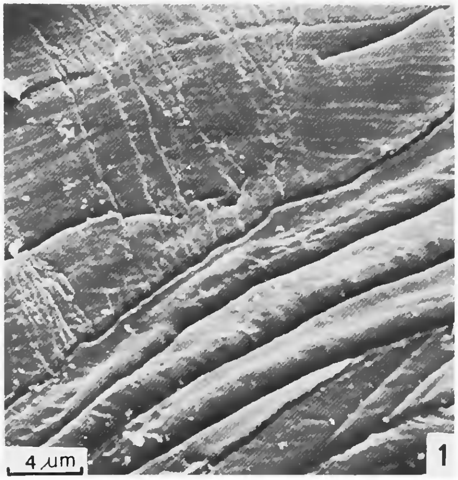


FIGURE 2.—Formation of a transgression (aa') in the periostracum of *Notosaria* shown in diagram (C), by forward movement of the cell surface from its normal depositional attitude (A) through the formation of a temporary loop-like contraction (B).



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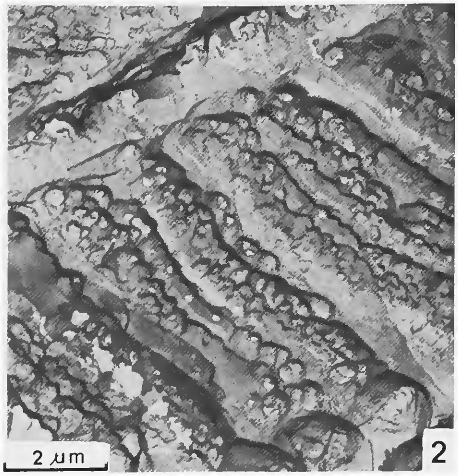

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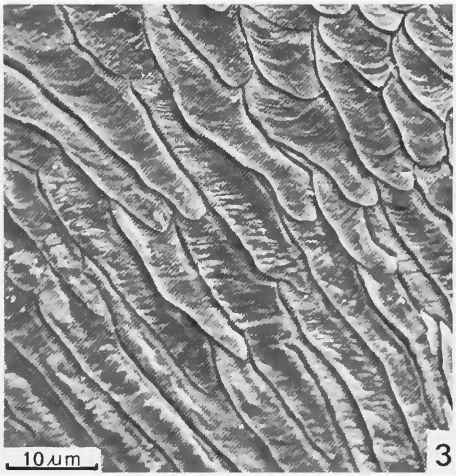

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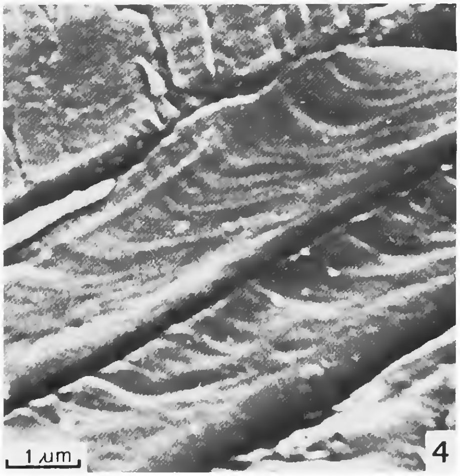

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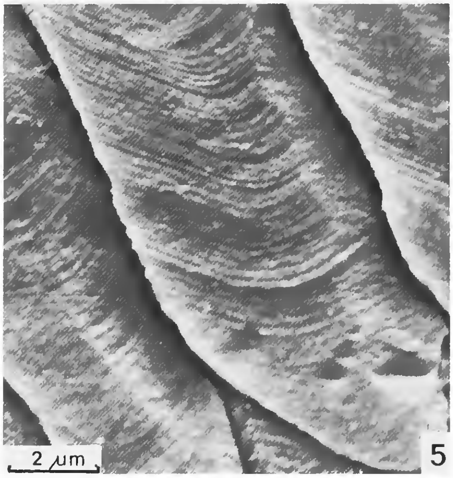

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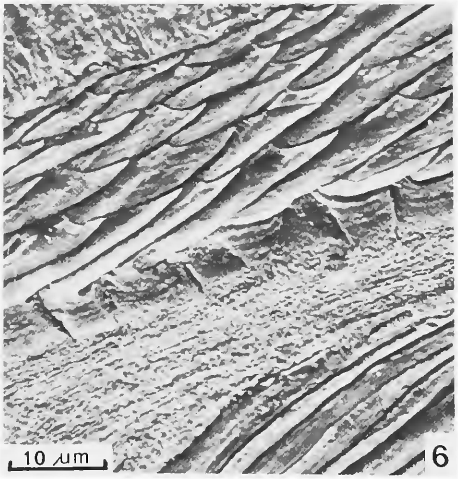

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PLATE 2

fused primary and secondary shell and erroneously asserted that shell deposition is normal to the long axes of secondary fibers.

Growth Features of the Periostracum

In *Notosaria,* the threefold layering of the periostracum greatly facilitates study of growth variation at the mantle edge. The two bounding membranes are physically distinguishable from each other by the nature of their distal constituents, although there are indications that the fibrils assembled during the construction of the inner bounding membrane may initially be coiled into rods, like those characteristic of the outer bounding membrane. Both surfaces are isotopic boundaries to the mucoproteinous filling which constitutes the bulk of the periostracum. They are simultaneously assembled on a cell plasmalemma(s) which subtends an outwardly facing angle of about 5 degrees with the membranes; and the various secreted products forming the surface immediately underlying the plasmalemma can be regarded as the superficial synchronous boundary to the periostracum. Variation in periostracal growth obviously will be related to biochemical changes in the cell(s) or positional shifts in the plasmalemma(s). Thus, one would expect to find features reflecting variation in the rate of secretion as well as the forward or backward slip of the outer mantle lobe. Such clues do occur and, in addition, indicate that different phases of the secretory regime can be repeated to give a rhythmic layering in parts of the periostracum.

The external surface of the periostracum of *Notosaria* is thrown into a series of impersistent folds arranged more or less concentrically to the shell edge (Plate 1: figure 2). In section, these are seen as anticlines and synclines with a wavelength of about 0.4 μm and an amplitude of 0.25 μm, which do not affect the inner bounding membrane. The folds therefore correspond to recurrent changes in the thickness of the mucoprotein layer. Yet, with rare exceptions, this layer is evenly exuded between the membranes, which are more or less parallel to one another when they lie on the inner surface of the outer mantle lobe. It is likely, therefore, that this folding is not an expression of variation in secretion but a postdepositional shrinkage, arising from polymerization and dehydration, which does not wrinkle the inner bounding membrane because it is kept taut across the underlying surface of the primary shell. There are, however, significant differences in the average thickness of the periostracum from one part of the shell surface to the other that do not arise from either folding of the outer membrane or movement of the secreting surface. More consistent variations may eventually prove to be controlled by periodically operating factors like temperature; but other variations must reflect innate differences in the biochemical efficiency of the outer mantle lobes. In one young shell of *Notosaria,* for example, a strip of periostracum on one valve, with an average thickness of about 0.6 μm, was three times as thick as contemporaneous periostracum on the opposing valve.

Repetition of one or more secretory operations, as indicated by recurrences of part of the periostracum within the same vertical section, is fairly common. Usually it is seen to have been brought about by minor displacements of the secretory surface; and even where short strips of the same membrane recur one above the other as rhythmic layering within a section, an oscillation of the cell plasmalemma rather than a repetition of its biochemical activity cannot be ruled out entirely. Rhythmic layering can be quite striking. One of the examples examined involved the repetition of the mucopolysaccharide and outer bounding membrane four times before periostracal deposition was completed with the exudation of the mucoprotein and the inner bounding membrane. This kind of repetition is the commonest (Plate 1: figure 3). Operations leading to the secretion of mucoprotein let alone the inner bounding membrane, without discernible displacement of the cell surface, have not yet been

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PLATE 2: figure 1.—Stereoscan view of a section of the primary-secondary shell of a young *Notosaria nigricans* (Sowerby) showing well-developed banding in the primary layer.

Figure 2.—Electron micrograph of the surface of the primary shell of *Notosaria nigricans* (Sowerby) immediately below the periostracum.

Figures 3, 5.—Stereoscan views of a tangential section of secondary fibers of *Terebratulina retusa* (Linn.) showing well-developed banding in individual fibers.

Figure 4.—Stereoscan view of a longitudinal section of the primary-secondary shell junction in *Notosaria nigricans* (Sowerby) showing the disposition of banding developed in the secondary fibers.

Figure 6.—Stereoscan view of a regressed lower succession of secondary shell, showing primary layer and calcite pads underlying the normal upper succession of secondary and primary shell.

seen; nor has evidence been found so far of any of the basic operations of the secretory regime being omitted during deposition of the periostracum.

The most spectacular changes in the periostracal succession are undoubtedly those brought about by removal of the secretory plasmalemma of the cell(s) from the superficial synchronous boundary of the periostracum, thereby terminating exudation on that particular surface. The displacement is the result of an abrupt forward extension or a sudden backward retraction of part or all of the outer mantle lobe, and it seems appropriate to refer to the physical effects on the exoskeleton of these respective movements as transgression and regression (Williams and Rowell, in Moore, 1965, p. H79). They differ from each other in the degree to which they affect the rest of the exoskeleton. Manifestation of transgressions as structural discontinuities appears to be limited to the periostracum; they probably are not represented by anything more spectacular than an acceleration in secretion in the rest of the shell. Regresions, on the other hand, can frequently be traced well into the secondary layer, reflecting a deep withdrawal of the entire mantle edge. Discussion of the latter, therefore, is best postponed until growth of the primary and secondary shell has been reviewed.

Transgressions are relatively rare and cannot involve more than ultramicroscopic slip because the forward moving tip of the outer lobe must still be accommodated within a comparatively rigid rim made up of completed periostracum and the first-formed primary shell. Indeed, the cell surface may never move much outside the area representing the superficial synchronous boundary of the periostracum because all known transgressions are like that shown in Plate 1: figure 2. In these examples, that part of the cell surface concerned with the deposition of the outer bounding membrane slips forward along the superficial synchronous boundary of the mucoprotein to make contact with the old inner bounding membrane (figure 2B). Thereafter, it continues to assemble the new outer bounding membrane but in physical continuity with the old inner one. The new inner bounding membrane also starts off in the vicinity of this junction. This suggests that transgression is really brought about by a sudden contraction of the cell(s) that carries the rear end of the secreting plasmalemma forward to lie adjacent to its front end. However, deposition soon starts up again and the plasmalemma, initially contracted into a loop, must revert very quickly to its normally extended contact with the superficial synchronous boundary of the periostracum. One interesting aspect of the transgressions so far examined is the way secretion of the outer bounding membrane is continued without any perceptible break or readjustment on the edge of the old inner boundary. Repetition in periostracal successions indicates that strips of outer bounding membranes can be secreted in isolation; but it may well be that as the plasmalemma(s) slides forward, the close physical and chemical similarity between the outer and inner bounding membranes promotes a linkage between the free end of the inner bounding membrane and that part of the plasmalemma responsible for the secretion of the outer bounding membrane, thereby putting a brake on further transgression.

Growth Features of the Primary Layer

Fabric studies of the primary shell show that it is made up of a succession of microscopic layers representing synchronous shell units that were deposited obliquely to two bounding surfaces (Figure 4). These outer and inner limiting surfaces are sharply defined isotopic boundaries and are, respectively, the periostracal-primary and primary-secondary interfaces. They coincide with profound biochemical changes that affect all migrating outer epithelial cells released from the intramarginal generative zone. The continuity of these boundaries throughout the growing shell is itself proof of the regularity with which separate operations of the secretory regime follow one another in strict order. In this regard, the most interesting aspect of the primary layer of *Notosaria* is the increase in its maximum thickness from umbo to anterior margin; in effect the periostracal-primary and primary-secondary interfaces become more widely separated as individuals grow older. The relationship is illustrated by variation in the thickness of the primary layer of a brachial valve of *Notosaria* along a medial surface length of 15.5 millimeters. Periodic retraction of the outer lobe of the mantle, which occurred throughout the growth of the shell, continually reduced the primary layer to a negligible thickness and greatly complicated the pattern (Figure 3B). However, the maximum thickness of the primary layer increases steadily from the umbo by

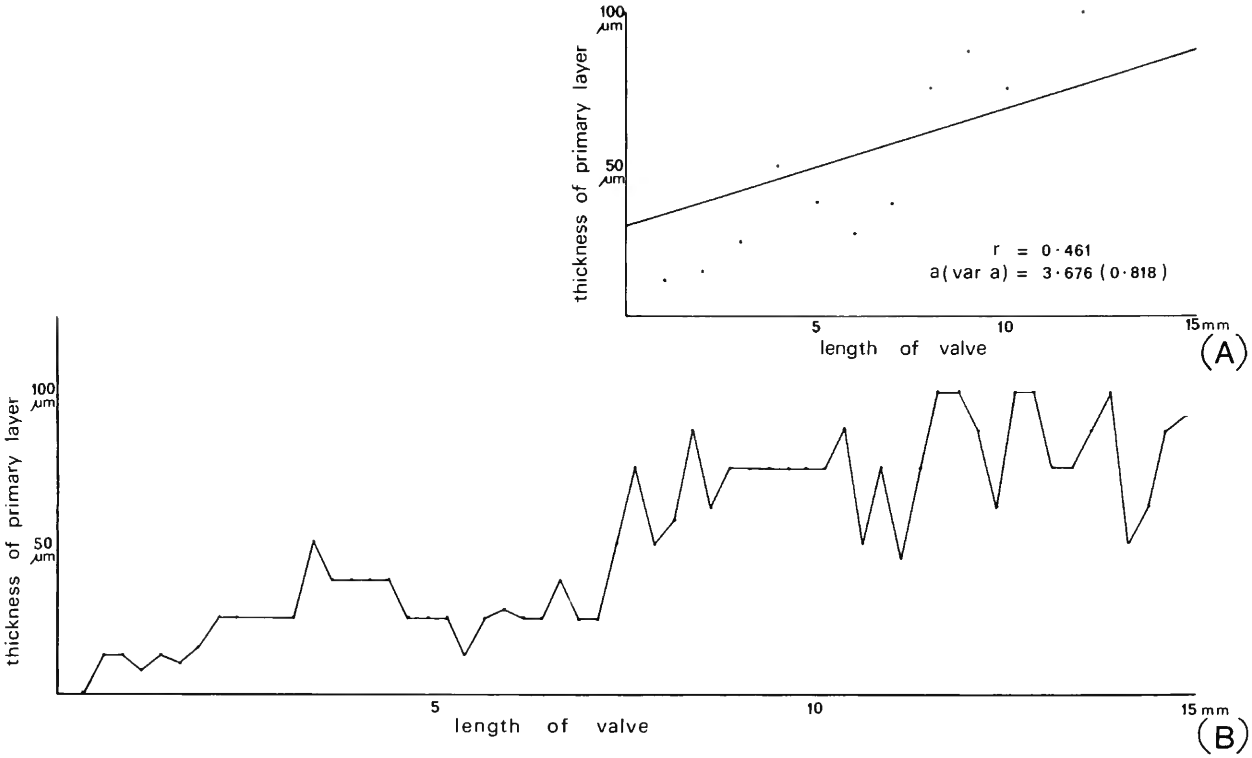

FIGURE 3.—Maximum thickness of the primary shell per mm (A) and per 0.25 mm (B) measured along a medial section of a brachial valve of *Notosaria*.

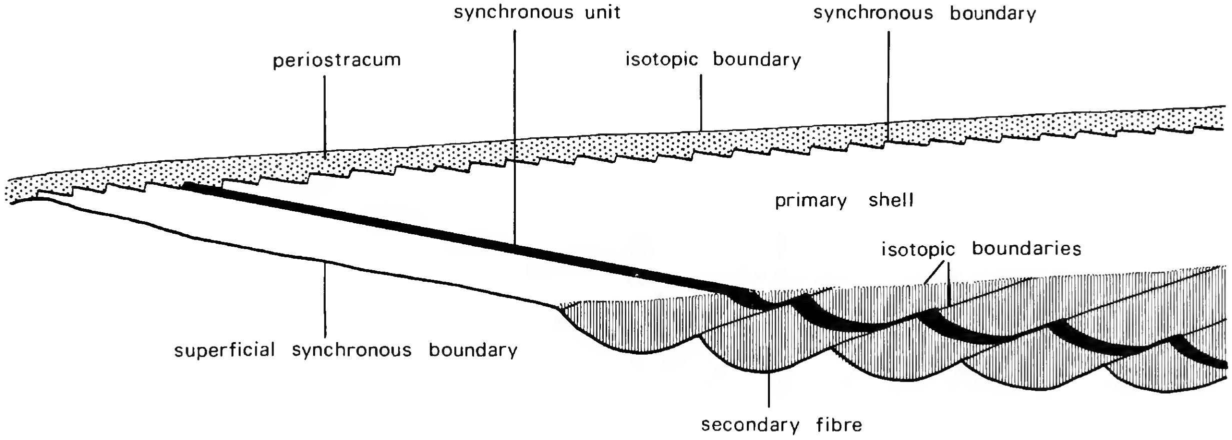

FIGURE 4.—Stylized medial longitudinal section of valve edge of young *Notosaria* showing the relationship between various isotopic and synchronous surfaces.

about 12μ per millimeter of surface length (Figure 3A), which represents the average increment accompanying full recovery from each retraction. The wider implications of this increase cannot be profitably discussed until the synchronous shell units have been considered.

Synchronous shell units are represented in sections of the primary layer by a distinct parallel banding which is inclined at an acute angle to the primary-secondary interface and opens out in the directions of growth, i.e., radially from the umbo (Figure 4 and

Plate 3: figure 1). In one segment of the primary layer of a brachial valve of *Notosaria,* 19 measurements of this angle averaged 13.9 degrees (range 10–25 degrees); and sampling of other sections indicates that such an estimate is typical not only of this species but others as well. The banding, being traces of old depositional surfaces, is parallel to the section of the superficial synchronous boundary on which the outer face of the outer lobe of the mantle rested at the moment of death of the animal. It is likely that the size of cells at the mantle edge does not vary very much throughout the life of the individual because enlargement of the mantle margin always takes place by the addition of new cells proliferated from the intramarginal generative zone. The average maximum widths (with ranges) of 7 and 14 newly formed fibers as an index of cell size at the junction between the primary and secondary layer were 6.7μm (4.8 to 7.9μm) and 6.5μm (4.9 to 8.2μm) for two brachial valves with median lengths of 3.2 and 13.5 millimeters respectively. The implications now become obvious. If the maximum thickness of the primary layer, measured normal to its isotopic boundaries, increases throughout growth, while the size of the cells occupying the superficial synchronous boundary and the disposition of that boundary remain more or less constant, the outer mantle lobe becomes absolutely longer through an increase in the number of cells secreting the primary layer. The relationship can even be used as a rough guide to the number of cells simultaneously depositing primary shell. The average medial length of 20 terminal faces of fibers seen in sequence immediately behind the primary-secondary junction was 10μm. Assuming this mean not to be significantly different from the average length of cells secreting primary shell, then:

$$N=\frac{Y}{10 \sin \theta}$$

where N is the number of cells along a radial vector of the mantle lobe, Y the thickness of the primary layer between its two isotopic boundaries expressed in μm; and $\angle\theta$ the disposition of the synchronous boundaries relative to the primary-secondary interface. In biochemical terms, cells arising at the intramarginal generative zone take an increasingly longer time to complete the preliminary stages of the secretory regime as the shell grows older. This is demonstrably so for that phase concerned with the deposition of the primary layer, and is likely also to prove true for the exudation of the periostracum. The slowing down is quite marked. In a young pedicle valve of *Notosaria,* 2.6 millimeters long, three times as many cells occupied a radial strip of the primary shell at the shell edge than at the umbo. Also, since there is no important difference in the thicknesses of the synchronous shell units in the compared sections, one can assume that each cell took three times as long to pass through the phase of depositing primary shell as did its predecessors near the umbo.

The synchronous shell units, which are seen in section as variably imprinted bands, constitute the depositional layering of the primary shell. The layers are of the right order of thickness to have been secreted diurnally (cf. Williams 1968a, p. 43) and, as is to be expected, vary more along the length of the shell than within any localized section normal to the isotopic boundaries. Thus, measurements taken near the anteromedian edge of two valves of *Notosaria* (one 2.6 millimeters long and the other between 7 and 9 millimeters long) gave mean thicknesses (with range) of 0.35μ (0.23–0.41μ) for 86 layers and 0.58μ (0.53–0.8μ) for 155 layers, respectively. The significance of such variation is still being studied. It may reflect seasonal changes, with the thinner layers representing winter deposition. Alternatively or additionally, daily secretion of calcite may be heavier in adult shells than in younger ones.

Removal of the periostracum shows that the synchronous shell units intersect the isotopic external surface of the primary shell as a series of microscopic scarps facing outward and disposed concentrically to the shell margin and to any growth lines ornamenting the surface (Plate 2: figure 2). When the surface is slightly fretted by the pulling away of the periostracum, the position of the first-formed calcite seeds is

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PLATE 3: figure 1.—Stereoscan view of a regression within the secondary shell of *Notosaria nigricans* (Sowerby) showing the calcite pads developed between two sets of fibers.

Figure 2.—Stereoscan view of a regression (indicated by a white crenulated band representing a resin replacement of an organic seal), affecting the primary and secondary layers and caeca of *Magasella sanguinea* (Leach).

Figures 3, 4.—Stereoscan view of the junction between a partition and the floor of the pedicle valve (extending from right to left in the lower half of figure 3) of *Syringospira prima* (Kindle) with a detail of the partition (in figure 4) showing the disposition of the secondary fibers.

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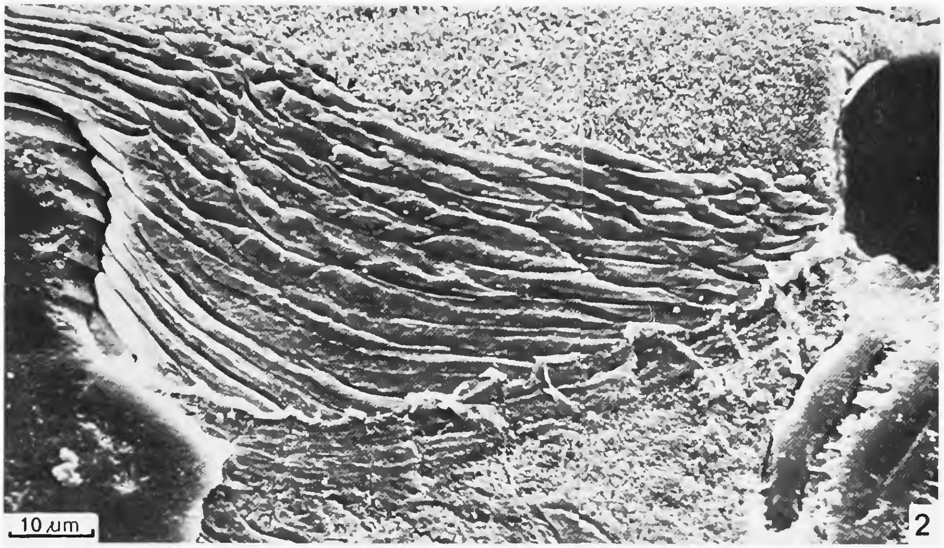

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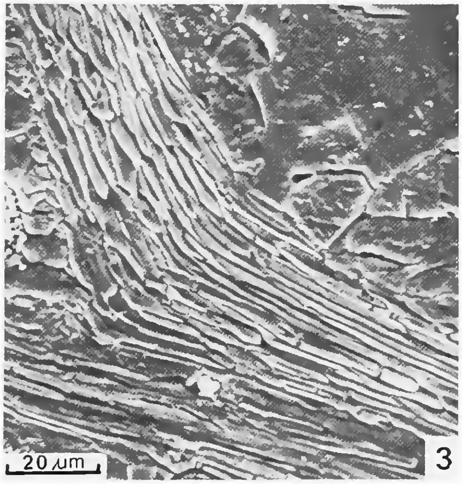

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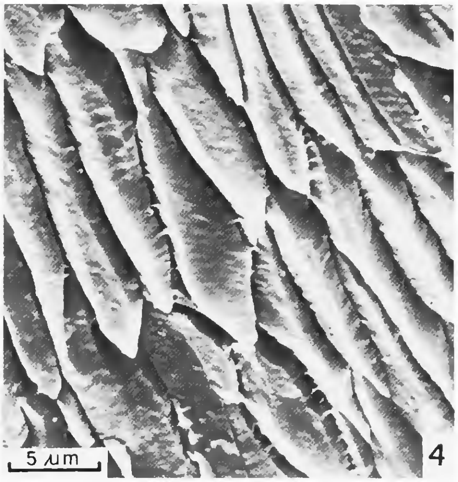

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PLATE 3

well seen as culminating rhombohedral peaks along the tops of each scarp (Williams 1968a, p. 3). The peaks stand on successively bigger crystal surfaces disposed as contour-like steps, which join with one another to form the dip slope surfaces behind the scarps. Each dip slope is the top of a simultaneously secreted layer of calcite; it is also the interface between the periostracum and the primary shell. The ultrastructural arrangement of the outer isotopic boundary to the primary layer, then, is a combination of isotopic and synchronous surfaces represented by the scarps and dip slopes respectively (Figure 4).

Growth Features of the Secondary Layer

The secondary shell accumulates by a more complicated process than either the periostracum or primary layer in that each cell involved in its secretion simultaneously exudes both organic and mineral compounds and, in so doing, initiates and controls the growth of a calcite fiber and its ensheathing membrane in the manner already described. Consequently, the secondary shell is defined by two sorts of isotopic boundaries as well as by a superficial synchronous boundary (Figure 4). One isotopic boundary separates the primary layer from the fibers making up the secondary shell (Plate 2: figures 1, 4). This boundary is less well defined than that between the periostracum and the primary shell. The change from primary to secondary shell deposition is rapid, but it is immediately distinguishable only by the presence of the first-formed ends of the membranes, the alinement of which traces the course of the boundary. The second kind of isotopic surface is that which segregates each fiber from its neighbors and is conveniently equated with the membranes pervading the secondary shell. Within its sheath, each fiber is an expression of cumulative growth because it is built up of a succession of synchronous shell units (Plate 2: figures 3–5), the nature of which was first recognized by Krans (1965, p. 84). The shape of a unit, which is determined by the disposition of the cell surface responsible for its secretion, is highly characteristic and comes about in the following way. The anterior arc of the external plasmalemma of a typical outer epithelial cell underlying the secondary shell secretes an organic membrane at a very much slower rate than the rest of the plasmalemma deposits calcite. The thickness of the membrane is about 14nm compared with an average of 354nm for 60 synchronous calcite shell units, measured medially immediately behind the membrane where the deposition of calcite is fastest. Away from this zone of maximum deposition, the section of calcite dwindles to nothing along the trail and sides of the exposed fiber, which are being covered by the membranes exuded by adjacent cells. Simultaneous secretion at these differential rates gives rise to a synchronous shell unit which is like a 74-degree sector of a circle in outline, corresponding to the margins of the terminal face of a fiber; and which is like a curved wedge in medial section with the thin end inserted between the stalk and the covering membrane. The concave surface of a synchronous shell unit, therefore, faces externally, as does the posterior part of the plasmalemma of the cell responsible for its secretion.

The course followed by fibers during their growth and the use of their mosaics (i.e., the arrangement of the exposed parts of fibers on the valve floor) to prepare growth maps of articulate shells have been described (Williams, 1968a, p. 9) and need only a brief review here. For such purposes, the long axis of the exposed part of a fiber can be taken as its growth vector at the moment of death, and average vectors for groups of adjacent fibers can be systematically plotted for the entire internal surface of a valve. The exercise is instructive not only for illustrating how the microscopic growth of various features takes place but also for revealing the characteristic growth of a fiber and the location of zones of secondary proliferations of cells and calcite resorption. In *Notosaria,* newly formed fibers bordering the junction of the primary and secondary shells develop normal to the shell margin. Within this narrow zone, however, in the two lateral areas of a valve interior, the terminal faces of fibers quickly become re-orientated more or less parallel to the commissure and grow towards the medial zone where fibers also tend to lie more or less normal to the anteromedian margin, unless they are involved in topographic complications like septa. Since these mature fibers were initially normal to the shell commissure, their growth away from the primary layer must trace a spiral arc, rotating clockwise in the right half of a valve and counterclockwise in the left half. Such a spiral course of growth may be described as the characteristic trace of fibers. The characteristic trace is greatly modified for those fibers contributing to the formation of skeletal outgrowths composed of secondary shell. It may also complete a spiral or double back on itself as a consequence of localized swirls or regroupings of cells.

Further specialization of the outer epithelium lining the secondary shell—as a preliminary to the secretion of elaborate internal features or the accommodation of growing tissue like muscle—can lead to gross alteration of the skeletal fabric. In particular, it can promote the formation of a number of distinctive isotopic shell units. Two of these, the units controlled by muscle bases and secondary generative zones, are closely associated (Williams, 1968a, pp. 14–19) but they receive only passing mention here because they are still under investigation. Essentially, muscle bases (including tendons binding the lophophore to the crura) change the biochemistry of the underlying outer epithelium sufficiently to inhibit membrane secretion with a consequential loss in identity of fibers. Calcite secretion also is greatly affected within an area occupied by a muscle complex and can vary from excessive deposition to form large scalenohedral or rhombohedral faces to differential resorption of calcareous surfaces. Resorption is especially important in controlling the size of features, such as lophophore supports, that have to accommodate growing soft parts of the animal. It also is involved in the growth of interlocking devices arising from both valves, like those defining the inner surfaces of the tooth ridge and the posterior part of the dental plate and the complementary outer surface of the inner socket ridge. Isotopic shell units such as these spread out and migrate across orthodox secondary layers as the shell grows. As they migrate, the disused parts of the isotopic units become buried by comparatively narrow zones of closely packed, small, regular fibers which are taken to indicate proliferation of cells from generative zones located well within the shell margin. So far, these secondary generative zones, are known to exist in *Notosaria* as confining posterior arcs to the main muscle areas on the floor of the valves, on the outer faces and the anterior part of the inner faces and dorsal edges of the dental plates, and on the anterodorsal surfaces of the crural bases. There is, therefore, a delicately balanced relationship between the differential growth and specialized functions of outgrowth composed of secondary shell; that relationship is reflected in the microstructure of such features.

Retraction of Outer Epithelium

Once the outer epithelium becomes detached from any part of the superficial synchronous boundary of the shell, retraction of the mantle or the posterior body wall can take place. The most profound changes in the exoskeleton arise from retraction of the mantle because the outer mantle lobe of punctate as well as impunctate brachiopods is free to retreat well within the primary-secondary junction, and in so doing interrupts every phase of the secretory regime being carried out by the affected outer epithelium. The actual operation is facilitated by the intervention of new forms of secretion which temporarily have precedence over all the orthodox secretory activities pursued by cells within the area of retraction. The area affected by retraction can vary from microscopic strips normally occupied by periostracum to macroscopic zones showing regression through the entire thickness of the shell. Both movements obviously involve the same sequence of events, and it is only a matter of descriptive convenience to treat them separately as has been done below. More spectacular morphologically but, in fact, less profound biochemically were the repeated retractions of the posterior body wall away from the floor of the pedicle valves of certain spiriferide and strophomenide species. Although they resulted in the growth of new elevated partitions within the valves, such movements could only have involved brief lapses from the normal secretory operation of mature outer epithelium.

Mantle Retraction in Impunctate Species

Restricted mantle retraction in *Notosaria* is immediately preceded by cessation of normal secretory activity, and the outer lobe of the mantle is pulled away from the superficial synchronous boundaries for the primary layer and periostracum (Figure 5 and Plate 3: figure 1). As the tip of the lobe retreats, newly formed outer bounding membrane is applied as a wrapping to the inner edge of the primary layer, as are the inner bounding membrane and mucoprotein layer after they have been sealed off by an irregular layer of a rapidly exuded, densely osmiophilic substance which is probably a protein. In fact, this substance is laid down as an undercoat to the primary layer for the entire distance of retreat away from the edge of the periostracum. It probably acts as an organic slide as well as a seal, which facilitates the breaking off of contact with the superficial synchronous surface and the smooth withdrawal of cells to their new positions. In all observed examples of periostracal regression the outer bounding membrane remains unbroken, implying that an acceleration in its secretion occurred during retraction of the mantle

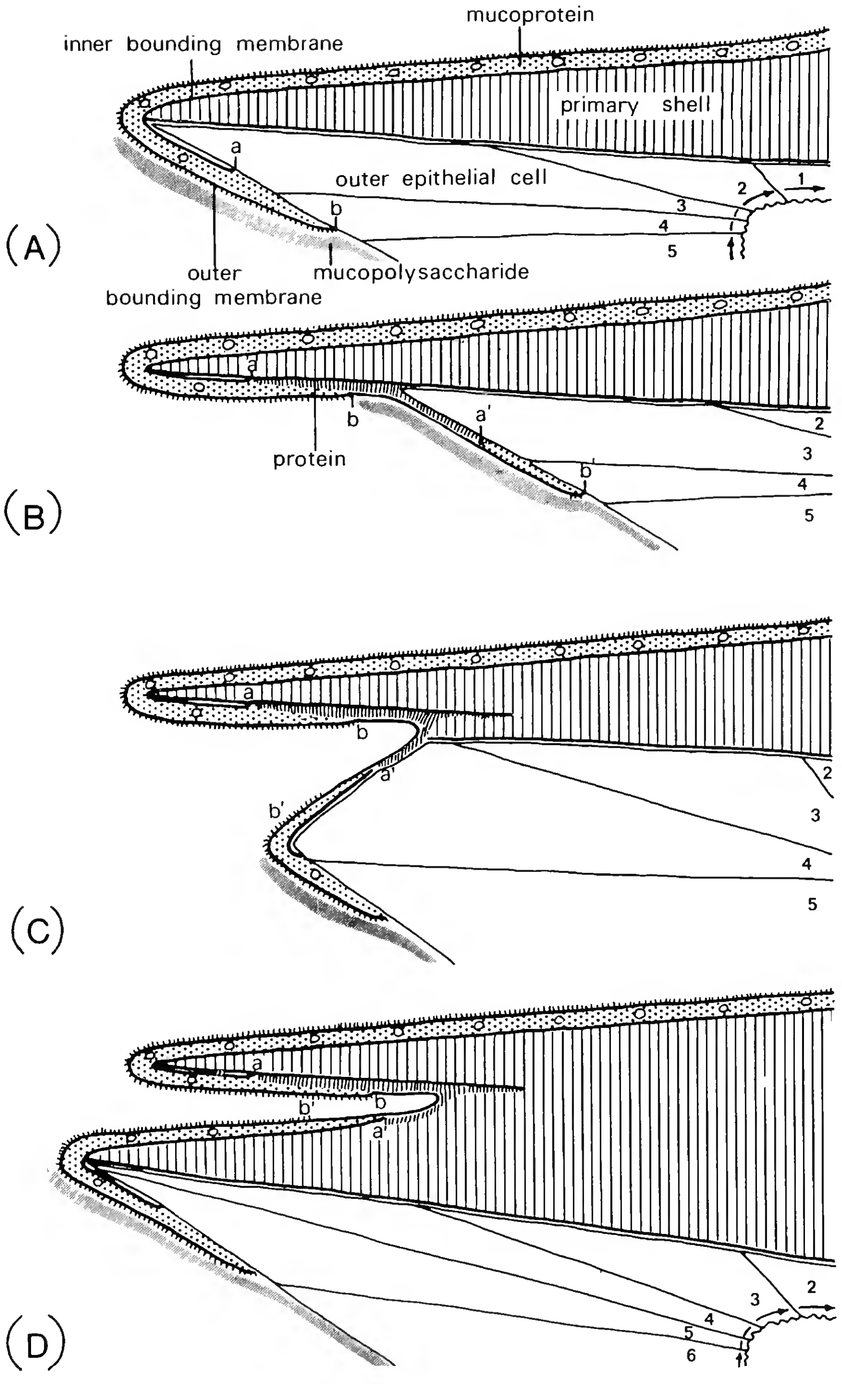

FIGURE 5.—Formation of a regression (aa′) in the periostracum of *Notosaria* shown embedded in primary shell in diagram (D), by retraction of the mantle lobe from its normal depositional attitude (A) and the concomitant secretion of the outer boundary membrane and a sealing proteinous layer (B) before forward movement of the mantle and normal depositon began again (C).

lobe. It is even possible that no matter how extensive the mantle's retreat from the shell edge, secretion of the outer bounding membrane keeps pace with retraction; and, even if this were not so, it is likely that exudation of protein always takes place in sufficient quantities to ensure a continuous organic seal.

Insofar as one can judge from such studies as have been carried out, protein actually is laid down by those cells which have already passed through that phase of the secretory regime concerned with the exudation of the inner bounding membrane. Cells previously depositing the inner bounding membrane and mucoprotein appear to suspend operations during retreat but start up again—when re-advance of the outer lobe takes place—at that phase in the secretory regime where they left off. Even those cells which secrete protein during mantle retraction revert to the correct phase of the regime once normal growth is restored. Thus, new primary shell is seeded on the protein undercoat of the old, the inner bounding membrane and mucoprotein start off anew from junctions with the protein layer, and secretion of the inner bounding membrane continues. In this way a fully operating regime is quickly re-established.

More powerful retractions, which cause the tip of the outer mantle lobe to retreat within the primary-secondary shell boundary, may or may not involve the widespread secretion of protein as has been observed in *Magasella sanguinea* (Leach) and *Notosaria*, respectively. Future work probably will confirm that these differences have no systematic significance because deposition of protein accompanies mantle retraction in *Hemithiris psittacea* (Gmelin) but occurs only discontinuously beneath a regression in the one specimen of *Terebratulina retusa* (Linnaeus) examined.

In the secondary shell of *Notosaria*, the first stages in mantle retraction involve an abrupt termination of all secretion, so that retreating outer epithelial cells move across calcitic cores separated from one another by proteinous strips which represent the terminal faces and the exposed ends of the organic sheaths of fibers. As soon as retreat has ended deposition begins again, but in a highly selective way (Figure 6; Plate 2: figure 6; Plate 3: figure 1). The retracted part of the mantle must undergo microscopic readjustments before forward growth is resumed, because that part of the plasmalemma of each cell which is responsible for the deposition of calcium carbonate starts secreting a calcitic pad in continuity with the terminal face of another fiber. In the specimen examined, diurnal banding indicated that the pads were built up by a steady accretion for about two weeks, by which time individual pads had joined up with one another to form a deposit about 5μ thick over the entire area of the former superficial synchronous surface of the secondary layer.

Two aspects of this phase of growth are noteworthy. The first is that these pads have a similar outline, at least in side-view, to outer epithelial cells engaged in the secretion of secondary shell. The likeness is accentuated by the presence of impersistent breaks between the pads, which lie, like tension gashes, more or less normal to the line of the fibers and occupy the same position as intercellular spaces in the outer epithelium. These breaks undoubtedly represent the lateral gaps that occur between the early growth stages of adjacent calcite pads before the pads make contact with one another by spreading beyond their original discrete centers of secretion (Figure 6c). It is even possible that they accommodate patches of protein exuded intercellularly from the outer epithelium at a time when secretion of protein from the external plasmalemmas of the cells was in abeyance. Thus, as calcite deposition about each terminal face proceeded, successive layers spread towards the limits imposed by such breaks, and the pads, with their characteristic shape, came into being.

The other significant feature of recovery from retraction is that the calcitic pads are secreted by *all* outer epithelial cells which have been brought into juxtaposition with the secondary shell surface irrespective of the particular phase of the secretory regime they were in prior to retraction. Thus, cells occupying the outer surface of the outer mantle lobe, which normally deposit primary shell, secrete pads of the same thickness and shape as those deposited by secondary outer epithelium. But once the pads have been deposited, cells revert to the normal secretory regime at precisely the point where they left off. The result is that, in shell sections, the isotopic boundaries displaced by a regression remain parallel to one another; and elimination of the effects of a regression enables the primary layer to be fitted neatly together in much the same way as faulted sedimentary rocks can be restored to stratigraphic continuity.

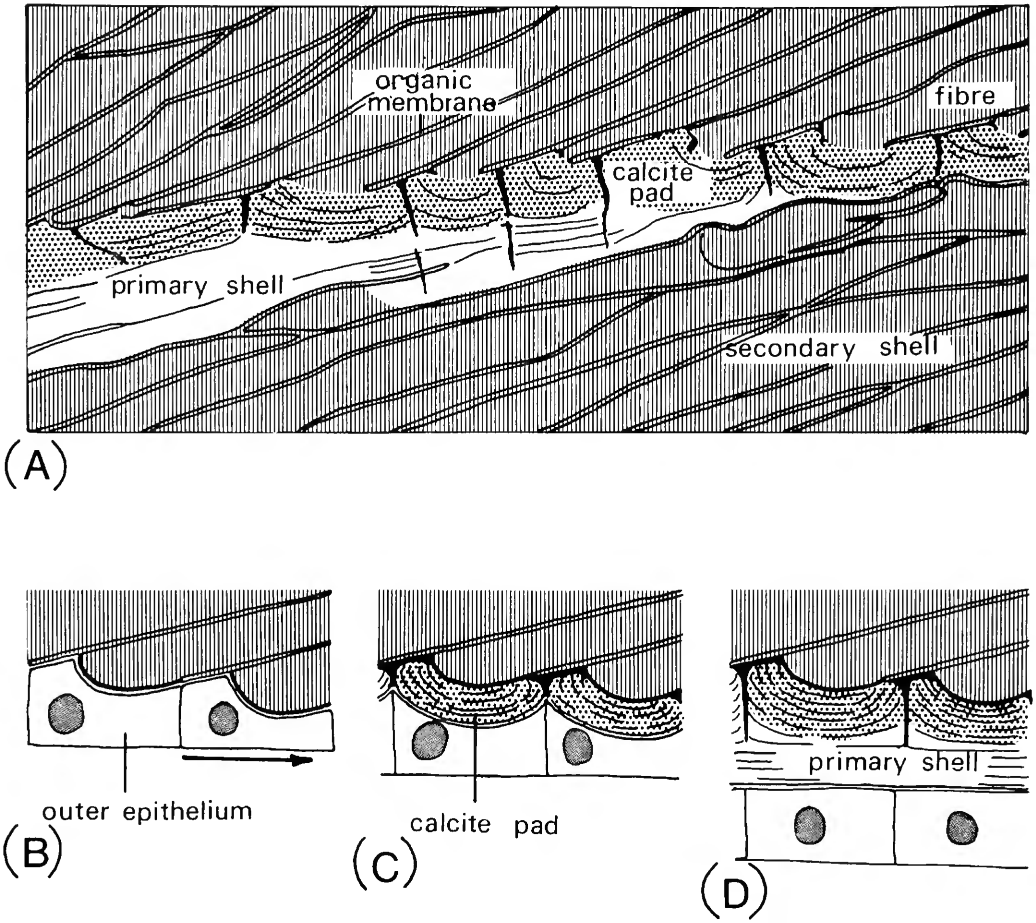

FIGURE 6.—Stylized tracing of an electron micrograph showing a regression affecting the calcareous layers of a valve of *Notosaria* (A); with reconstructions of how calcite pads (C) and primary shell (D) are deposited on the exposed faces of fibers by a retracted mantle lobe after withdrawal of the outer epithelium responsible for the normal growth of the fibers (B).

Mantle Retraction in Punctate Species

Evidence for the retraction of the terebratulide mantle is worth considering because the terebratulide shell is permeated by densely distributed caeca of the mantle that originate at the mantle edge and would appear to prevent any withdrawal whatsoever. The shells of many species, like *Magasella sanguinea*, however, become rutted with coarse growth lines as they approach maturity, and sections show that these breaks in growth can be accompanied by mantle retraction penetrating deep into the secondary layer. In fact, the operation is exactly the same as that described for *Notosaria* except that all outer epithelial cells secrete an organic cover for the superficial synchronous surface either before or during retreat (Figure 7 and Plate 3: figure 2). So far, this cover has been examined only under the scanning electron microscope, which has afforded no clue to its composition, although it is likely to be a protein or mucoprotein because it is continuous with such substances lining the canals (punctae) that contain the caeca. Indeed, it is this continuity which is a key to the disengagement of those caeca involved in retraction. The protein lining not only separates every caecum from the calcareous sides of the puncta accommodating it but also forms

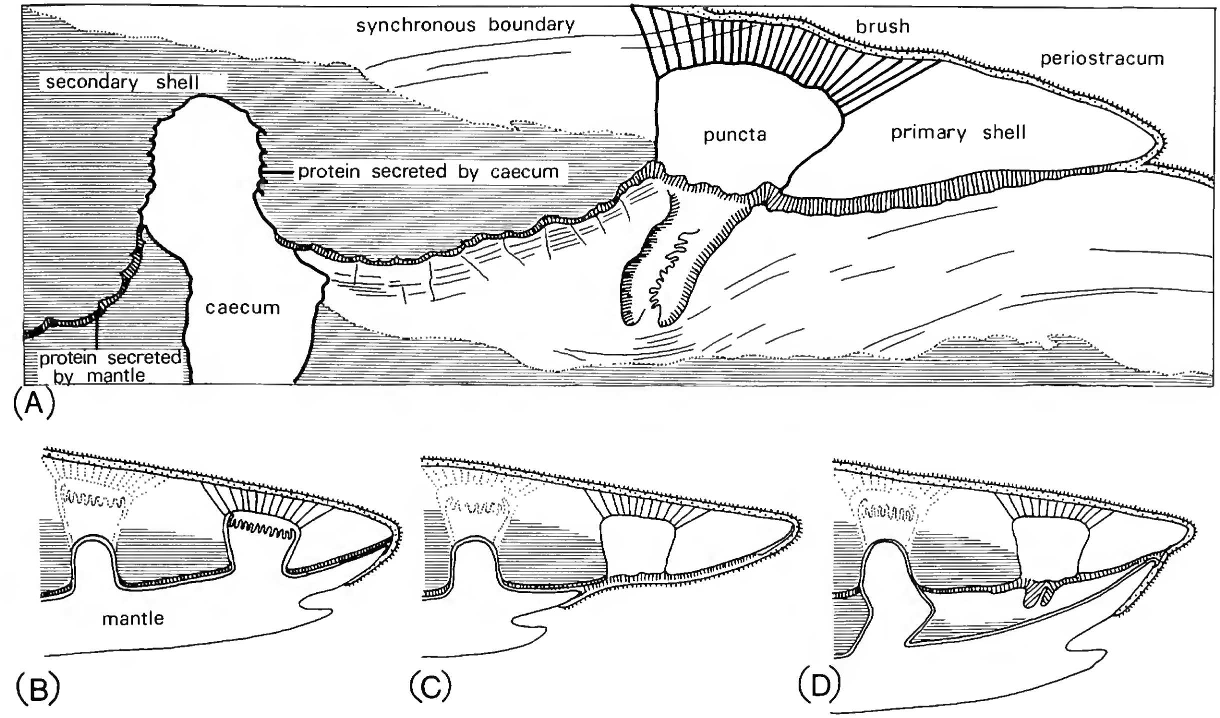

FIGURE 7.—Stylized tracing of an electron micrograph, partly represented in figure 2 of Plate 3, showing a regression affecting the calcareous layers and caeca of a valve of *Magasella* (A); with reconstruction of how retraction of the mantle lobe leads to the transference of an anteriorly placed caecum (B) into a more posteriorly sited puncta (C) and the sealing off of the forward puncta during subsequent mantle growth (D).

the brush of fine tubules connecting with the periostracum.

The microvilli covering the distal surface of the caecal head, which must have occupied the brush when it was being formed, are withdrawn shortly after completion of the brush and remain so throughout the life of the animal.[2] The withdrawal is accompanied by slide out from the lubricated organic lining of the punctae like fingers out of a glove. When retraction has ended and before shell deposition is resumed, some caeca probably become inserted in punctae other than those originally containing them. But it would also not be surprising to find that many caeca get trapped along the regression between the old superficial surface and the newly formed shell and eventually are pinched out, and that many punctal heads in the immediate vicinity of the coarser growth lines are empty of living cells.

Retraction of the Posterior Body Wall

Causes of retraction have still to be explored, although obviously it may occur randomly as well as periodically in response to environmental factors. Among genetically controlled retractions can be reckoned the sporadic sag of the posterior body wall away from the floor of pedicle valves of certain extinct species such as those of *Richthofenia, Scacchinella,* and *Syringo-* the exudation of mucopolysaccharide which fills the brush; and a similar arrangement is envisaged for caeca attached to the retreating part of the mantle that *spira* (see Cooper 1954, p. 326). In these unrelated stocks, the volume of the pedicle valves must have increased at a much faster rate than that of the coelomic cavity, so that the bounding outer epithelium moved

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[2] G. Owen and A. Williams, "The Caecum of Articulate Brachiopoda," in press.

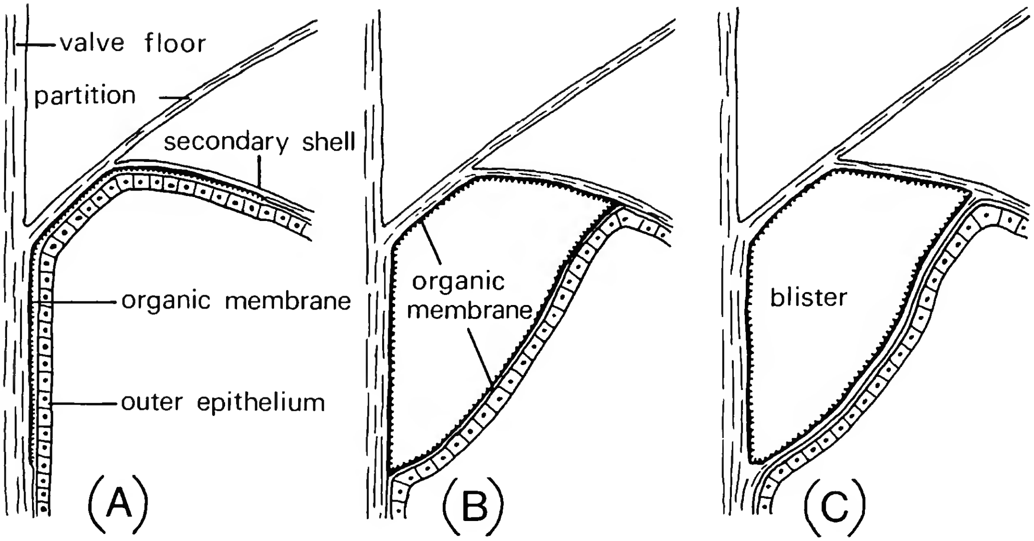

FIGURE 8.—Reconstructions to show the formation of a blister in the pedicle valve of *Syringospira*.

suddenly in a dorsal direction from time to time and, on each occasion, deposited a partition (or blister) sealing off the vacated part of the valve floor. Examination of *Syringospira* shows that these blisters are composed of orthodoxly stacked fibers lying at a very acute angle to the surface (Plate 3: figures 3, 4). There is no trace of any extra first-formed calcareous layer like the pads of *Notosaria*. Indeed, this is to be expected because secretion of an organic seeding sheet must have preceded the deposition of a fibrous sheet away from the valve floor (Figure 8). Deposition of a blister, therefore, must have involved a sudden termination of accretion on the valve floor, followed by a retraction of the outer epithelium of the body wall. The space created by this movement, possibly filled temporarily with fluid, must then have been sealed off by the exudation of a protein layer which, in turn, afforded the foundation for the secretion of a stronger partition composed of fibers and their organic sheaths.

Conclusions

This review, which is necessarily only a cursory look at a few of the problems concerning exoskeletal growth in articulate brachiopods, has been devoted mainly to abnormalities of shell deposition. The intention was to present some new data that have come to light during a comprehensive study of the shell and mantle that currently is underway. Two aspects of exoskeletal growth are newly described. The first is that interruptions in the processes of shell expansion, whether they involve forward or backward displacement of the mantle or just a simple suspension of deposition, do not upset the normal course of the secretory regime. As soon as the effects of interruption disappear, each outer epithelial cell reverts to its original phase in the secretory regime. The second aspect is that when an interruption involves a retraction of the mantle, disengagement from organic and mineral superficial synchronous surfaces usually is facilitated by the secretion of an organic (probably proteinous) layer. The recognition of both features probably will be helpful in future palaeontological studies. It follows from the former that shell successions, no matter how much they are displaced in, for example, a regression, can be correlated like strata on either side of a break. This rule will enable some realistic assessment to be made of the mobility of mantle in extinct stocks. The latter feature, i.e., exudation of an organic seal prior to mantle movement, also is important. Hydrolysis of such seals and removal of derived products during fossilization will leave only fabric evidence of their former presence, mainly as abrupt changes in the orientation of fibers. Yet, these are likely to be easily discernible and therefore indicative of the vagaries of the mantle even in those fossil species for which there is no obvious living morphological model.

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PRECAMBRIAN-CAMBRIAN

A. J. Rowell

Supposed Pre-Cambrian Brachiopods

ABSTRACT

Examination of all reported occurrences of Pre-Cambrian brachiopods reveals that all but one are most likely not brachiopods at all. Indian and Iranian material is most likely algal; the single Australian occurrence is thought to be inorganic; and the supposed specimens of *Lingulella* from the Belt Series of Montana are probably dolomitic segregations deformed by slippage. By way of contrast, well-preserved fossil brachiopods do occur in Arctic Canada, but they were collected from strata now thought to be of Cambrian rather than Pre-Cambrian age.

Because of the diversity of shelled brachiopods that are known from the early Cambrian, the existence of Pre-Cambrian brachiopods with no mineralized shells is considered likely. However, exceptionally well-preserved material would be needed to demonstrate convincingly that any such fossil remains truly represented the Brachiopoda.

The nature of Pre-Cambrian life and the problems posed by the appearance of relatively abundant fossils in the Lower Cambrian have long been subjects of interest. During the past 15 years, intensive collecting in some areas of the world, coupled with the use of improved techniques and equipment, has enabled the known age of the oldest authenticated fossils to be greatly extended. Sufficient evidence has been accumulated to convince all but the most skeptical of the existence of primitive plants some 2,000 million years old from the Gunflint Chert of Ontario (Barghorn and Tyler, 1965; Cloud, 1965). Some simple bacteria may be even older than these plants, for minute (0.5μ), rodlike bodies, seemingly bacteria, have been recorded from the Fig Tree Series of South Africa in beds which are thought to be 3,100 million years old (Barghorn and Schopf, 1966).

There have been many recorded finds of Pre-Cambrian metazoan animals, but in several cases the organic origin of the "fossils" has been questioned, and, in some instances, their Pre-Cambrian age is in dispute. Perhaps the most spectacular discovery has been the Ediacara fauna from Ediacara, South Australia, where Glaessner and Wade (1966) have reported the occurrence of 25 species based on over 1,400 specimens. There has been no challenge of the organic nature of this diverse fauna, although there is room for differences of opinion on its age, whether it is Late Pre-Cambrian or Early Cambrian (Cloud and Nelson, 1966; Ford, 1967). In part, these differences are semantic and reflect a lack of accord in the definition of the base of the Cambrian. Although the base of the Cambrian is not operationally well defined, the existence of elements of the Ediacara fauna in the Charnian of England (Ford, 1958) and the report of *Cyclomedusa plana* Glaessner from the Vendian of the Russian platform (Zaika-Novatskiy et al., 1968) suggest that at least part of the fauna was extant before Cambrian times. The possibility remains that the fauna persisted into the Cambrian, as Ford (1967) and Cowie (1967) have noted.

It is not the purpose of this account to review all metazoan Pre-Cambrian fossils, as several such reviews have been published, with those of Glaessner (1966) and Cowie (1967) being the most recent. It will suffice to note that, apart from pennatulacean spicules, no commonly accepted Pre-Cambrian metazoan fossil is known to possess a mineralized skeleton. In this respect, the Ediacara fauna, although unusually rich, is typical of all reputedly late Pre-Cambrian faunas.

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Brachiopods are unknown at Ediacara and none have been reported in association with elements of the typical fauna from other regions. The Australian occurrences have been intensively collected, and the preservation is such that one would have expected representatives of the phylum to have been discovered if, indeed, they were ever present in significant numbers. Reputedly, Pre-Cambrian brachiopods have been described from four major regions—India (Chapman, 1935), Iran (Stöcklin, et al., 1964), Australia (Chapman, 1929), and North America (Fenton and Fenton, 1936; McNair, 1965); in every case, however, either their Pre-Cambrian age of their systematic assignment (or both) has been disputed.

I am indebted to Dr. D. J. McLaren and Dr. A. H. McNair, who first invited me to study the Victoria Island material, and to Dr. McNair for discussions on the age of the specimens. I am grateful also to Dr. P. Kier and R. H. Hansman for arranging the loan of specimens of *Protobolella minima* and *Lingulella montana* from the collections of the United States National Museum and Princeton University, respectively.

The following abbreviations of repositories are used in this paper: USNM, United States National Museum; PU, Department of Geological and Geophysical Science, Princeton University; and GSC, Geological Survey of Canada.

Indian and Iranian Occurrences

Fossils have been known for 60 years from the Vindhyan System of India—since the time that Middlemiss and Jones collected numerous, small black discs from the Suket shales. According to Holland (1909), Jones was uncertain of their affinity. Jones suggested that they might be referred to the brachiopod *Obolella,* or possibly they might be the operculum of *Hyolithellus,* or, alternatively, they might belong to *Chuaria circularis* Walcott. The difficulty in finding a defendable systematic assignment of these fossils, apparent in their initial description, characterizes much of the history of later investigations of them.

For a few years, the specimens generally were regarded as brachiopods. They were examined by several paleontologists in the 1920s, and the consensus of Walcott, Ulrich, Bassler, and Resser was that they were definitely brachiopods and agreed most closely with *Acrothele* (Pascoe, 1928, p. 21). Chapman (in Fermor, 1932, p. 29; 1933, p. 20) also believed that these black discs were the remains of brachiopods; he initially referred them to *Neobolus* and *Obolella,* but subsequently (Chapman, 1935) endeavored to erect two new genera, *Fermoria* and *Protobolella* to include them.

Sahni (1936), who reinvestigated the type collections of *Fermoria* and *Protobolella,* came to the conclusion that such differences as were apparent between the specimens were differences of preservation, and he synonymized all of Chapman's species under the name *Fermoria minima.* At that time he was uncertain of their systematic position. Misra (in Rao, 1952), regarded the disks as ostracodes, but he soon abandoned that view, believing them to be of inorganic origin (Misra, 1952).

Although several investigators considered the possibility that the specimens were the remains of fossil plants, Howell (in Pascoe, 1928, p. 21) was the first to express the opinion that they probably were plants, and later he drew further comparisons with other plantlike material (Howell, 1956). Some two years earlier Sahni and Shrivastava (1954) described additional material, collected in 1950, that seemingly confirmed the view that these discs were primitive plants, possibly algae. In these new specimens, the discs occupied terminal positions on long filaments and were regarded as some form of spore sac.

The collections of "*Fermoria*" in the United States National Museum that were made by H. C. Jones from the Vindhyans of Neemuch are, at least in a loose sense, topotypes of "*F.*" *minima.* Like most of the described material, they reveal only the black disks (Plate 1: figures 1–3), with no indication of attached filaments. Superficially, these objects resemble the Ordovician inarticulate brachiopod *Paterula*; they are of a comparable size, have a flattened brim, and seemingly have the brim interrupted by a notch, which could be homologized with the pedicle notch of *Paterula.* These resemblances, however, are believed to be misleading. The black material of the disks is not an apatite and is probably carbonaceous; on two occasions when X-rayed, it failed to produce a picture, although the fragments of *Paterula* used as a control produced the characteristic lines. In some specimens the notch breaching the flattened brim (Plate 1: figure 1) is demonstrably an artifact, and the carbonaceous material is broken. There are no indications of musculature or mantle canal patterns; in fact, there is nothing other than outline that might lead one to accept these specimens as brachiopods. When considered together with material figured by Sahni and Shrivastava, I lean to the view of those authors—that "*Fermoria*" is probably algal.

Stöcklin et al. (1964) have figured specimens which they refer to *Fermoria* from the Chapoghlu Shale Member of the Soltanieh Dolomite of Iran. From the available figures, the fossils are certainly similar to the Indian material, and I would regard them also as primitive plants.

There is a nomenclatural point which, although briefly noted by Rowell (1965b, p. H864), has been generally overlooked. The specimens in question usually are referred to the generic name *Fermoria* of Chapman (1935), but the generic name is not available with that author and date. As noted above, Chapman (1935) regarded the fossils as brachiopods and consequently worked under the International Code of Zoological Nomenclature. In his initial account, Chapman (1935, pp. 115–117) described three new species—*F. minima, F. granulosa,* and *F. capsella,* but, unfortunately, he failed to make the generic name available as he neither designated nor indicated a type-species for the genus as required by Article 13(b) of the Code of Zoological Nomenclature. Under Article 17(3) of the Code, however, the three species-group names are available, and take date and authorship of Chapman, 1935. It will be recalled that in the same paper Chapman also proposed the new genus *Protobolella,* which was erected as a monotypic genus, including only *P. jonesi.* As the latter is automatically the type-species by indication (Article 68(c) of the Code), the generic name *Protobolella* was made available in 1935. In the following year, Sahni (1936) synonymized all of the species described by Chapman (1935), referring them to *Fermoria minima.* In his publication Sahni (1936), inadvertently perhaps, met all the conditions necessary to make *Fermoria* an available generic name. Consequently, *Fermoria* takes authorship of Sahni, 1936, with type-species *F. minima* (Chapman), 1935, by indication (monotypy).

If Sahni was correct in synonymizing the four species—and I accept his treatment—then *Fermoria* Sahni, 1936, although an available name, is, none-the-less, not a valid name because it is a junior synonym of *Protobolella* Chapman, 1935. This is an unfortunate situation, and one made even more untidy by the consequences of Sahni's action in synomymizing *Protobolella jonesi* with *Fermora minima,* for both species names were published simultaneously in 1935 with Chapman as their author. Both names are available, but, as subjective synonyms, only one can be valid. In these circumstances, Sahni (1936) was acting as a "first reviser" (Article 24(a)(i) of the Code) and his action determined the relative priority of the two; regrettably, he chose *Fermoria minima* as senior.

In summary, the legal aspects of the case are seemingly as follows: the valid name of the nominal taxon usually referred to as "*Fermoria*" is *Protobolella* Chapman, 1935; and the type species of this nominal genus is *Protobolella jonesi* Chapman, 1935, which is a junior subjective synonym of *Fermoria minima* (Chapman), 1935.

There is also some doubt concerning the age of the beds containing *Protobolella,* both in India and Iran. The Indian fossiliferous horizons are in the Rhotas Stage at the top of the Semri Series of the Vindhyan System (Sahni, 1962a). The evidence of the age of the Vindhyans has been reviewed by both Howell (1956) and Sahni (1962b). Unfortunately, there are no undisputed faunal or floral elements that provide reliable information. Both Howell and Sahni consider the problem unsolved; both concede that at least the upper part may be Cambrian, but Howell, in particular, is inclined to regard part of them as Pre-Cambrian. The stratigraphic control is only slightly better in Iran, where the oldest horizons with a diagnostic fauna are Middle Cambrian in age (Stöcklin et al., 1964). The beds yielding forms like *Protobolella* are around 2,000 meters lower in the section and are regarded as either Lower Cambrian or Upper Pre-Cambrian (Stöcklin et al., 1964, fig. 4).

Australian Occurrence

In 1929, Chapman described two species which he referred to the inarticulate genera *Lingulella* and *Obolella* from the Blue Metal Limestone, Adelaide Series. The Blue Metal Limestone lies some 14,000 feet below the top of the Series (David and Browne, 1950) and its Pre-Cambrian age has not been disputed. The original material on which Chapman's account was based has not been seen, but the available illustrations give little support to Chapman's opinion. Their form and described mode of preservation strongly suggest that they are inorganic and possibly were produced by weathering.

North American Occurrences

Belt Series, Montana

In 1932, the Fentons found remains of what they considered to be the pedicle valve of *Lingulella* (Fenton and Fenton, 1933). This material, from the Newland Formation, was formally described by Fenton and Fenton (1936) as *Lingulella montana.* The Pre-Cambrian age of the beds is not in question; indeed, if the remains are really those of a brachiopod they could lay claim to being the oldest known coelomate, with only the problematic *Telemarkites* Dons (1958) being a potential contender for the position. The question critical to the present study is whether the Montana specimens are brachiopods.

Schindewolf (1956) had doubts that the specimens were *Lingulella,* observing that they were from 5 to 10 times larger than typical Cambrian species of the genus. They certainly are much bigger than common Cambrian forms (Plate 1: figures 7, 9), but this argument alone is not very convincing. If one accepts that the beds from which they come are some 400 to 500 million years older than any Lower Cambrian species, then there seems no particular reason why the Belt specimens should not be *Lingulella* and belong to species substantially larger than Cambrian ones. Undoubtedly there are Lower Paleozoic lingulaceans that are separated from the Lower Cambrian by a time gap of much less than 400 million years yet are much larger than Cambrian species and noticeably larger than any of the specimens of *Lingulella montana.*

Although the possible taxonomic position of these specimens cannot be refuted by merely considering size, there are other possible approaches to the problem. Glaessner (1962) noted that the slippage which the specimens have clearly suffered would tend to destroy growth lines rather than enhance them. He was of the opinion that they were not brachiopods, but that they resembled stromatolites.

A detailed reexamination of the type collection of *Lingulella montana* reveals features that I believe show, beyond reasonable doubt, that the "species" is not a brachiopod and probably is not even of organic origin.

There are only two characteristics of the specimens that suggest they are brachiopods—their gross shape and the presence of concentric wrinkles which resemble growth lines. Fenton and Fenton (1936, p. 620) stated that the outline of the figured specimens had been emphasized, and this is readily apparent when one compares unfigured (and unprepared) paratypes with the illustrations in the original description (compare figures 7 and 9 of Plate 1, herein). The margins of the unprepared material are much more diffuse; it is, of course, impossible to say to what extent the sharp outlines of the previously figured specimens reflect the activities of the preparator and to what degree they are natural. At least at one point on the holotype, the outline departs markedly from any organic structure (Plate 1: figure 10), for the dolomite forming the "shell" is seemingly extended out into the matrix as a veinlet.

One can be more confident of the interpretation of the concentric wrinkles. In detail, these wrinkles are not continuous and show little resemblance to growth lines in any known lingulide. Their relation to the margin of the specimens is also unlike that of any lingulide, or, indeed, that of any brachiopod. The wrinkles intersect the margin at high angles, whereas in lingulides they curve gently toward the margin, becoming asymptotic to it near the beak. The wrinkles seemingly are deformation features consisting of a large number of small, steeply dipping, shear planes, all oriented in a comparable manner. Along the shear planes there is a preferred orientation of small elongate crystals, all of which lie parallel to the dip of the planes (Plate 1: figure 11). Thus, neither outline nor "ornament" can be utilized to support the claim that the specimens should be referred to the phylum Brachiopoda. The possibility that they are stromatolites remains open, but more probably they are inorganic segregations of dolomite that have been deformed by slippage.

Victoria Island-Arctic Canada

In 1965, McNair briefly described the occurrence of "primitive, very thin-shelled brachiopods" from what were thought to be beds of the Shaler Group, late Pre-Cambrian of western Victoria Island. This announcement of well-preserved fossils of seemingly Pre-Cambrian age attracted, not surprisingly, considerable attention. It was, however, somewhat premature, for although the majority of the original specimens were forms which could provide little stratigraphic information, the material identified by McNair as Brachiopoda undoubtedly belongs to the phylum and strongly suggests an Early or Middle Cambrian age for the beds. After completion of more detailed field work, McNair (personal communication, 1968) now believes that the beds which yielded the fauna are Cambrian and are preserved in a local graben, being down-faulted into the Pre-Cambrian.

Thus, in contrast to the previous cases that have been discussed, the supposed Pre-Cambrian brachiopods of Victoria Island are sufficiently well-preserved and morphologically distinct that their taxonomic position is readily accepted, but they are not Pre-Cambrian in age. All of the identifiable specimens are paterinaceans and seemingly are best referred to the genus *Dictyonina*.

Order PATERINIDA Rowell, 1965

Superfamily PATERINACEA Schuchert, 1893

Family PATERINIDAE Schuchert, 1893

Genus *Dictyonina* Cooper, 1952

The brief diagnosis given by Rowell (in Moore, 1965, p. H295) is accepted here, but more information still is needed about many features of paterinacean genera. *Dictyonina* is being used for those members of the family that have a pitted ornament. It is recognized that this probably is a gross simplification of a complex phylogenetic pattern and that the ornament may have arisen independently in several stocks of the family. Indeed this seems probable, for at least two types of pitted ornament are recognizable: in some species the pits are arranged in quincunx; in others, they are hexagonal in outline and are disposed in rows radiating from the beak. It is unknown, at present, the extent to which a classification based on ornament is congruent with classifications based on other features. As yet we are unable to discern any probable evolutionary pathways within the group, and the simpler approach is preferred.

TYPE-SPECIES.—*Trematis pannulus* White, 1874.

Dictyonina sp.

PLATE 1: FIGURES 4–6, 8

DESCRIPTION.—Specimens relatively large for the genus; maximum observed width, 13 mm. Ornament of fine pits arranged in quincunx, formed by intersection of two sets of narrow ridges. Ornament never well preserved, but seemingly about 10 pits/mm at a distance of 5 mm from the ventral umbo. Concentric growth lines conspicuous anteriorly and anterolaterally.

Brachial valve low, gently convex, sub-semicircular in outline with straight posterior margin, maximum width 20 to 30 percent greater than length, occurring at about one-quarter valve length in front of beak. Pseudointerarea short, homeochilidium not observed.

Outline of pedicle valve rounded subtriangular, apsacline. Length and maximum width approximately equal, maximum width occurring near midlength of valve. Pseudointerarea conspicuous, bounded laterally by abrupt change in slope of valve surface, ornamented only by growth striae. Homeodeltidium well developed, covering apical one-third to one-half of delthyrium, strongly convex externally, marked off from pseudointerarea by narrow groove.

Internal structures unknown.

DISCUSSION.—All the material is crushed to a varying degree, and adequate biometric treatment is not possible. The above dimensions and ratios can be regarded only as indicators of order of magnitude.

The genus occurs in high Lower Cambrian beds and is known to range into the Upper Cambrian. The ornament of described Late Cambrian species, however, is not closely comparable to that of the Victoria Island material; moreover, the Late Cambrian forms are all typically much smaller. Thus, the fauna is consistent with a late Early Cambrian to Middle Cambrian age for the beds.

Recognition of the Earliest Brachiopods

Although it has been claimed that Pre-Cambrian brachiopods have been found on several occasions, all such claims seemingly are not justifiable. As discussed above, either the specimens are not brachiopods or, alternatively, they belong to the phylum but are not Pre-Cambrian. To date, we have no direct fossil evidence for the existence of the phylum prior to Cambrian times; indeed, we still know remarkably little about the group from the lower beds of the Lower Cambrian. In several parts of the world there is a sequence of archeocyathid-bearing limestones that underlies the lowest beds with trilobites. In some areas, at least, brachiopods are reported to occur in these horizons carrying an archeocyathid fauna (Sokolov, 1968), but little work as yet has been done with them. We know that by late Early Cambrian times the phylum was represented by all four orders of inarticulate brachiopods together with kutorginaceans and primitive orthides. Seemingly, the ability to secrete a shell of calcium phosphate or calcium carbonate was acquired early in the Early Cambrian.

The form and mode of life of any possible Pre-Cambrian ancestor is still in the realm of speculation, but the morphology of both fossil and living brachiopods is thought to provide reasonable guidelines for such conjectures. Because of the diversity of late Early Cambrian brachiopods, it seems probable that common ancestral forms existed that lacked mineralized skeletons. All known brachiopods have two valves that are underlain by very thin mantles, the valves being opened and closed by musculature of varying complexity. Almost by definition, our postulated shell-less brachiopod would need to possess such mantles; and for the musculature to be effective in controlling their movement they would have to possess a degree of rigidity. The rigidity conceivably could be produced by a hydrostatic skeleton; and the mantle canals, a feature of all known brachiopods, could have functioned secondarily in this manner. More probably, the rigidity was achieved by the secretion of an entirely organic integument. Williams (1968) has shown that the outer organic periostracum functions as a seeding sheet for calcite in Recent brachiopods and has suggested that it may have constituted the only skeletal cover in ancestral, pre-shell forms prior to attaining its present function. Regardless of how rigidity of the mantle was attained, consideration of brachiopod musculature and the torque stresses involved in its use suggest that in the absence of a mineralized shell the animals could attain only a small size.

If such primitive brachiopods existed, one wonders how readily they would be recognized as members of the phylum in the fossilized state. In this condition, they would presumably form small, flattened carbonaceous impressions, hopefully retaining some indication of bilateral symmetry. It seems doubtful if such characterless objects would be universally accepted as brachiopods unless additional features, typical of the phylum, were also developed. Traces of two such features are known as fossils, for indications of the pedicle (Craig, 1952) and the form of the feeding organ, the lophophore (Steinich, 1963; Rowell and Rundle, 1967), have been described from fossil brachiopods, but both are very rare. Amongst fossil forms, the lophophore is known only in the terebratulide Cancellothyrididae, a family which characteristically has very heavy development of calcareous spicules in the lophophore; these spicules are responsible for retaining some indication of the nature and disposition of the lophophore after death. Also unusual is a preserved pedicle, which is known only in *Lingula*, a genus whose pedicle is atypical of the phylum in its great length and unusual proximal thickness. A pedicle is typical of most brachiopods, but commonly it is relatively short and its position beneath the beak of the pedicle valve hinders its recognition in fossil specimens. Thus, preservation of either of these organs requires not only exceptional environmental conditions but also rather unusual development of the organs in the living animal.

There are, however, additional structures which, although exceedingly fine, are characteristic of nearly all brachiopods. These are the setae, "chitinous" in composition, bristle-like in form, and projecting from the valve margins. They occur in living species of both classes, inarticulates and articulates, and it seems reasonable to believe that they may well have been present in their ancestors that lacked mineralized shells. Although they are not commonly preserved in fossilized

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PLATE 1: figures 1–3.—*Protobolella minima* (Chapman), from Vindhyan System, Neemuch, India. 1, Severely exfoliated disk, showing marginal brim; USNM 116016 (× 15). 2, Specimen showing traces of concentric ornament on marginal brim; USNM 116012 (×15). 3, Specimen showing vague concentric marks probably due to crushing; USNM 116015 (×15). All specimens coated with ammonium chloride.

Figures 4–6, 8, 12.—*Dictyonina* sp., from Cambrian, Minto Inlet, Victoria Island, Northwest Territories, Canada. 4, Damaged shell with pedicle valve displaced posteriorly relative to brachial valve; GSC 24568 (× 4). 5, Posterior view of pedicle valve showing conspicuous homeodeltidium; GSC 24571 (× 9). 6, External view of brachial valve showing low pseudointerarea; GSC 24570 (× 4). 8, Ventral exterior of exfoliated pedicle valve, specimen crushed on right posterior; GSC 24569 (× 5). 12, Detail of ornament (× 25) of specimen shown in figure 4. All specimens coated with ammonium chloride.

Figures 7, 9–11.—*Lingulella montana* Fenton and Fenton, from Newland Limestone, Belt Series, Birch Creek, eight miles west of Sulphur Spring, Montana. 7, Unfigured paratype material showing four aligned specimens whose margins are locally diffuse; PU 40769 (× 1). 9, Holotype, PU 40767 (× 2), showing linguloid form and "ornament." 10, Detail (× 20) of right posterior margin of holotype, below vein cutting "shell"; the "shell" material is drawn out into the matrix. 11, Detail (× 20) of "ornament" of holotype, showing alignment of crystals. Specimens in figures 7 and 9 coated with ammonium chloride; specimen in figure 10 photographed under water.


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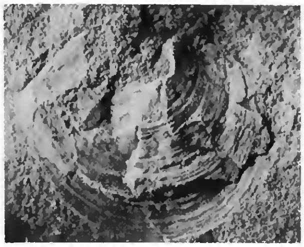
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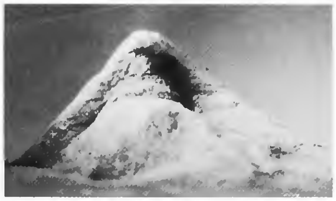
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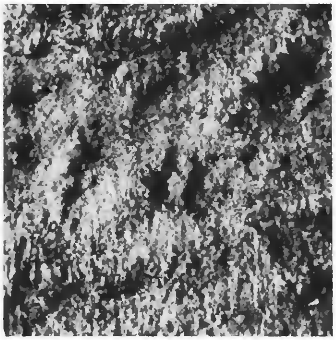
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PLATE 1

material, given very fine-grained sediments and freedom from scavengers their form may be retained as casts—for example, *Dictyonina pannula* from the Middle Cambrian Burgess Shale of Mt. Stephen (Walcott, 1912, p. 362). It would appear that these structures are the most likely ones to confirm the identification of a bilaterally symmetrical, carbonaceous impression as the remains of a brachiopod as opposed to traces of plant material or the representative of another phylum.

As yet we know nothing of the evolution of the Brachiopoda prior to the acquisition of a mineralized shell, and it is apparent that if such shell-less forms existed it would require exceptionally well-preserved material to demonstrate convincingy that their fossil remains indeed belong to the phylum.

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ORDOVICIAN

Gertruda Biernat

On Branched Surface Spines in Some Inarticulate Brachiopods

ABSTRACT

Multiple bifurcation of surface spines is considered one of the characteristic features of a Lower Ordovician *?Siphonotreta* sp. The general morphology (the arborescent part excluded) and morphogenesis are judged to be similar to those of single spines of other spinose brachiopods. The function of branched spines is discussed in general.

One of the most interesting, unusual and, as yet, almost unknown features of siphonotretids is their dichotomously bifurcating surface spines. That phenomenon within this group of inarticulate brachiopods was first recorded by Professor R. Kozłowski (1948, p. 6). Prior to 1939, while dissolving Lower Ordovician chalcedonites from Wysoczki, Holy Cross Mountains (Góry Swiętokrzyskie), in diluted hydrofluoric acid he found a rich faunal assemblage containing, among others, many valves of siphonotretids, numerous detached bifurcating spines and (Kozłowski, personal communication) one pedicle valve of a comparatively large siphonotretid with preserved branched spines. Unfortunately, all this material was lost during World War II.

After the war, Professor Kozłowski continued dissolving the chalcedonites from Wysoczki, obtaining in the residuum, among other microfossils, a number of separate valves of phosphatic inarticulate brachiopods and numerous, but only detached, branched spines. All this chalcedonic material of brachiopods was passed on to me by Professor Kozłowski in 1958.

In 1965, with a view of enriching this material, I began dissolving chalcedonites from Wysoczki in diluted hydrofluoric acid and obtained complete specimens of siphonotretids with bifurcating spines. Two years of dissolving about 400 kilograms of rock yielded numerous and differentiated inarticulates—especially the genera *Lingulella* Salter, *Oxlosia* Cooper, *Conotreta* Walcott, *Schizambon* Walcott, *Helmersenia* Pander, and *Siphonotreta* de Verneuil—and a number of separate dichotomous and multiple dichotomously bifurcating spines.

It was only quite recently, however, that I succeeded in obtaining three almost complete brachial valves of *?Siphonotreta* sp., each with a few preserved dichotomously branched spines. These specimens supply concrete evidence of the occurrence of this phenomenon within siphonotretids.

The work here presented has been carried out in the Paleozoological Institute of the Polish Academy of Sciences in Warsaw. The studied collection is housed in that Institute and is abbreviated herein as Z. Pal. Bp. XIII.

I sincerely thank Professor Kozłowski for having interested me in this field of investigation. Thanks also are due to Miss M. Witkowska, laboratory assistant, for dissolving the chalcedonites; to J. Kazimierczak for the photographs of specimens and spines; and to Mrs. K. Budzyńska for the ink drawings—all of whom are with the Paleozoological Institute of the Polish Academy of Sciences, Warsaw.

Remarks on the Chalcedonites at Wysoczki

The Lower Ordovician chalcedonites, the source of the siphonotretids, come from Wysoczki, about 51.5 kilometers southeast of Kielce (Figure 1). This outcrop was studied mainly from the lithological point of view by Czarnocki (1928), Samsonowicz (1948) and petrographically, with some considerations on the origins

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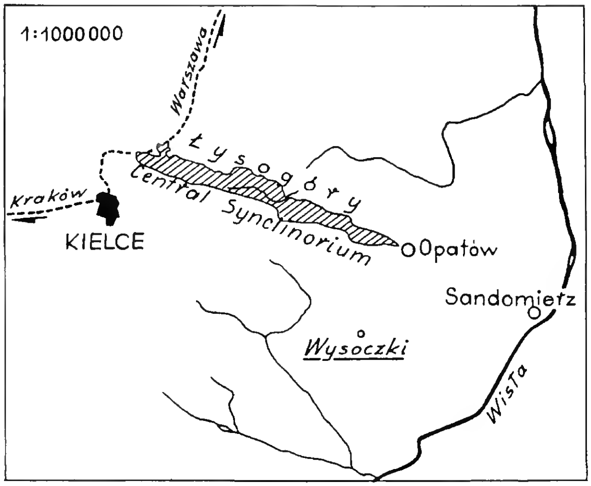

FIGURE 1.—Locality where Lower Ordovician chalcedonites occur.

of chalcedonites, by Turnau-Morawska (1957). As shown by the above studies, the outcrop consists of a 16-meter-thick sedimentary series of chalcedonites and associated rocks composed of rhythmically interbedded thin layers of glauconitic sandstones, each from 5 to 20 centimeters thick, and chalcedonites in parallel beds or sometimes as nodules or lenses. The chalcedonic intercalations, 46 in number and each from 7 to 15 centimeters thick, constitute about 2.8 meters (17.5 percent) of the total thickness of the entire outcrop. These chalcedonites are interesting from the petrographic point of view as a rather rare occurrence of pure silica in clastic sediments (Turnau-Morawaska, 1957). The decomposition of the pelitic detrital material which reached the sea probably was the main source of the silica in this rock.

The unweathered chalcedonites are bluish and transparent, with suspended granules of glauconite, spicules of sponges, and fragments of graptolites and inarticulate brachiopods. All the above (mineral fragments included) often constitute the centers of nearly pure silica gel that crystallized into large spherulites of chalcedony. In this way, these fragments are well preserved.

Material

The chalcedonites contain a differentiated assemblage of microfossils (among others): algae of Osciliatoracea (Starmach, 1963); Acritarcha of incertae sedis (Gorka, 1967); and sponges, brachiopods and graptolites (Kozłowski, 1948). The number of representatives of individual groups varies to some extent; some are less numerous (such as graptolites) while others (Acritarcha, for example) occur in abundance. Sponge spicules are very numerous, with those of monactinellids dominating and with hexactinellids and lithistids in the minority. Somewhat less numerous are the thin-shelled phosphatic inarticulate brachiopods, including mainly lingulellids, acrotretids, and siphonotretids. These latter are represented by small, sometimes densely spinose genera: *Helmersenia* Pander, *Schizambon* Walcott, *Siphonotreta* de Verneuil and *?Siphonotreta* sp. with branched spines.

The state of preservation of the faunule—although the chemical method (diluted hydrofluoric acid, about 30 percent) was used—is, in general, satisfactory, indicating suitable environmental conditions for their preservation as fossils. The percentage of complete valves of spinose inarticulate brachiopods, however, is not high in comparison with their fragments, which are of various sizes. A number of fragments that probably are *?Siphonotreta* sp., usually bear stumps, and sometimes branched spines, all of which are preserved in only one-fourth to one-half their full lengths.

The rare occurrence of branched spines on more or less complete valves of *?Siphonotreta* sp. is due to the delicate structure and extreme fragility of the branched part. These distal parts, being the youngest and thus more delicate and thin, no doubt are more readily destroyed or dissolved. When a fragment of a valve with a few stumps and one bifurcating spine was accidentally left in weakly acid water for two days, the distal bifurcated part of the spine was dissolved and only the stump remained.

In residuum, the number of detached, very diversified branched spines is considerable, comprising more than a hundred nearly complete or fragmentary examples. The valves of *?Siphonotreta* sp., weakened by the action of the hydrofluoric acid, were easily fragmented, with the bifurcated spines becoming detached during the subsequent washing of the specimens. Single spines of other siphonotretids at hand often were preserved in their full length and, in varying degrees of density, covered the valves, almost completely, but only rarely were they found detached.

General Appearance of Brachial Valve of *?Siphonotreta* sp.

The preserved brachial valves are small, with length and width slightly exceeding one millimeter, and they belong to younger individuals. These valves are thin and of moderate convexity (especially their umbonal part); their cardinal margins are a little thickened; and the pseudointerarea is like a very low, thin, laterally elongated plate, slightly concave medially and covered with horizontal growth lines.

The valves under consideration are true siphonotretids in external appearance, differing mainly in their spines. No doubt they represent a new genus which, for the present, must remain unnamed due to the lack of a pedicle valve with branched spines.

On the basis of fragments of valves and detached branched spines of different sizes, it seems that an adult shell of *?Siphonotreta* sp. would attain a size considered large for siphonotretids—up to about 10 millimeters in length. The largest branched spine in our collection—the corona is only partly preserved—is about 2.5 millimeters long (Figure 2:9). According to Kozłowski (personal communication) the pedicle valve with branched spines that he found before the war also was larger and thicker in comparison with other siphonotretids and possessed a larger foramen with a distinct siphonal extension. It is unfortunate that no other pedicle valve of *?Siphonotreta* sp. has been found.

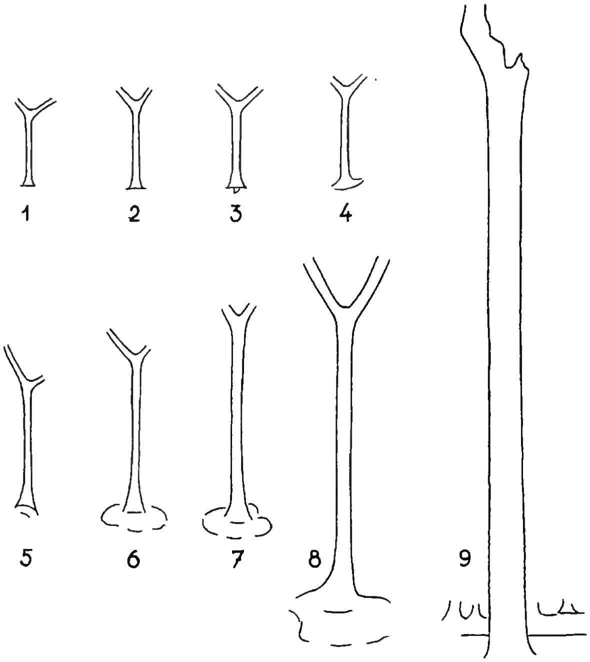

FIGURE 2.—Spines of *?Siphonotreta* sp. Length of stems to the first cycle of bifurcation (subsequent growth stages). Bp. XIII/30–33, 20, 29, 18–19, 1; approximately × 40.

Morphological Remarks on Spines

The examined spines are true hollow tubes, usually opening into the interior of the shell, like all the single spines of the other siphonotretids at hand or the spinose representatives of articulate brachiopods such as productoids. Characteristics of the spines of *?Siphonotreta* sp. are as follows: short basal tube communicating with the external hollow spine and the shell interior; the stem; and the arborescent part, or corona. These three parts are variable, especially the arborescent one (Figures 3, 4; and Plate 1).

The short internal tube penetrates the thin shell substance extending into the shell interior—somewhat similar to productoids (Grant, 1968)—at slightly different angles, depending upon the growth stage, but usually rather low to the inner shell surface. This tube, sometimes vesicular in appearance, bears a small open terminal orifice leading into the spine, its diameter being almost equal to the central lumen of the stem. This orifice becomes gradually blocked with growth.

The stem is, of course, the thickest and the longest, usually half or more than half the total spine length, and its walls are thin, attaining about one-fourth to one-third of the stem thickness at each growth stage. In general, it is slightly thicker in its basal part, especially in the adult stage, insignificantly tapering, if at all, distally. As a rule it is almost uniform in appearance. The differences that do occur refer only to length, width and thickness of walls; and these are mainly growth changes, as the individual variability is very limited (Figures 2, 4).

The arborescent part comprises about one-third to one-half of the entire length of the spine and takes the form of a spreading tree, or of antlers, in different degrees of variation. It can attain a quite remarkable development, as shown on Figures 3, 4, and Plate 1. In general, there are only a few variants of arborescence, the most common being the types shown on Figure 3.

Occasionally, in the residuum there are spines simultaneously branching in three directions, as well as dichotomously bifurcating spines with both branches slightly coiled laterally. These kinds of spines are rare and are preserved as detached fragments. No such kinds have been found on the larger fragments of valves (Plate 2: Figures 10, 11).

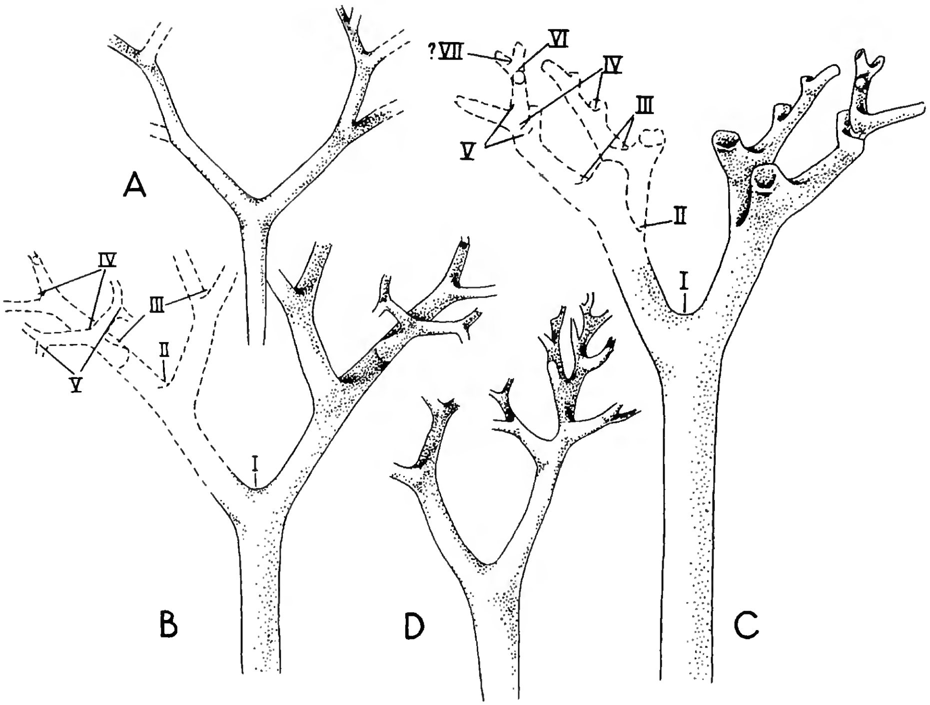

FIGURE 3A–D.—Appearance of the corona of four spines of *?Siphonotreta* sp. In B and C the left sides of the spines (broken lines) are reconstructed on the basis of the preserved right sides, with the number of bifurcations shown. Bp. XIII/15, 7a, 7, 7b; approximately × 79.

Morphogenesis and Growth of Spines

The spines in question must have originated in a manner similar to the way in which single ones originated (Rudwick, 1965; Williams, 1956, 1968). Their development, however, occurs in two phases—first of the stem and then of the corona.

The stem appears by periodic budding-off from the wavy edge of the valve, anteriorly closing with growth to form a ring. This gradually lengthens into a distinct tube by the continual addition of circular increments (their traces sometimes observed) at their distal ends which are always open. With growth of the shell, the tube becomes gradually removed from the valve margin (Figure 5). This budding-off of the valve is accompanied simultaneously by budding-off of the mantle edge from the outer, earlier evaginated, mantle lobe. The mantle tissue lining the spine grows in length due to the long period of proliferation of the mantle's outer epithelial cells at their distal, generative tips.

After the stem has attained a certain length, the second phase of development begins. The distal epithelial cells divide, the first cycle of bifurcation always parallel to the valve surface. The growth of the two new spinose parts continues in the same way as in the stem to the moment of their next division. The second cycle has four branches turned outwards at angles from about 30 to 45 degrees. This growth continues, as a rule, as long as the connection exists between the mantle tissue lining the growing spine and the remaining lobe of the shell (Rudwick, 1965). In our case, this connection was maintained over a long period. The repeated process of bifurcation for each new branch until the final condition is reached is evidence of this long period of growth. The secretory activity of the mantle tissue was at a faster rate than in single spines of many spinose species, but it slowed gradually as the distance between each further division became shorter. The rate of the shell growth was comparatively slower.

In the present material, seven cycles of subsequent branching of spines are indicated. This branching may not be the maximum attained as it depends, among other factors, mainly upon the thickness of the stem;

that is, the growth stage. In the residuum occur straight (or almost straight) younger spines that bifurcate a maximum of four times, vary only slightly in their appearance, and cover the posterior part of young (preadolescent and early adolescent) individuals. These are not preserved, having been broken off. They can partly disappear with growth, becoming blocked from the interior, and only their short stumps, small surface tubercles, or even only traces are present. There also are adult spines, generally curved, that bifurcate seven times or more, vary greatly in appearance, and cover the anterior third of the shell in mature individuals. All these spines represent different cycles of branching, corresponding to the different growth stages (Figure 3). The process of branching starts early in ontogeny (Figure 2:1). Specimens of the smallest (youngest) bifurcated spines occur at a distance of about 0.3 millimeter from the beak. They are delicate and thin, about 0.6 to 0.7 millimeters long, and have a stem length to approximately 0.4 millimeter. They are, however, sufficiently large for further branching and strong enough to support the increasing size of the corona.

The corona, with four branches, is about two-thirds to one-half the stem length and about one-third to one-half the stem thickness. With further growth, the diameter and length of the stem, as well as the number of branches, increase. Each of the subsequent branches is comparatively shorter and thinner, being about one-fourth to one-third of the preceding one, with the central lumen also being gradually restricted. A typical adult spine in the collection appears to be approximately 1.9 millimeters long, with a stem of about 0.9 millimeter to 1.1 millimeters long. There also are a few spines with comparatively long stems, attaining a length of about 2.2 millimeters and a thickness of about 0.2 millimeter before the first cycle of bifurcation.

In summary, it may be said that there are some characteristic properties associated with the process of growth of these spines: a regular, always dichotomous, repeating bifurcation; both branches of the first cycle are always parallel to the valve surface; in each later cycle the newly bifurcated branches are turned outwards at angles that vary from about 30 to 45 degrees; and the general rule for single spines (that is, the gradual tapering and corresponding constriction of the central lumen) holds also for the branched spines. This kind of arborescent branching can be explained as probably useful for balancing the weight of the spine, the weight of the whole corona being disposed equally in all possible directions. In addition, there seems to be no significant difference between the branched and single spines except for bifurcation.

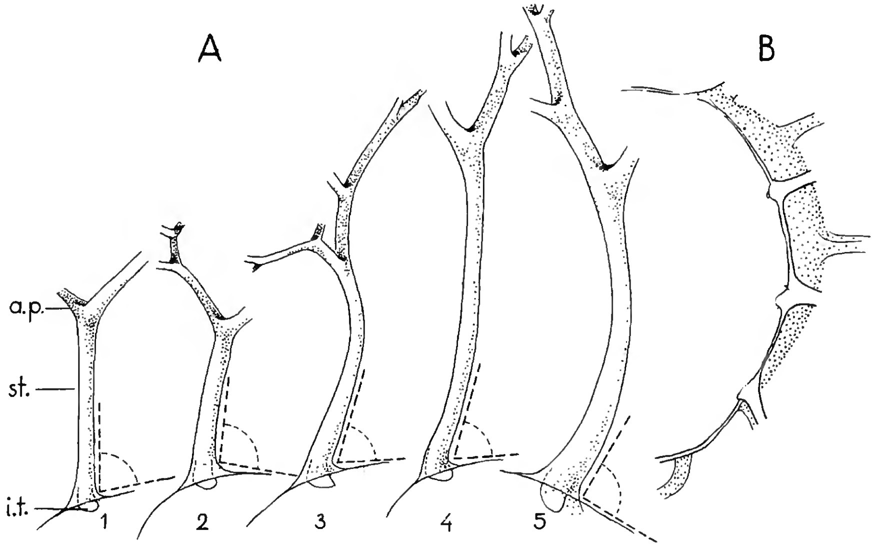

FIGURE 4.—A (1–5): Different angles of spine projection to the shell surface of *?Siphonotreta* sp. (Bp. XIII/16, 16a–b, 22, 6); a.p., arborescent part; st., stem; i.t., internal tube. B: Side view of small (young) brachial valve (Bp. XIII/17) showing projection of spines to the shell surfaces. All approximately × 36.

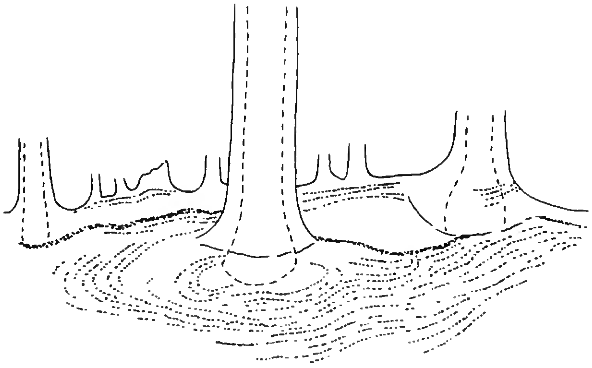

FIGURE 5.—Fragment of marginal part of valve of *?Siphonotreta* sp. (Bp. XIII/1) showing fragments of smaller and larger spines and arrangement of microlines. Approximately × 79.

Spacing and Arrangement of Spines

The spines in *?Siphonotreta* are, generally speaking, arranged in regular concentric rows or in a somewhat quincunx fashion very analogous to that in the pedicle valve of productellids. In general, there are four spines in a row, at a distance of about 0.7 millimeter from the dorsal beak, whereas in other associated siphonotretids there are from seven to nine spines in a row. The number and thickness of spines in each new row slowly and gradually increase, hence their average spacing changes only slightly with time. This change in spacing may be connected with the degree of arborescence of the spine because more space is needed. The spines are not, of course, of stable appearance, varying somewhat in thickness and length. Even in the same row they are slightly differentiated.

As a rule, the spines project at different angles to the shell surface. This angle, closely depending upon the growth of the shell as well as that of the spine, is always higher for younger spines—that is, for those on the posterior half of the shell (Figures 4, 5).

The spines on the hinge lateral extensions (usually one or two on each) are, judging from their preserved basal portions, directed posteriorly, extending beyond the posterior umbonal part, just as in the other siphonotretids with single spines. The younger spines usually are perpendicular (or almost perpendicular) to the shell surface on the median portion of the valve and are more inclined on both lateral slopes. The angle becomes progressively lower anteriorly for adult spines. At first, for a very short distance, they grow almost perpendicularly to the shell surface but then change direction to run nearly parallel to it, extending much beyond the anterolateral commissure of the shell (Figure 4B).

General Conclusions

It is difficult at present to discuss in detail all the aspects of branched spines because those preserved on the shell surface are incomplete. Their arborescent nature, however, is not in doubt. They are, above all, additional evidence of the great developmental activity so characteristic of brachiopods, and they underlie the many morphological possibilities displayed by these animals. These spines also have been observed recently by Gorjansky (in press) in a new siphonotretoid genus from the Caradoc of the Leningrad district and from Estonia. The spines, well-preserved along the anterolateral margins of three specimens, are comparatively long and thick, extending anteriorly beyond the shell margins. There also are many separate spines in Gorjansky's collection. Bifurcation, as in the Polish *?Siphonotreta* sp., although found, seems to be rare. Spines with slender branches arranged spirally up to the stem are most common.

These spines probably are not exclusively associated with inarticulate brachiopods. In addition to their presence in *?Siphonotreta* sp., they appear to occur also in spinose articulate brachiopods as shown in drawings by Jux (1962, Abb. 2). Some of the spines in the Devonian atrypids, *"aspera"* group, from the "Röhrer horizon" of Wachberg at Sötenich, Eifel, bifurcate at about half their length, extending anteriorly from the anterolateral parts of the shell. They seem to be very similar in appearance to those of *?Siphonotreta* sp. If Jux's illustration is correct, it would suggest that branching spines were fairly widespread and may have evolved independently several times in different spinose groups. G. A. Cooper (personal communication, September 1968) has observed bifurcation in a productoid specimen and, quite possibly also, in an inarticulate brachiopod; however, as these were just isolated cases he considered the phenomenon accidental.

Some very interesting observations on branching spines were made by Kozłowski (1914, pp. 73, 74, fig. 18d) for the Upper Carboniferous reticulariids from Bolivia. These spines do not communicate with the shell interior and are bi-tubed for five-sixths of their length, both tubes lying very close together. The tubes

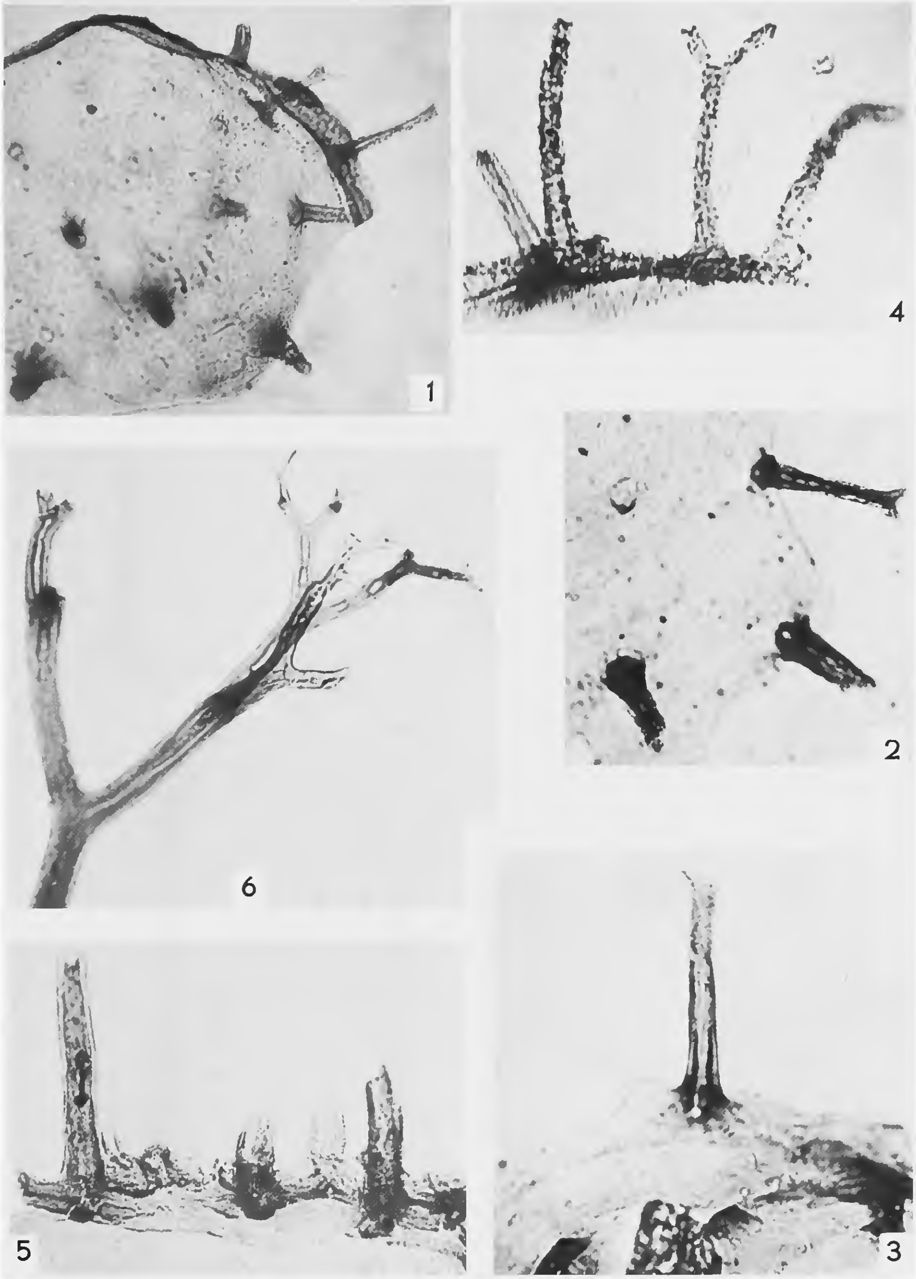

PLATE 1.—?*Siphonotreta* sp. and its spines; from chalcedonites at Wysoczki, Holy Cross Mountains, Poland: 1, exterior of brachial valve (Bp. XIII/12) showing arrangement of spines preserved as tubercles or stumps, one bifurcating; 2, fragment of brachial valve (Bp. XIII/13) with two stumps and one incomplete branched spine; 3, incomplete branched spine with a fragment of valve (Bp. XIII/28); 4, young spines, two of them bifurcating, on a fragment of valve (Bp. XIII/21); 5, stumps of adult spines, their basal parts preserved (Bp. XIII/14); 6, fragment of corona of adult spine (Bp. XIII/10). Approximate magnifications: 1, × 40; others, × 85.

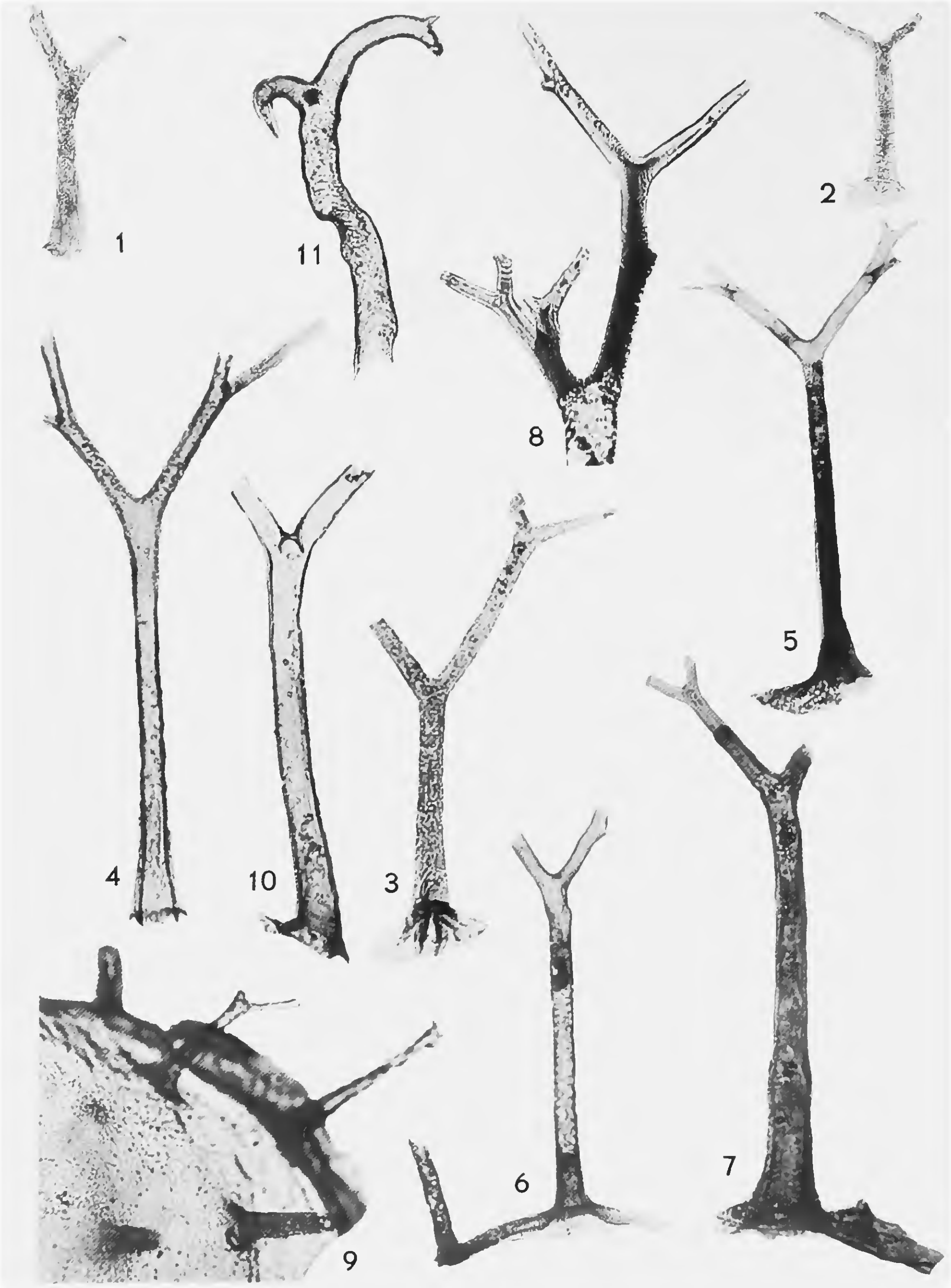

PLATE 2.—Spines of ?*Siphonotreta* sp. from chalcedonites at Wysoczki, Holy Cross Mountains, Poland: 1–7, detached branched spines (Bp. XIII/26, 27, 3, 4, 5, 9, 2) at different growth stages; 8, fragment of corona of adult spine (Bp. XIII/8); 9, enlarged fragment of the bracial valve (Bp. XIII/12) shown as figure 1 of Plate 1; 10, incomplete, detached spine (Bp. XIII/25) branching in three directions; 11, fragment of spine (Bp. XIII/11) with branches slightly coiled laterally. All approximately × 85.

are bordered laterally by a range of very small, delicate spines that bifurcate distally, similar to those of *?Siphonotreta* sp. in the first cycle of bifurcation. These "Carboniferous" spines, although quite different from ours, merit mention as one further kind of bifurcation.

The fact that branched spines have been so rarely recorded up to now could be due to the considerable difficulty in finding them in fossil state. While it cannot be completely ruled out that these spines did not have a rather common occurrence, it seems more reasonable to ascribe to them a limited range.

On the basis of the scarcity of the specimens of *?Siphonotreta* sp. as compared with the number of other preserved siphonotretids with single spines, these complicated spines—so spectacular in their full development—presumably were not a very fortunate specialization for the animals. This feature was specific and, in all probability, not very adaptable, being developed only in some special external environments, which could explain its presence with algae, colonial corals, bryozoans, and other forms.

Considering this aborescent feature from its functional aspect, it is difficult to ascribe a definite role, the more so as the correct interpretation of single spines within brachiopods still is not clear. At any rate, spines in general seem to have a very diverse function, being regarded as anchors (Muir-Wood and Cooper, 1960; Grant, 1968) or some kind of camouflage for shells living in colonial corals (Jux, 1962, p. 511; Rudwick, 1965).

In the case of the spines in *?Siphonotreta* sp., it would seem that they were more than just anchors for the animals. That they served to enlarge the gaseous area to any great extent is questionable. On the basis of petrographic data (Turnau-Morawska, 1957, p. 184), the environment of the Lower Ordovician seas in which these animals lived was shallow water, with the sea being open and well-aerated, as indicated by the numerous grains of glauconite and, above all, by the great number of spicules of sponges.

Apart from the theory that the spines acted as anchors or were useful for aeration, it could be considered (as suggested by Rudwick, 1965) that they served as particularly good filters, aiding in the protection of the animal against the incursion of non-nutritious particles into the body cavity. That the degree of this protection could have been high is suggested by the arborescent development of the spines, their strength and arrangement on the anterior third of the shell. One might say that the arborescent spines formed a protective thicket around the shell, at some distance from its anterolateral commissure. This thicket could both reduce, to some degree, the speed of the sea currents and have served as a very useful sieve for eliminating indigestible foreign particles suspended in the sea water. Part of this mineral suspension became transformed into siliceous gel (Turnau-Morawska, 1957).

Another possibility is that the spines could, to some extent, have served as sensitive receptors to inform the animals of danger, so that, in an emergency, the gap between the two valves of the shell could be diminished considerably. If one accepts the observation that all the branches of the corona were distally open as a result of the almost continuous growth of spines, this latter explanation appears to be quite reasonable. A similar suggestion was made by Rudwick (1965) for, among other genera, *Acanthothiris* Buckman.

Finally, the presence of arborescent surface spines within siphonotretids poses additional questions, one of which concerns their systematic value. The use of these spines as a diagnostic generic character in brachiopods cannot be justified, however, at present. In this collection, as already mentioned, their occurrence on valves is rare, and those at hand are not in a complete state of preservation. It is difficult to determine from the available data whether this feature is a stable one.

Another problem which awaits clarification is whether all the surface spines in *?Siphonotreta* sp. are branched. It would appear that they are differentiated in their degree of final development. Single spines presumably may occur on the hinge extensions, in addition to very delicate ones on the valve surface. All these "single" spines in the present collection are, however, not fully preserved, so this question must remain unresolved until further material becomes available.

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Shou-Hwa Chuang

The Morphology and Paleobiology of *Trematis elliptopora* Cooper (Inarticulata, Brachiopoda)

ABSTRACT

The brachial valve of *Trematis elliptopora* Cooper has hemiperipheral growth, notothyrium, and pseudointerarea. The pedicle valve, flat anteriorly, has a depressed posterior sector that faces posteriorly. The pedicle, attached to the outer surface of this depression, is presumed to point posteriorly and pass partly through the notothyrium. Muscle scars provide evidence for the occurrence of two components of the anterior occlusors, posterior occlusors, lateral oblique muscles, and internal oblique muscles. The longitudinal subdivision of the depressed posterior sector indicates the presence of at least two pairs of muscles in the lumen of the pedicle, namely the rectus muscles and the inner oblique muscles. The life history consists of three stages—embryonic, planktonic larval, and sessile postlarval. The transversely oval embryonic shells average 0.145 millimeter long and 0.183 millimeter wide. The larval shell valves average 0.412 millimeter long and 0.471 millimeter wide. The morphology and paleobiology of *Trematis* are discussed and comparison with recent *Discinisca* is made.

The genus *Trematis* was proposed by Sharpe (1848) for several species of *Orbicula* "attached by a ligament passing through a longitudinal fissure in the posterior part of the ventral valve" (1848, p. 68) and with external, regular punctation. Hall and Clarke (1892) discussed the available species and illustrated the muscle scars and the pedicle-callosity of *Trematis millipunctata* Hall. They believed that the pedicle-callosity at the posterior end of the inner surface of the brachial valve formed a surface for the passage of the pedicle. In other words, there is a notothyrium on the brachial valve. Several new species were described by Cooper (1956), who, with his fine acid-etched specimens, contributed further information to our knowledge of the morphology of the genus *Trematis*. In addition to other details, he noted the lightly impressed external ornamentation of the pedicle valve in contrast to the conspicuous sculpturing of the brachial valve.

Some well-preserved acid-etched specimens of *Trematis elliptopora* Cooper in the collection of the Natural History Museum, Smithsonian Institution, were examined in the present study of the morphology and paleobiology of *Trematis*. Comparison with *Discinisca*, with which it has close affinity, is made possible by dissection of *Discinisca laevis* Sowerby from the collection of the Peabody Museum of Yale University. Further comparison was made with dissected specimens of an undescribed species of *Discinisca* collected by the International Indian Ocean Expedition.

This study was carried out in the Paleobiology Department, Natural History Museum, Smithsonian Institution, Washington, D.C. The author thanks Dr. G. Arthur Cooper, senior geologist, for permission to examine types and other specimens, and for all arrangements made for the study at the Smithsonian, and Dr. Porter M. Kier, head of the Paleobiology Department, Mr. Frederick J. Collier, and other members of the Smithsonian staff for all facilities enjoyed at that Institution; Dr. Alan H. Cheetham for taking the photo-

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graphs of *Trematis* and for other photographic facilities, and Mr. Hoi Kee Yip for making the enlargements; Professor Willard D. Hartman of the Peabody Museum of Natural History, Yale University, for specimens of *Discinisca laevis*; and Dr. H. Adair Fehlmann, Miss Patsy A. McLaughlin, and Mrs. L. W. Peterson of the Smithsonian Oceanographic Sorting Center for specimens of *Discinisca* from the Indian Ocean.

In this paper the names of muscles are those of Blochmann (1900). Other terms used are current ones occurring in the literature and redefined as follows:

Anterior occlusor: One of a pair of muscles at the anterior end of the visceral cavity with dorsoventrally directed fibers; each member of the pair consists of a separate medial or anterior and a lateral or posterior component.

Anterior sector: Sector of shell anterior to the protegulum.

Brachia: Cirri-bearing projections of anterior body wall into the mantle cavity.

Brachial retractor: One of a pair of muscles with origin near the anterior occlusor on the brachial valve and inserted in the anterior body wall in the vicinity of the base of each brachium.

Brachial valve: The valve other than the pedicle valve.

Hemiperipheral growth: Growth of shell material in anterior and lateral sectors but with little or no growth in the posterior sector.

Holoperipheral growth: Growth of shell material in all sectors including the posterior.

Inner oblique muscle: One of a pair of muscles with origin in the anterior part of the median strip on the outer surface of the depressed posterior sector of the pedicle valve.

Internal oblique muscle: One of a pair of muscles with origin on the brachial valve anterolateral to the posterior occlusor and inserted to the median region between the bases of the anterior occlusors on the pedicle valve.

Larval shell: Shell valves secreted during the planktonic larval stage.

Lateral oblique muscle: One of a pair of muscles with origin on the pedicle valve along part of the lateral reigon of the visceral cavity and inserted to the brachial valve anterior to the anterior occlusor.

Notothyrium: Groove on median part of pseudointerarea at the posterior end of the brachial valve.

Outer oblique muscle: One of a pair of muscles with origin on the outer surface of the pedicle valve along the lateral region of the depressed posterior sector.

Pedicle attachment area: Outer surface of the concave posterior sector of the pedicle valve for attachment of pedicle and of the muscles in the coelomic space inside the pedicle.

Pedicle valve: Shell valve to which the pedicle is directly attached.

Posterior oblique muscle: One of a pair of muscles with origin on the brachial valve near the median plane at the posterior end of the visceral cavity.

Posterior occlusor: One of a pair of muscles with dorsoventrally directed fibers at the posterolateral region of the visceral cavity.

Protegulum: Shell valve formed in the embryo from substances stored in ovum.

Pseudointerarea: The inner surface of the posterior end of the brachial valve in inarticulate brachiopods—secreted by the edge of the reflexed mantle.

Rectus muscle: One of a pair of muscles with origin on the outer surface of the lateral strip within the depressed posterior sector of the pedicle valve and inserted to the distal end of the pedicle at its attachment to the substratum.

Morphology

THE SHELL.—The brachial valve in *Trematis elliptopora* is convex and with the protegulum and larval shell valve marginally placed at the posterior end, as Cooper (1956) has noted. In posterior view (Figure 1*a*) the external profile gently slopes from the sagittal plane towards the lateral edge on each side. The posterior edge also describes a similar curve, thus forming a considerable concavity facing the opposite valve. The larval valve is smooth and of a color different from that of the pitted postlarval valve. The postlarval valve appears to have a thick periostracum, and its outer surface is ornamented with many concentric ridges suggesting growth lines. As Cooper (1956) has indicated, the regularly arranged pits increase in size anteriorly. Measurements indicate that the pits at the anterior end have twice the diameter of those about halfway between the two ends along the sagittal plane of the brachial valve in a large specimen.

The pedicle valve is flat anteriorly, with its anterior sector longer than the posterior one. The posterior sector of the larval valve is notched and that of the

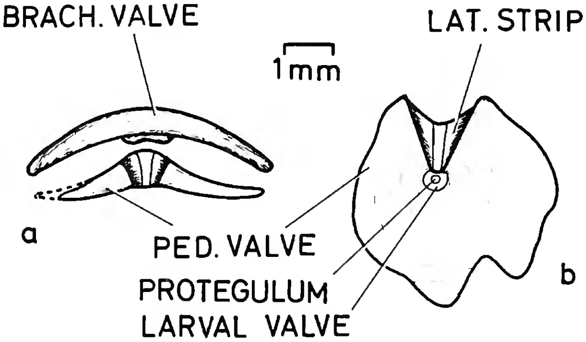

FIGURE 1.—*Trematis elliptopora* Cooper: *a*, upper, posterior view of brachial valve, USNM 116809g, paratype; and lower, posterior view of external surface of pedicle valve, USNM 116809d, paratype; *b*, ventral view of external surface of pedicle valve, USNM 116809d, paratype. All from Pratt Ferry, Blocton Quadrangle, Alabama.

postlarval valve is depressed to form a posteriorly ever-widening triangular concavity (Figure 1). This concavity faces posteroventrally in the young postlarva but almost posteriorly in later stages. As Cooper (1956) has indicated, the ornamental or growth ridges between the rows of pits and the pits themselves on the outer surface are less conspicuous than in the brachial valve and are easily visible only in certain regions of the pedicle valve. In posterior view the curved posterior edge of the valve (Figure 1*a*) has its convex side facing dorsally, thus fitting into the ventrally concave posterior edge of the brachial valve. This close fit between the brachial and pedicle valves provides further evidence for, and also seems to confirm, Cooper's (1956) assignment of these valves to a single species.

At the posterior end on the inner surface of the brachial valve there is a pseudointerarea, as reported by Hall and Clarke (1892). This shows distinct, transversely directed lines or wrinkles that represent the successive attachments of the growing reflexed posterior edge of the mantle during ontogeny. The median part of this pseudointerarea shows a slight concavity—Cooper's (1956) "more or less deep triangular pit under the beak." This concavity suggests a slight notothyrium (Figures 1*a*, 2*b*), as noted by Hall and Clarke (1892). Immediately anterior to the pseudointerarea is a deep depression, the anterior and lateral slopes of which are steep.

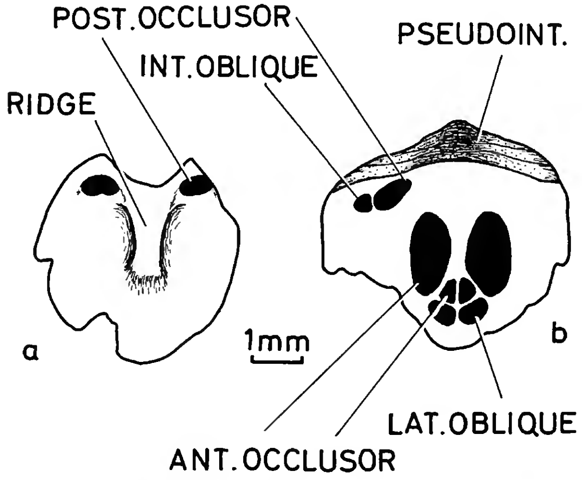

FIGURE 2.—*Trematis elliptopora* Cooper.—*a*, dorsal view of inner surface of pedicle valve, USNM 116809d, paratype; *b*, ventral view of inner surface of brachial valve, USNM 116809g, paratype. Both from Pratt Ferry, Blocton Quadrangle, Alabama.

The inner surface of the ventral valve has a Y-shaped ridge with the prongs lying in a crescent along the posterior edge of the valve. The stem occupies an anterior median position and gradually lopes anteriorly. The ridge corresponds in position to the triangular concavity on the outer surface in the posterior sector of the valve, thus indicating that the ridge is not purely a thickening of the shell but is due partly to folding of the posterior sector.

MUSCLE SCARS.—The musculature is not preserved as Cooper stated (1956). However, detailed examination of the inner surface of the valves under the microscope reveals certain regions with a different texture or a different shade of color from the rest. These regions correspond in position to muscle scars described by Hall and Clarke (1892) in *Trematis millipunctata* Hall and in *T. terminalis* Emmons, and are here presumed to be such, though they are not as distinct as in those species.

Three pairs of scars occur in the central part on the inner surface of the brachial valve in *T. elliptopora* (Figure 2*b*). They correspond in position to the three muscles in a new *Discinisca* species to be described by the author. The anteriormost of these scars are the lateral oblique muscles. Next to them near the median line are the medial components of the anterior occlusors. The largest pair of scars posterolateral to the other two pairs are the lateral components of the anterior occlusors. The small scars called "posterior centrals" by Hall and Clarke (1892, pl. 4c, figs. 4, 9) at the posterior end of this group of scars in *Trematis millipunctata* have not been observed in *T. elliptopora*.

At the left posterolateral region on the inner surface of the brachial valve is a long oval scar (Figure 2*b*) which corresponds to the posterior occlusor. Lateral to this is a less-distinct, triangular scar of the internal oblique muscle. This scar has the same triangular shape in both *Trematis* and *Discinisca*. On the opposite side on the same fragment of the illustrated brachial valve only the more medial part of the posterior occlusor muscle scar is present. In USNM 116809c and 116809e (the larger of the two specimens) a raised area, presumably for the attachment of muscles, occurs at the posterolateral region of the brachial valve.

On the inner surface of the pedicle valve (Figure 2*a*) only an oval scar is recognizable on the slope of each prong of the Y-shaped ridge in the posterolateral region. It represents the posterior occlusor.

The pedicle and its attachment area.—The depressed triangular area on the outer surface of the posterior sector of the pedicle valve (Plate 1) resembles that in recent *Discinisca* and therefore is presumed to serve the same purpose. As in *Discinisca* it is divided longitudinally into three regions providing origins for the muscles in the lumen of the pedicle. A narrow median region for a pair of inner oblique muscles in the center is flanked by lateral strips of posteriorly widening area for the origin of the two rectus muscles. Presumably, the cuticular wall of the pedicle is mostly attached to the outer edge of the depressed triangular area as in recent *Discinisca.* Whether there is a pair of outer oblique muscles along the anterolateral region of each rectus muscle as in *Discinisca* is not known.

The median one of the three longitudinal strips on the outer surface of the depressed posterior sector shows a different texture and also rows of pits along its lateral boundaries with the two lateral strips (Plate 1). These indicate a different mode of formation, as in recent *Discinisca.* In this the posterior continuation of the median strip is membranous and contains the pedicle canal that serves as a tubular connection between the coelom in the visceral cavity and the coelom in the pedicle. This membranous part anterior to the pedicle canal grows posteriorly and becomes calcified to provide accretion to the posterior border of the calcified median strip. A similar mode of formation is presumed to occur in the pedicle valve of *Trematis.*

While the depressed triangular area on the pedicle valve faces ventrally in *Discinisca,* it faces almost posteriorly in *Trematis.* Moreover, its posterior edge is concave, while it is convex in *Discinisca.* These differences indicate a different orientation of the pedicle. Presumably the pedicle in *Trematis* is directed posteriorly, necessitating the presence of a notothyrium and a pseudointerarea at the posterior end of the brachial valve (Figure 3 and Plate 2).

Reconstruction of soft parts.—From what is known of the anatomy of *Discinisca* and from the available data on the muscle scars and ridges in *Trematis,* the muscles that have a structural basis for their presence in *Trematis* are the medial (anterior) and lateral (posterior) components of the anterior occlusors, the posterior occlusors, the lateral oblique muscles, and the internal oblique muscles. The tripartite outer surface of the posterior sector of the pedicle valve provides evidence for the presence of at least the rectus muscles and the inner oblique muscles, which occupy the coelomic cavity of the pedicle. The disposition of the anterior and posterior occlusors and of other muscles indicates that the muscular system of *Trematis* is similar to that of *Discinisca.* Since the muscle scars in recent *Discinisca* are hardly recognizable, the absence of scars of other muscles in *Trematis* does not preclude their presence. It is presumed, therefore, that other muscles in *Discinisca* also are represented in *Trematis.* Thus, in the reconstruction of the soft parts in the latter, the following muscles are included: the posterior oblique muscles, the brachial retractors, and the outer oblique muscles in the pedicle lumen.

The area of attachment of the body wall to the inner surface of the shell valves is not recognizable. From the disposition of the muscles in *Trematis* it is assumed that the attachment of the body wall to the pedicle valve and to the brachial valve follows the pattern of *Discinisca.*

Again from the disposition of the muscles it is assumed that the gut in *Trematis* resembles that in *Discinisca,* with a curved pharynx and oesophagus, and a stomach with two dorsal and one ventral digestive diverticula. The intestine, as in *Discinisca,* presumably turns laterally to the right from the sagittal plane of the animal towards the right body wall, from the vicinity of which it then continues anterolaterally as the rectum before opening on the body wall on the right side of the body as the anus (Figure 3). Presumably there are two nephridia occupying a lateral position, as in *Discinisca.*

The brachia, as in *Discinisca,* presumably consist of a large proximal whorl on each side with other whorls reduced in size to form a minor spiral that has its apex facing anteroventrally (Figure 3). The fragments of

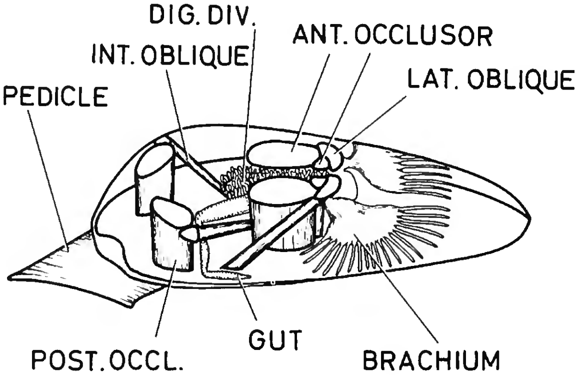

Figure 3.—*Trematis elliptopora* Cooper. Dorsolateral view (× 20) of reconstruction of entire animal, based on USNM 116809d,g,h.

PLATE 1.—*Trematis elliptopora* Cooper. Dorsal view (× 69) of the external surface of part of the posterior sector of pedicle valve; USNM 116809d, paratype, from Pratt Ferry, Blocton Quadrangle, Alabama. Note the median strip (M) and lateral strip (L) of the depressed area; and the protegulum (edge arrowed) inside the larval shell valve (edge arrowed).

Trematis elliptopora examined in this study do not have the anterior and lateral borders of the shell preserved for observations of the setal impressions to be made. However, it is here assumed that the mantle setae occur in *Trematis.*

Paleobiology

Adult *Trematis* lives attached to the substratum presumably with a short stumpy pedicle that issues posteriorly. Its life history, as in recent *Discinisca* (Chuang, 1968), consists of an embryonic stage, a planktonic larval stage, and an attached postlarval stage. During the embryonic stage the shell valves or protegula generally are transversely oval in shape and have a distinct growth line at the stage when they have reached a length of about 0.041 millimeter (average of 3 specimens) and a width of 0.052 millimeter (average of 4 specimens). The embryonic shell valves or protegula reached a final length of 0.145 millimeter (average of 7 specimens) and a final width of 0.183 millimeter (average of 7 specimens). However, the completed protegula in the brachial valve may vary from transversely oval (0.120 mm long and 0.187 mm wide in USNM 116809a) to almost circular (0.180 mm long and 0.187 mm wide in USNM 116809b). The completed protegula have a smooth outer surface and are conspicuously marked off from the larval shell valve by a prominent growth line that separates it from the larval shell valve (Plate 1). The completed protegula mark the size of the shell at the end of the embryonic stage, and presumably they are produced by the embryo from substances stored in the ovum.

The larval shell valve is secreted on the inner surface of the protegulum during the larval stage and outgrows this along the periphery. On both the brachial and pedicle valves the growth of the larval shell valve is holoperipheral. But whereas the outline of the larval shell on the brachial valve is oval, that on the pedicle valve develops a notch in the posterior sector during the later larval stage (Plate 1), as in *Discinisca* (Chuang, 1968). This notch serves as an exit for extrusion of the pedicle during settlement to the post-larval life. The larval shell valve presumably is produced during the planktonic larval stage, as in *Discinisca.* The outer surface of the larval shell valve is smooth and thus contrasts strongly with the pitted post-larval shell outside it. A prominent growth line separates it from the postlarval shell (Plate 1). The completed larval shell valve is a transverse oval, 0.375–0.435 millimeter long (average length of 4 specimens, 0.412 mm) and 0.450–0.510 millimeter wide (average width of 7 specimens, 0.471 mm). As in the protegula, the completed larval shell valve varies from a transverse oval (0.375 mm long and 0.495 mm wide in the ventral valve of USNM 116809d) to a subcircle (0.435 mm long and 0.450 mm wide in USNM 116809b).

The postlarval shell is produced after settlement to sessile life. The brachial valve pursues a hemiperipheral growth pattern, with the larval valve occupying a marginal position at the posterior end. Here the growing edge forms a reflected pseudointerarea, the central part of which is weakly grooved to show a slight notothyrium for the passage of the pedicle. The pedicle valve grows holoperipherally with most rapid increase in shell length along the anterior sector, with next most rapid increase along the lateral sectors, and with least rapid increase along the posterior sector. The notch of the late larval stage is repaired, and the external surface of the posterior sector develops a fold during the postlarval shell growth to give rise to a depression or concavity. In this concavity the pedicle and the muscles inside its coelomic cavity become attached to the external surface of the shell.

While in all known species of *Discinisca* the brachial valve has a holoperipheral shell growth with no pseudointerarea, the brachial valve of *Trematis* has a hemiperipheral shell growth with a prominent pseudointerarea and recognizable notothyrium. While the concave posterior sector of the pedicle valve faces ventrally, that in *Trematis elliptopora* faces posteriorly. Since the pedicle emerges from between the two shell valves in *Lingula* and *Glottidia*—in both of which a pseudointerarea occurs on the brachial valve—it is presumed that in *Trematis* the pedicle similarly is directed posteriorly from the outer surface of the posterior sector of the pedicle valve and passes through the notothyrium of the brachial valve during its course. The pedicle is presumably slightly longer than in recent *Discinisca* species and passes beyond the posterior edge of the brachial valve. *Trematis* lives attached to the substratum and does not seem to live in a burrow, since the sculpture on the outer surface of only the pedicle valve is eroded. A burrowing life would have abraded the sculpture of both shell valves. Since there is a tendency for *Discinisca* species from shallower habitats to be thicker and also larger than those from the deep, it is assumed that this thick-shelled *Trematis elliptopora* is a shallow-water species.

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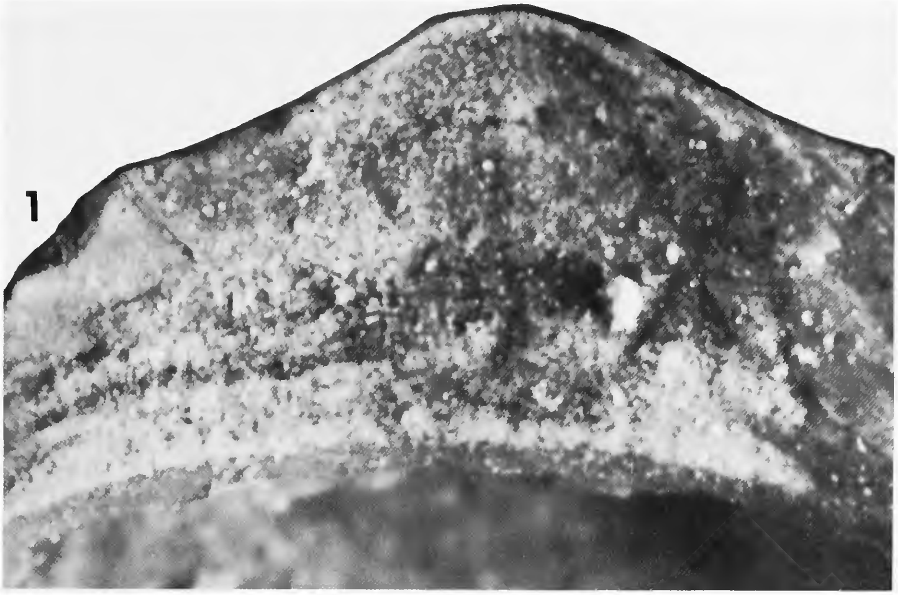

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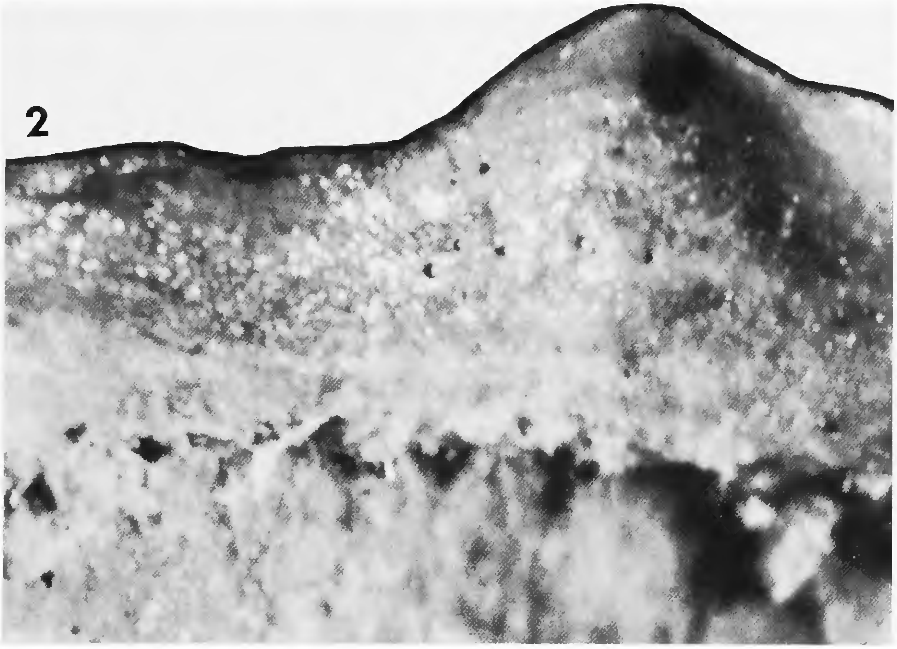

Plate 2.—*Trematis elliptopora* Cooper. 1, Ventral view (× 75) of the inner surface of the posterior part of brachial valve; USNM 116809g, paratype, from Pratt Ferry, Blocton Quadrangle, Alabama. 2, Ventral view (× 119) of inner surface of posterior part of brachial valve; USNM 116809h, paratype, from same locality.

In recent *Discinisca* the posterior part of the pedicle attachment area in the depressed posterior sector of the pedicle valve is covered ventrally by a thin layer of uncalcified shell material. Into this the posterior or dorsal wall of the pedicle continues, as reported by Blochmann (1900). Hall and Clarke (1892, p. 131) also referred to this part of the shell when they remarked: "By examining a specimen of the recent *Discinisca lamellosa,* it will be seen that the callous margins of the groove in this part of the shell are connected by only a thin transparent lamella, which, if broken, as is often the case, would leave the valve with a slit extending to the margin, as in *Schizocrania* or *Trematis.*" Lack of material on *Schizocrania* prevents the writer from comparing that genus with *Trematis.* Williams and Rowell (1965) also regarded the gap in the posterior sector of *Trematis* as comparable to that in a discinid. The surface of this uncalcified piece is covered by mantle and bears the growing mantle edge. Presumably a similar piece occurs in *Trematis.*

Discussion

There is no doubt about the affinity of *Trematis* with *Discinisca.* A life history with three stages—the embryonic stage, the planktonic larval stage, and the sessile postlarval stage—is a common feature of *Trematis* and *Discinisca.* The dimensions of both the protegulum and the larval shell valve in *Trematis* are comparable to those of *Discinisca.* From the information available, the muscular system presumably is similar to that of some species of *Discinisca.* The depressed posterior sector of the pedicle valve and the longitudinally divided external surface of the depressed area are features shared by *Trematis* and *Discinisca.* These features point to the presence of a relatively short, muscular pedicle attached to the external surface. However, Williams and Rowell (1965, p. H173) believed that "the pedicle emerged through a triangular opening which breached the posterior margin of the circular to subcircular pedicle valve in all stages of growth."

Discinisca, however, with its ventrally directed pedicle, differs from *Trematis,* in which the pedicle points posteriorly and emerges partly through the notothyrium of the brachial valve. Evidence for this lies in the noticeable notothyrium and the pseudointerarea. The hemiperipheral growth of the brachial valve of *Trematis,* in contrast to holoperipheral growth in *Discinisca,* is another important difference between the two genera.

Trematis thus differs sufficiently from *Discinisca,* and Schuchert's (1893) erection of a separate family Trematidae to accommodate *Trematis* is fully justified. Williams and Rowell (in Moore, 1965, p. H173) stated: "The discinaceans are first recorded from the Ordovician and, whereas it is almost certain that they arose from the acrotretaceans, it is also probable that the acrothelids were their ancestors." However, the attachment of the pedicle, the muscular system, and the size of the protegula are so different between the discinaceans such as *Trematis* and *Discinisca* on the one hand and the acrotretaceans and acrothelids on the other that, in the present writer's view, neither the acrotretaceans nor the acrothelids could have given rise to the discinaceans.

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Rousseau H. Flower

Cephalopods of the Whiterock Stage

ABSTRACT

Cephalopods now known from beds of Whiterock age fall into four categories: (1) survivors of Canadian stocks unknown in the Chazyan; (2) beginnings of stocks formerly thought to have begun in the Chazyan; (3) continuations of lineages known from both intervals; and (4) distinctive genera occurring only in the Whiterock. Not unexpectedly, the beginnings of some genera formerly known only from Chazyan or younger beds are found in the Whiterock. There are, however, surprisingly few genera in common to both the Whiterock and the Chazyan.

The validity of the Whiterock Stage is supported by the record of the cephalopods, not so much to allow time for the extinction or decline of dominant Canadian lineages as to account for the diversification of those which are found in the Chazyan.

Four new genera, one each from the Ellesmeroceratida and Discosorida and two from the Endoceratida, including five new species, are known only from the Whiterock.

Prior to the recognition of the Whiterock Stage, the Canadian-Chazyan hiatus seemingly marked a most profound change (see Flower, 1964a). No genera pass the boundary. Of the dominant Canadian orders, the Ellesmeroceratida is represented by seven families in the Canadian and two in the Upper Cambrian that do not survive; one family, the Baltoceratidae, does continue. The Middle Ordovician contains three new families, the Cyrtocerinidae, the Shideleroceratidae, and Bathmoceratidae, though formerly there were some questions of correlation concerning the beds yielding *Bathmoceras.* Of the Tarphyceratida, two families, the Bassleroceratidae and the Tarphyceratidae, disappear; the Trocholitidae continue; and the Lituitidae probably are completely post-Ordovician.

In the Endoceratida, changes are less marked because major taxonomic groups still are rather generalized, but the close of the Canadian marks the decline of the Proterocameroceratidae, a few of which persist into the Chazyan; the disappearance of the Manchuroceratidae; and the decline of the Piloceratidae, with the Silurian genus *Humeoceras,* known from three species and less than a dozen specimens, being the sole known post-Canadian survivor of that family. The Chazyan is marked by the appearance of the Endoceratidae, the Emmonsoceratidae, and the Allotrioceratidae, with the Cyrtendoceratidae coming from beds rather broadly classed as Chazyan in Europe.

In the Michelinoceratida, we have the sparse beginnings of two families, the Michelinoceratidae and the Troedssonellidae, in the Canadian. In the Chazyan they are diverse and are augmented by the Allumettoceratidae, the Proteoceratidae, and the Clinoceratidae.

The remarkable genus *Ecdyceras,* sole occupant of the Ecdyceratida, also appears. Collins' (1967) claim that the phragmocone described for this genus (Flower, 1961) actually is an endoceroid siphuncle cannot be right, since it is enclosed in the unique lamellar conch of the genus. His interpretation of the siphuncle as a commensal worm tube is opposed by (1) the position of the siphuncle in the plane of symmetry and (2) its position well away from the juncture of the conch and the mural parts of the septa, where all other known commensal worms occur.

Orders appearing for the first time in the Chazyan include (1) the Ascoceratida, represented by the Hebetoceratidae, (2) the Oncoceratida, represented by the Graciloceratidae, Oncoceratidae, and Valcouroceratidae, (3) the Barrandeoceratida, represented by the Plectoceratidae and Barrandeoceratidae, and (4) the Discosorida, represented by the Ruedemannoceratidae. Even assuming a more imperfect knowledge of cepha-

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lopod occurrences than seems reasonable, a time break is needed, not so much for the extinction and decline of the dominant Canadian lineages as for the diversification of those which appear in the Chazyan.

Cooper (1956) proposed the Whiterock Stage as occupying the Canadian-Chazyan hiatus. It was a matter of particular interest to ascertain which forms were (1) survivors of Canadian stocks unknown in the Chazyan, (2) beginnings of stocks formerly thought to have begun in the Chazyan, (3) continuations of lineages known from both intervals, and (4) distinctive genera common to the three regions in which the Whiterock is known in North America; also, it was of interest to determine to what extent the genera suggested equivalance with the Whiterock of beds in other continents.

The Whiterock cephalopods known so far fall into these categories, as shown in the following summary by orders. It must be noted that in approaching fossils of a time interval only recently recognized, and in which the fossils have largely escaped description until recently, one should be prepared to find the beginnings of some genera formerly known only from Chazyan or younger beds. The presence of such forms is not necessarily an indication of Chazyan age. Indeed, it is surprising that so few cephalopod genera are common to the Whiterock and the Chazyan.

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Order ELLESMEROCERATIDA

As noted under the generic discussion (below), *Meikeloceras,* new genus, is the youngest known survivor of the Ellesmeroceratidae, which dominate the Lower Canadian and are sparse in both the Middle and Upper Canadian. The Protocycloceratidae, Cyclostomiceratidae, Eothinoceratidae, and Apocrinoceratidae are unknown above the top of the Canadian. The Baltoceratidae continue, and seemingly *Cyptendoceras* and *Rhabdiferoceras* are represented by quite similar species in the late Canadian and in the Whiterock Stage. *Cyptendoceras* is possibly the ancestor of *Murrayoceras,* known from the Marmor through the Wilderness Stages; and *Cartersoceras,* known only from the Wilderness Stage, may be a modification either of *Murrayoceras* or *Rhabdiferoceras.*

The exact position of the beds yielding *Baltoceras, Eobactrites,* and *Bactroceras* in the eastern hemisphere has been a matter of perplexingly different opinions. The writer suggests that they are largely, if not completely, Whiterock equivalents. The American forms include one species of *Bactroceras* from the lower Antelope Valley Limestone and one of *Baltoceras* from the sponge beds of Ikes Canyon of Nevada and another species of *Baltoceras* from the Day Point Limestone of the Champlain Valley, which the writer believes is better placed faunally with the Whiterock below than with the Chazyan (Crown Point and Valcour Limestones) above. Certainly all of the three genera occupy a rather short time-span in the early post-Canadian.

Recent observations suggest that the beds yielding *Bathmoceras* (the Sarka of Bohemia and the Kunda of the Baltic) are of Whiterock rather than late Canadian age. Sweet (1958) described *B. norvegicum* from the *Orthoceras* shale of Norway, which is younger, as he has indicated. *B. norvegicum* is an exogastric shell and, for that reason, might well represent a new genus.

The Cyrtocerinidae are known to range from Black River to Richmond, and the Shideleroceratidae are known only in the Richmond. Their connection with Canadian ancestors must be through species as yet unknown.

Meikeloceras, new genus

Diagnosis.—The shell is an endogastric cyrtocone, moderately rapidly expanding, with a section more broadly rounded ventrally than dorsally, slightly higher than wide in the young, width equal to or slightly greater than the height in the adult. Sutures show lateral lobes, even where the section is broad, but do not slope conspicuously forward on the dorsum. Septa are very close. The ventral siphuncle shows faintly concave segments of ellesmeroceroid aspect, with vestigial necks and moderately thick rings; its interior is abundantly supplied with diaphragms. The siphuncle expands in diameter more rapidly than does the conch. The shell is smooth, and the aperture is not contracted.

Type-species.—*Meikeloceras parvum,* new species.

Discussion.—In form this genus resembles *Levisoceras* in general aspect, except for the broadening of the cross section. The Middle Canadian *Cumber-*

loceras is somewhat similar in form and in the rapid enlargement of the siphuncle, but shells are compressed in section and conspicuously costate. *Clelandoceras* of the Upper Canadian is similar in that the cross section is more narrowly rounded dorsally than ventrally, but is a tiny, strongly compressed shell. *Oelandoceras,* of the Glauconitkalk of the Baltic region, is a much larger shell, with the section higher than wide, and is more gently expanding.

As has been noted (Flower, 1954), the nucleus of the Ellesmeroceratida is found in the Lower Canadian, where 25 of the known genera occur. In addition, *Robsonoceras,* which is of doubtful position, may well come from the lower *Kainella-Leiostegium* beds, now assigned to the Lower Canadian. *Beekmanoceras* is known from one Middle Canadian species, and *Cumberloceras* ranges from the Demingian into the Jeffersonian. The Cassinian has yielded *Copiceras* and *Clelandoceras;* and *Oelandoceras* probably is late Canadian. *Meikeloceras* is the youngest member of the family so far known; only the type-species is recognized.

Meikeloceras parvum, new species

PLATE 2: FIGURE 11

DESCRIPTION.—The shell has the characteristics of the genus. The holotype is a specimen exposed in a section slightly oblique to the plane of symmetry but nearly vertical. It shows a cyrtoconic shell expanding in a phragmocone of 14 mm, from 2 mm to 11 mm in height, containing 22 camerae. The siphuncle increases in height from 1 mm to 3 mm. The living chamber has a dorsal length of 11 mm and increases to 13 mm in height. Only one side of the cut is here illustrated.

A paratype (not figured) is an incomplete specimen 14 mm long, showing an increase within 8 mm from a section of 3 mm and 5 mm, slightly compressed—the dorsum more narrowly rounded than the venter—to a width of 8 mm and a height of 7 mm.

TYPES.—Holotype and paratype, RHF 1358 (in collection of the writer), from biohermal limestones, low in the Antelope Valley Limestone of Meikeljohn Peak, Bare Mountain Quadrangle, Nevada (see Ross, 1964, pp. C24ff).

Order ENDOCERATIDA

The Endoceratida begin with the Proterocameroceratidae, slender forms with short septal necks. In the Canadian are recognized also the Thylacoceratidae, forms with small siphuncles and longer necks; the breviconic Piloceratidae; and the Manchuroceratidae. The Chazyan contains survivors of the Proterocameroceratidae; with more knowledge, more of these forms possibly will be placed in derived families as yet undefined. Extensive material of the endoceroids in the Whiterock remains to be studied, but *Najaceras,* new genus, seems to be the first of the true Endoceratidae; *Williamsoceras* and *Cacheoceras* are the oldest of the Allotrioceratidae, suggesting an origin in *Coreanoceras* of the Canadian Manchuroceratidae; and *Juaboceras* is intermediate between the Canadian Manchuroceratidae and the Chazyan *Emmonsoceras. Williamsoceras,* or a new allied genus, is represented in the Baltic. Mutvei (1964, pl. 5, fig. 8; pl. 6, fig. 1) has figured specimens such as *Dideroceras wahlenbergi* (Foord) of the Oetinkian (Raniceps Limestone) and others, such as *Nanno belemnitiforme* (Holm), from the Aseri Stage. Some material attributed to the later species is that described by Holm (1885) as *Endoceras gladius.*

Najaceras, new genus, is the forerunner of the Chazyan *Meniscoceras;* possibly these two genera should be set apart in a family distinct from the Proterocameroceratidae. *Rossoceras,* apparently allied to the "Interjoceratina," is characteristic. Though the Piloceratidae are unknown in Whiterock or Marmor beds, or from any higher strata in the Ordovician, *Humeoceras* of the early Middle Silurian is a descendant of *Piloceras* and is very close to it in all known structures. Flower (1968b, p. 20) had noted a form from Newfoundland reminiscent of the Canadian genus *Oderoceras,* but additional material has shown that this form is a slightly endogastric shell allied to *Kiotoceras,* new genus, but distinct from *"Orthoceras insulare"* Barrande.

Kiotoceras, new genus

DIAGNOSIS.—This genus is a slender endoceroid, with the shell slender and straight and with sutures transverse except close to the siphuncle, where they form deep lobes; the siphuncle is in broad contact with the venter and usually is conspicuously flattened there. The siphuncle wall is holochoanitic. The genus is characterized mainly by the endosiphuncle, which extends forward on the dorsum, grows laterally, and has its ventral closure sometimes lying appreciably apicad of its anterior dorsal limit. The speiss becomes depressed (rarely, it is hexagonal anteriorly) and then becomes rectilinear, terminating in an extremely small transverse tube, from the corners of which four blades extend toward the siphuncle margin. The tube may be subcentral in late growth stages, but it is well ventrad of the center apically. Exposed siphuncles are characterized by septal ridges that are steep laterally, describing broad saddles over the flattened venter and lobes on the dorsum.

TYPE-SPECIES.—*Kiotoceras quadratum,* new species.

DISCUSSION.—This genus is characteristic of the Whiterock Stage. The type-species is from the Oil Creek Limestone of Oklahoma, from which there are two additional species not now described. The genus occurs in the high Kanosh of western Utah, in the lower part of Zone N, and in the upper part of Zone N, in the Lehman Limestone. Also, it has been found in Zone N in the Ely Springs Range of Nevada. It occurs in the Table Head Limestone of Newfoundland, where it is represented by most, if not all, of the specimens which Barrande (1870, pl. 430, figs. 1–11; pl. 431, figs. 1–10) figured and described as *Orthoceras insulare.*

Siphuncles showing good septal ridges of similar aspect are found in *Rossoceras,* where the endosiphuncle is very different. In addition, though we have seen no specimens thus preserved, the exterior of siphuncles of *Najaceras* may be quite similar. Phragmocones failing to show the septal necks of the endosiphuncle cannot be distinguished with certainty. *Cyptendoceras* of the Baltoceratidae is very similar in aspect.

The genus is known only from the Whiterock Stage of Utah, Nevada, Oklahoma, and Newfoundland.

Kiotoceras quadratum, **new species**

PLATE 1: FIGURES 1–8, 10

DESCRIPTION.—A large, straight endoceroid of depressed section, with transverse sutures sloping apicad, where they approach the sides of the siphuncle, which is in broad contact with the ventral wall of the shell. The holotype is a somewhat crushed part of a phragmocone of 200 mm in which the siphuncle is 14 mm high and 21 mm wide, in a shell 36 mm wide and with an estimated height of 24 mm, expanding to a siphuncle 24 mm high, 34 mm wide, in a shell 63 mm wide and an estimated 55–60 mm high. Camerae are very short, averaging 4 mm in length apically and 6 mm adorally. A thin-section shows the siphuncle wall to be holochoanitic. A cross section at the break near the anterior end of the holotype (Plate 1: figure 2) shows the endosiphuncle thin and developed only dorsally and laterally. A second break, 44 mm farther apicad (Plate 1: figure 3) shows a cone with four sharp angles and with two obscure angles at the top and bottom, making the section obscurely hexagonal. In another 18 mm, the section shown as figure 4 of Plate 1 is attained; here the cone is rectilinear, with the top and bottom faintly convex, and traces of four blades coming from the four corners are obscurely indicated. Apicad of this region lies the longitudinal section (Plate 1: figure 10, which shows the maximum width of neither the shell nor of the siphuncle). A part of the surface opposing this section was used in making a thin-section. Just orad of that region another cross section (Plate 1: figure 5) was cut; here there is a small quadrangular tube with four straightblades extending from its corners, better shown in an enlargement (Plate 1: figure 6).

A paratype (Plate 1: figures 7, 8) shows strongly oblique septal ridges (in lateral view) that arch across the strongly flattened venter. At the anterior end of this specimen, the endosiphuncle presents an appearance much like that the one shown in Plate 1: figure 2.

TYPES.—Holotype, USNM 162058, from the upper quarter of the Oil Creek Limestone, West Spring Creek, three miles east of Poolville, Oklahoma. Paratype, USNM 162059, from "Basal Simpson," four to five miles southeast of Daugherty, Oklahoma.

Najaceras, new genus

DIAGNOSIS.—This genus is a slender, straight, smooth endoceroid, depressed in section, with the siphuncle commonly in broad contact with the venter and with sutures forming a ventral lobe close to the siphuncle but elsewhere transverse. The siphuncle wall is holochoanitic; the apex is blunt, straight ventrally, expanding and convex dorsally and laterally, but not swollen, and then contracted as in *Nanno.* The endosiphuncle supplies the main features of the genus, beginning with a dorsal process, convex and projecting into the cavity of the siphuncle but developing a narrow median emargination as it grows. Beyond sharp lateral angles, the endosiphuncle then expands down along the sides but is rather massive dorsally before its two sides finally close on the venter. The speiss tends to be concave dorsally except for a faint median ridge and is somewhat triangular in section. A blade forming an axis of the dorsal process is bifurcated once (or even twice) close to the dorsal margin. A strong infula develops, and apicad of the speiss is a small median tube that is hardly larger or more conspicuous than discrete beadlike elements along the length of the infula, which are partly and imperfectly preserved sheaths but which in cross section may appear as discrete tubes—some rounded, some triangular—with the long apex directed laterally, the base toward the final tube. Oddly, the dorsal blade may show a very similar structure.

TYPE-SPECIES.—*Najaceras triangulatum,* new species.

DISCUSSION.—Vexingly, without the endosiphuncle, phragmocones of this genus cannot be distinguished with certainty from those of *Kiotoceras,* new genus, with which it is associated. The genus is closely related to the Chazyan *Meniscoceras* but differs from it mainly in that the dorsal process extends convexly into the siphuncle (in cross section) so that the speiss is at all times concave dorsally; in *Meniscoceras* it is transverse until the dorsal half of the siphuncle is filled by the calcareous material. It has been suggested elsewhere that *Meniscoceras* is not holochoanitic—an opinion which rests upon a rather poor thin-section and which, in view of the long necks of this genus, now seems suspect. Endosiphuncles apicad of the speiss resemble those of *Williamsoceras* in cross section, except that they are upside down. It therefore is necessary to ascertain the orientation of siphuncles, which commonly is at the flattening of the siphuncle wall where it lies against the ventral wall of the shell.

The genus takes its name from the "naja," the crescent that is placed at the bottom of the Navajo squash-blossom or wedding necklace.

Najaceras triangulatum, new species

PLATE 2: FIGURES 1–3, 8, 9

DESCRIPTION. The holotype, here illustrated only by a series of cross sections, is a part of a slender phragmocone of depressed section with a rather depressed siphuncle in broad contact with the venter. The sutures are transverse over most of the shell but slope apicad close to the siphuncle. The type is 86 mm long, expanding from 30 mm and 46 mm to 37 mm and 50 mm; and its siphuncle expands from 20 mm and 24 mm to an estimated height of 20 mm and a width of 27 mm. Camerae average 5 mm in length. A section near the anterior end (Plate 2: figure 1) shows the dorsal process of the endosiphuncle as an almost semicircular calcareous body. A second section, 26 mm farther apicad, shows this body larger; and a third section, 26 mm still farther apicad, shows the endosiphuncle growing down around the sides, leaving the speiss as a triangular cavity, with the dorsal wall concave and each of the lateral walls sinuate. At the very apex, the cavity is smaller but similar in shape. The sections show—in spite of some replacement—an infula curving up from the angles of the speiss and an axis in the dorsal process which is bifurcated above.

A paratype that is part of a siphuncle shows a blunt apex of the aspect of *Cameroceras,* beyond which the siphuncle is slender. It expands from 9 mm high and 12 mm wide (the apex missing) to 18 mm and 24 mm in a length of 20 mm. The venter is straight, with the sides and dorsum oblique and convex. In the remaining 60 mm, the siphuncle becomes 22 mm high and 27 mm wide. This specimen represents a part of the endosiphuncle apicad of the speiss, or endocone, and shows in several sections an infula curving across the venter and reaching the margin dorsolaterally. The dorsal process shows an axis which is Y-shaped, dividing into two curved arms above. Some sections show traces of incompletley preserved bands in the dorsal process. A section at the anterior end is illustrated (Plate 2: figure 9).

The proportions and the subtriangular cross section of the endosiphocone characterize this species.

TYPES.—Holotype USNM 162062 and paratype USNM 162063, both from the upper fourth of the Oil Creek Limestone, West Spring Creek, three miles east of Poolville, Oklahoma.

Najaceras bilobatum, new species

PLATE 2: FIGURES 4–6

DESCRIPTION.—This large species, similar to *N. triangulatum* in general aspect, is distinguished by the emargination of the dorsal process of the endosiphuncle so that it has a bilobed appearance in cross section. (Only cross sections are illustrated.) The holotype is part of a phragmocone that increases from a height of 48 mm to 56 mm and from a width of 64 mm to 72 mm, with a siphuncle increasing from 28 mm and 32 mm to 30 mm and 37 mm in a length of 120 mm. The septum at the base is deeply curved, having a depth of 17 mm, which is more than half the shell width. Camerae in this part of the shell average 8 mm long. An anterior section with the bilobed dorsal process beginning to curve down at the sides is shown in Plate 2: figure 4. A more apical section (Plate 2: figure 4) shows the downward extension of the endosiphuncle more advanced at the sides. Figure 6 of Plate 2 shows an apical section in which the cone is enclosed—a small lens-shaped mass, from the ends of which the infula curves up toward the dorsum. Traces of the Y-shaped axis of the dorsal process are shown.

A paratype (not figured) shows 70 mm of a phragmocone expanding from 49 mm and 54 mm to 50 mm and 60 mm, with a siphuncle that is 24 mm and 30 mm at the base. Five camerae occur in 15 mm. The siphuncle here contained lies apicad of the endosiphocone, showing the infula and the Y-shaped axis of the dorsal process with the upper limbs convex.

The different proportions, the large size, and the bilobed dorsal process distinguish this species from *Najaceras triangulatum.*

TYPES.—Holotype and paratype (USNM 162065–6) are from the upper fourth of the Oil Creek Limestone, West Spring Creek, three miles east of Poolville, Oklahoma.

Najaceras chevroniferum, new species

PLATE 1: FIGURE 9; PLATE 2: FIGURE 10

DESCRIPTION.—The type is an isolated endosiphuncle, slender down to a much smaller dimension than the blunt apex of *Najaceras triangulatum* and much smaller than any known specimens of *N. bilobatum.* It is figured and described here mainly to show a remarkable phase of preservation. It is an endosiphuncle, 173 mm long, partly enclosed in matrix, and expanding from 14 mm and 18 mm to an estimated height of 15 mm and a width of 21 mm. The exposed surface shows color-differentiated, chevron-like bands, which posed a problem in interpretation until the preceding species and the features of *Najaceras* were recognized. The exposed surface is dorsal, and the chevron-like markings point orad, marking sheaths in the dorsal process of a *Najaceras.* Sections cut at either end show the infula; and, although there is advanced replacement, fine blades are apparent in the dorsal process and also in part of the endosiphuncle below the infula.

TYPE.—The holotype, USNM 162067, is from the lower Simpson Group, from "greenish shale below the third sandstone," Joins or Oil Creek Limestone (probably the latter), from Henryhouse Creek, Oklahoma.

Order ACTINOCERATIDA

As discussed previously (Flower, 1968a), the family Wutinoceratidae is confined to beds of Whiterock age in Utah, Nevada, Oklahoma, and the Table Head of Newfoundland. Related forms suggest Whiterock equivalence of the Vaginatum Limestone and the overlying Aserian of the Baltic, the Wuting of Manchuria, and an unnamed limestone in Tasmania. Some doubt surrounds the equivalence of the Maruyama Limestone, which yielded the ancestral *Maruyamaceras,* but it is either latest Canadian or early Whiterock. In Utah and Nevada, the Wutinoceratidae occur rather high in the section—in the *Palliseria* beds of Nevada, and in the Lehman and possibly in the upper Kanosh in Utah.

Order MICHELINOCERATIDA

By-passing nomenclatorial problems and differences in interpretation that have been discussed earlier (Flower, 1968b), the late Canadian has yielded *Michelinoceras* with cameral deposits and annuli in the siphuncle. Forms of this aspect are now known as low as the *Ceratopea ankylosa* zone of the El Paso, which is equivalent to the Cotter of eastern North America. *Michelinoceras primum* is from the lower part of the Scenic Drive, of Fort Cassin equivalence, and

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PLATE 1: figures 1–6, 10.—*Kiotoceras quadratum,* new species; holotype, USNM 162058, from upper quarter of the Oil Creek Limestone, West Spring Creek, three miles east of Poolville, Oklahoma: 1, ventral view of complete specimen (approximately × 0.33); 2, siphuncle at break near anterior end, showing speiss enclosed only dorsally and laterally (× 1); 3, cross section farther apicad, speiss rectilinear and obscurely hexagonal (× 1); 4, cross section farther apicad, showing speiss rectilinear (× 1); 5, cross section near apex (× 1); 6, same section enlarged, showing small rectilinear tube and bases of four blades (× 2); 10, transverse longitudinal section from apical part (× 1).

Figures 7, 8.—*Kiotoceras quadratum,* new species; paratype, USNM 162059, from "Basal Simpson Group," four to five miles southeast of Daugherty, Oklahoma: lateral and ventral views (× 1) showing course of septal ridges, the section at the anterior end being comparable to that shown in figure 2.

Figure 9.—*Najaceras chevroniferum,* new species; holotype, USNM 162067, from Simpson Group, "greenish shale below the third sandstone," Henryhouse Creek, Oklahoma: dorsum of an incompletely exposed endosiphuncle with chevrons marking growth lines around the dorsal process (× 1).

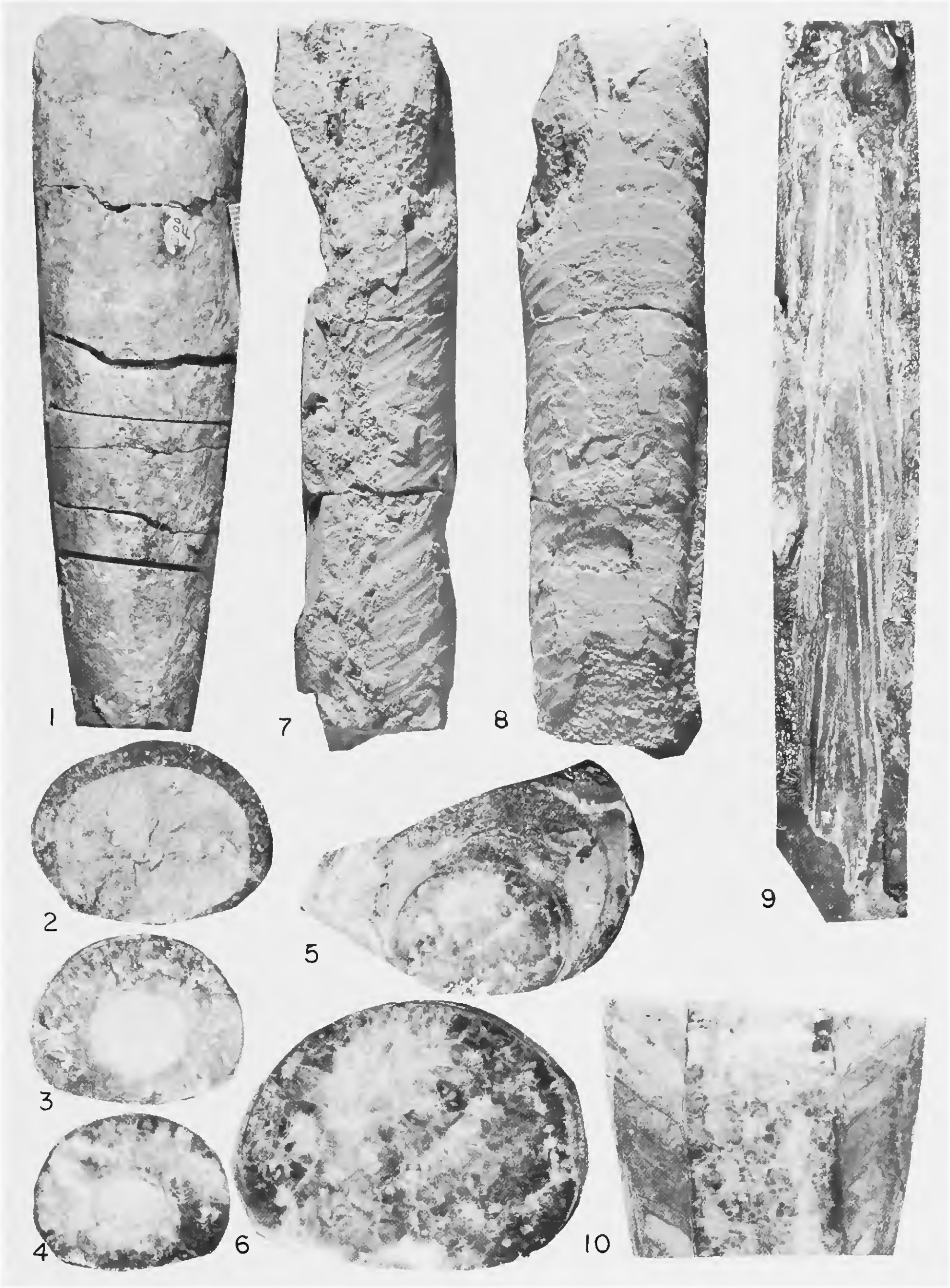

PLATE 1

either Zone H or Zone I of Ross (1951) and of Hintze (1951). Undescribed material shows the presence of similar forms in the Florida Mountain Formation of the El Paso Group and in the Wahwah Limestone of Utah. *Buttsoceras,* the first of the Troedssonellidae, michelinoceroids with a lining of thin growth increments in the siphuncle, occurs in the latest Canadian, the Odenville of Alabama, the Florida Mountain Formation of the El Paso Group, the highest Arbuckle of Oklahoma, the high Garden City, and the Wahwah Limestone (Zones J and K) of Utah. Both the Michelinoceratidae and the Troedssonellidae continue into the Whiterock, where they are joined by a group of species with tubular siphuncles and with cameral and siphonal deposits greatly retarded, in some cases perhaps obliterated. For such forms, which include *Orthoceras regulare, Sinoceras, Nevadaceras,* and *Aethiosolen,* it would seem desirable to use a family name, and extension of the Orthoceratidae for such use might be appropriate. What is significant is that these forms occur in the Whiterock. They are the dominant "*Orthoceras*" of the *Orthoceras* Limestone, continuing into the Chazyan, where they are joined by forms of more advanced families, notably of the Proteoceratidae and Tripteroceratidae. Astonishingly, the Michelinoceratida, with tubular siphuncles, seem to be minor constituents of later Ordovician faunas in both Europe and North America. *Clinoceras* is from probable Whiterock equivalents in the Baltic.

Order ASCOCERATIDA

Flower (1941) suggested that *Clinoceras* was the possible ancestor of the Ascoceratida (then called the Mixochoanites). Jaanusson (1960) lists this genus as occurring in the Lasnamägian, which contains cephalopods suggestive of the Whiterock. The first of the true Ascoceratida, *Montyoceras* and *Hebetoceras,* are unknown prior to the Chazy Limestone. *Redpathoceras* of the Black River of Quebec supplies a connection between the slender, truncated Hebetoceratinae and the inflated *Probillingsites* of the later Ordovician.

Order TARPHYCERATIDA

The first family of this order, the Bassleroceratidae, ranges from early Middle to late Upper Canadian. The Tarphyceratidae have the same range. The Trocholitidae appear in the Jeffersonian, expand in the late Canadian, and continue through the Ordovician—the youngest genus being the Silurian *Graftonoceras,* which is somewhat isolated stratigraphically. As now interpreted, *Litoceras* is a genus peculiar to the Whiterock, known from Utah, Nevada, Oklahoma, and Newfoundland. *Plectolites,* first described from Nevada, is represented in the Table Head of Newfoundland by *Trochoceras incipiens* Barrande (1870, pl. 433, figs. 1–5). True *Trocholites* ranges from the Chazyan to the Richmond. The *Discoceras perornatus* described from the Whiterock may well prove to be a distinct genus, but it can be separated only on the assumption, not clearly demonstrable at present, that similar frills apparently are absent in *Discoceras* because of the mode of preservation. The Lituitidae, known only from Europe and Asia, probably begin in the Whiterock, where they show their widest development.

Order BARRANDEOCERATIDA

No forms of Barrandeoceratida are known in the Whiterock, though it would seem logical that *Plectoceras* is derived by thinning of the ring from the Ca-

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PLATE 2: figures 1–3.—*Najaceras triangulatum,* new species. Cross sections (× 1) of holotype, USNM, 162062, from upper quarter of the Oil Creek Limestone, West Spring Creek, three miles east of Poolville, Oklahoma: 1, anterior, showing dorsal process; 2, median, showing dorsal process enlarged; 3, apical, showing dorsal process larger and endosiphuncle extending downward laterally.

Figures 4–6.—*Najaceras bilobatum,* new species. Cross sections (× 1) of siphuncle of holotype, USNM 162065, from same horizon and locality as preceding: 4, anterior, showing bilobed dorsal process; 5, showing endosiphuncle more advanced, extending down the sides, but with the endosiphocone still open below; 6, more apical, showing crescentic cone with traces of infula and axis of the dorsal process.

Figure 7.—*Kiotoceras* sp.; USNM 162061, from same horizon and locality as preceding: transverse break across siphuncle showing endosiphuncle wanting ventrally (× 1).

Figures 8, 9.—*Najaceras triangulatum,* new species; paratype, USNM 162063, from same horizon and locality as preceding: 8, apical part of siphuncle showing blunt apex, venter on left (× 1); 9, cross section at anterior end showing infula and axis of dorsal process bifurcated above (× 2).

Figure 10.—*Najaceras chevroniferum,* new species; holotype (see figure 9 of Plate 1): cross section (× 2.5) near apical end, showing infula and rays in endosiphuncle.

Figure 11.—*Meikeloceras parvum,* new species; holotype, RHF 1358, from Antelope Valley Limestone, lower biohermal beds, Meikeljohn Peak, near Beatty, Nevada: nearly vertical section, venter on left (× 2.5).

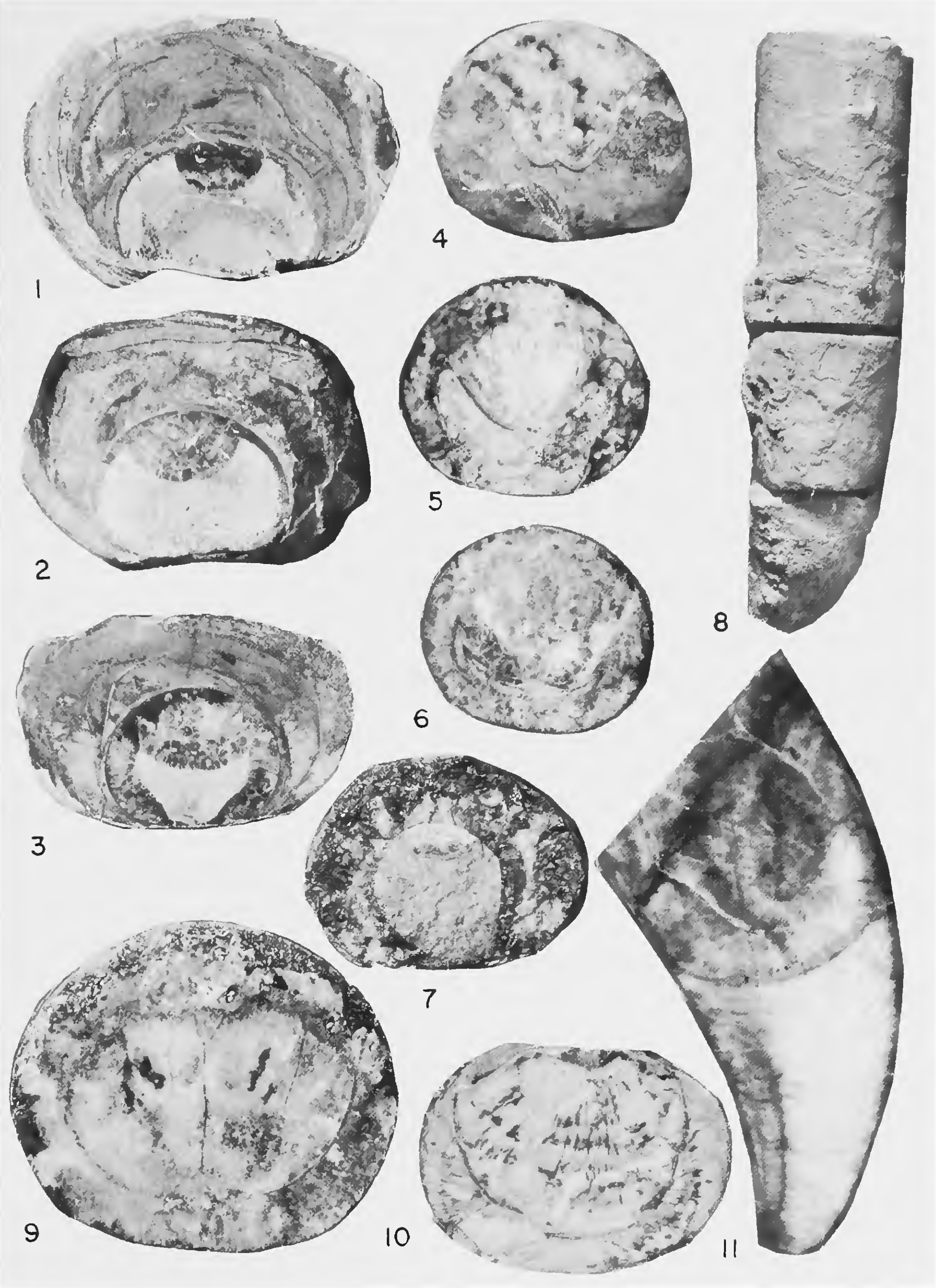

PLATE 2

nadian *Campbelloceras* and the allied *Alaskoceras*. In the Chazy Limestone are found *Plectoceras* and *Avilionella* of the Plectoceratidae and *Barrandeoceras* and *Centrocyrtoceras* of the Barrandeoceratidae.

Order ONCOCERATIDA

The Graciloceratidae, the archaic family of this order, is regarded as intermediate between the ancestral Bassleroceratidae of the Canadian and the more advanced families, Valcouroceratidae and Oncoceratidae—with expanded siphuncle segments—of the Chazyan. *Leonardoceras* of the Whiterock possibly is the archaic genus of the Graciloceratidae, having much the form of the ancestral *Bassleroceras*. A more specialized genus of the Whiterock is *Ikesoceras*. Recently, the Lehman Limestone yielded an apparent *Graciloceras*, a crushed brevicone with inflated siphuncle segments, that belongs either to the Valcouroceratidae or the Oncoceratidae, and a small shell of the aspect of *Diestoceras*. Too much emphasis must not be placed on the presence of these more advanced types here; identity of small and large *Diestoceras* is an assumption, and the origin of the family is as yet unproved. We cannot demonstrate that the small shell is an oncoceroid rather than a specialization of the discosorids.

Order DISCOSORIDA

As has been pointed out (Flower and Teichert, 1957), the early stages of *Ruedemannoceras* suggest an origin in the family Plectronoceratidae, known only from the Trempealeauan and the early Gasconadian (Wanwanian) of Manchuria. One fragmentary *Ruedemannoceras* has been illustrated from the Whiterock of Nevada (Flower, 1964b). Ancestral forms in the Middle and Upper Canadian connecting the Ruedemannoceratidae with their ancestors morphologically and stratigraphically are as yet unknown.

Elkanoceras, new genus

Diagnosis.—Similar to *Ruedemannoceras* except that the siphuncle lies slightly removed from the convex side of the shell.

Type-species.—*Lituites pluto* Billings 1865, from Table Head Limestone, Newfoundland.

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Robert B. Neuman

An Early Middle Ordovician Brachiopod Assemblage from Maine, New Brunswick, and Northern Newfoundland

ABSTRACT

Brachiopods from rocks largely of volcanic composition in Maine, New Brunswick, and Newfoundland include several genera not heretofore found in North America and not known to occur together anywhere.

Of fifteen genera identified, four are newly described herein: a clitambonitid, *Fistulogonites;* an orthid, *Munhella;* a syntrophid, *Rugostrophia;* and a probable plectambonitid, *Schedophyla.* If previously recorded ranges of established genera and genera most closely related to the new genera are averaged, a Whiterock or Llanvirn age for these rocks is indicated.

The abundance of volcanic rocks near the edge of the present continent and the diversity of the brachiopod stocks present, especially those represented by new genera, may be a record of volcanic islands at the border of Ordovician continental and oceanic masses.

An exotic assemblage of probable early Middle Ordovician (Whiterock) brachiopods occurs in the Shin Brook Formation in Maine and in its unnamed equivalents in central New Brunswick and northern Newfoundland (New World Island). Genera known so far only in this group of rocks include the clitambonitids *Platytoechia* (Neuman, 1964) from Maine and *Fistulogonites,* new genus, from Newfoundland; and the orthid *Munhella,* new genus, the syntrophid *Rugostrophia,* new genus, and the probable plectambonitid *Schedophyla,* new genus, all from New Brunswick.

Many new genera of several different distantly related stocks occur at the few localities that have been discovered. Other brachiopod genera that elsewhere occur at widely separated levels and in different geographic provinces occur together here. The occurrence of this suite near the edge of the continent in association with volcanic rocks seems to have special paleogeographic implications.

I am greatly indebted to several colleagues for their part in helping me to obtain collections and information from Canada. Professor Marshall Kay of Columbia University indicated the Newfoundland occurrence; funds that enabled me to collect there in 1966 were granted from the Charles D. and Mary Vaux Walcott Research Fund of the United States National Museum (USNM). L. M. Cumming of the Geological Survey of Canada (GSC) arranged for the loan of collections from his organization, and guidance to the localities and information concerning the geology in New Brunswick were supplied by R. R. Potter of the New Brunswick Department of Natural Resources and by F. C. Anderson of the Geological Survey of Canada. All type specimens have been deposited with the Geological Survey of Canada.

Geology of the Fossiliferous Rocks

Small, widely separated outcrop areas in Maine, New Brunswick, and Newfoundland have yielded the fossils under discussion here (Figure 1). The rocks, largely of volcanic composition and considerably deformed, are poorly exposed in most places, and knowledge of their stratigraphy is incomplete. The Shin Brook Formation in Maine is best known (Neuman, 1964);

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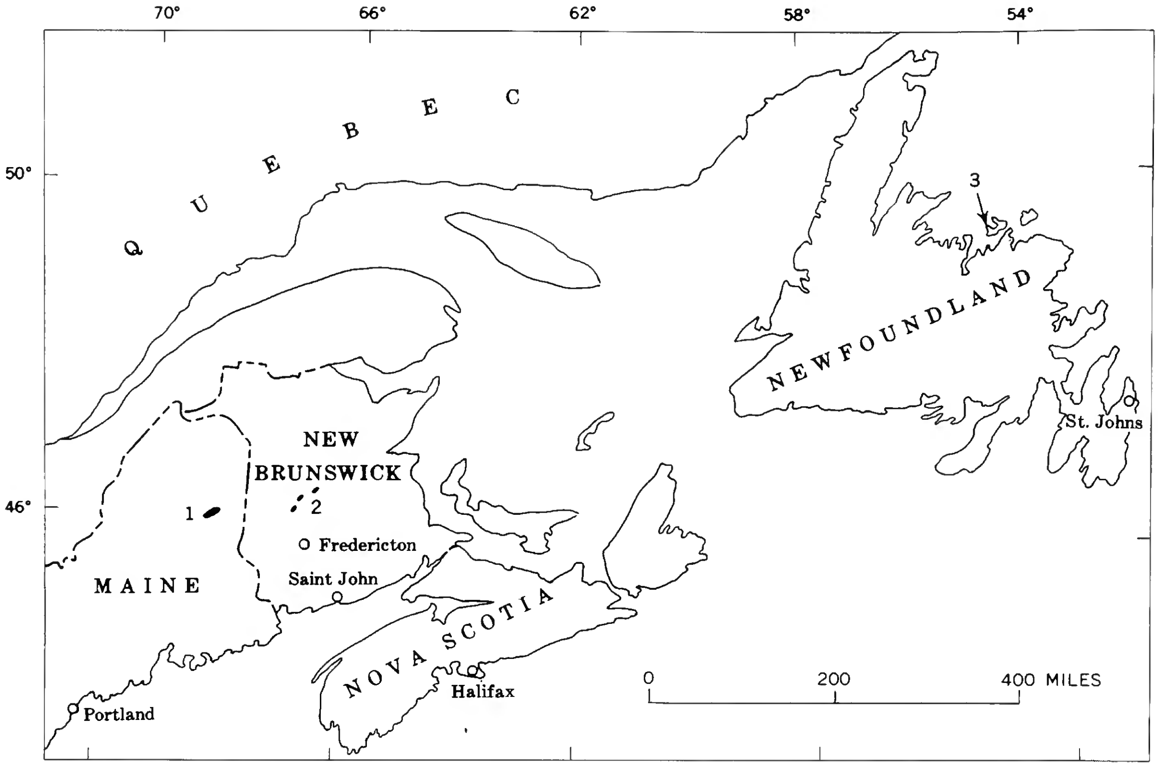

FIGURE 1.—Location of Shin Brook Formation in Maine (1) and of correlative rocks having similar fossils in New Brunswick (2) and on New World Island, Newfoundland (3).

it consists of tuff, tuffaceous sandstone and conglomerate, and lava flows aggregating about 1,000 feet in thickness and exposed for 14 miles on both flanks of a doubly plunging syncline. The Shin Brook unconformably overlies rocks of Early Cambrian(?)—late Precambrian or Early Cambrian—age, but its relations to younger fossiliferous rocks have not been observed.

Equivalent rocks in central New Brunswick are quartzitic siltstones with no apparent volcanic constituents; these rocks crop out in a complex of folds and faults in an anticlinal area 80 miles east of the Shin Brook outcrop area. Geologic relations of these rocks remain to be worked out definitively, although rocks similar to those in Maine of Early Cambrian(?) age beneath the Shin Brook Formation are present in the area as are carbonaceous slate and chert of Middle Ordovician age (Poole, 1963) containing *Climacograptus bicornis* (Poole, personal communication, 1968).

A distance of more than 700 miles separates these rocks in New Brunswick from similar equivalent rocks on New World Island, off the north coast of Newfoundland. The fossiliferous rock here is tuffaceous sandstone very similar to that of the Shin Brook Formation, apparently a minor component of a unit dominated by lava flows. The relations of rocks of this age to younger and older rocks are under study by G. S. Horne, of Wesleyan University, who has found limestone containing fossils like those under consideration here.

The present outcrop areas are probably erosion remnants of the thicker and more resistant parts of a more continuous body of sediment (Neuman, 1968, p. 40). In the same region, younger Ordovician volcanic-rich graywacke that contains brachiopods is locally interbedded or associated with more widespread dark, fine-grained rock that contains graptolites and other pelagic fossils; together these are evidence for deposition in a deep-sea basin of debris derived from volcanic islands. Although pelagic deposits of early Middle Ordovician age are presently known at only one place in the region of the volcanic rocks, a similar pattern of volcanic islands near the border of a deep-sea basin may have prevailed in this region at that time.

Age and Provincial Affinities of the Brachiopods

The rocks and their fossils at all three localities are considered to be of the same age because of the occurrence of similar if not identical species of three genera of brachiopods and the general similarity of the brachiopods at all three places. The age determination within the early half of the Ordovician is uncertain because the assemblage, at one place or in composite, cannot be matched with another assemblage anywhere else in the world and because brachiopod genera are present that are not known together elsewhere.

Ranges of previously described genera found in these rocks are plotted in Figure 2, together with ranges of genera most closely related to the four genera that so far are known only from these rocks. Recorded ranges of some genera in North America are considerably different from ranges elsewhere; most notable are the ranges of *Platystrophia* and (to a lesser degree) of *Productorthis, Valcourea,* and *Christiania,* all of which occur in older rocks outside North America.

The brachiopods and trilobites of the Shin Brook Formation (Neuman, 1964, p. E24; Whittington, in Neuman, 1964, p. E34) suggest a Whiterock age assignment. Such fossils as *Multispinula, Platystrophia, Christiania,* and *Eoplectodonta* suggest an age somewhat younger than Whiterock. The presence, however, of *Tritoechia* and the syntrophid *Rugostrophia* (which has affinities with the Late Cambrian genus *Huenellina*) provide arguments against the younger age.

Dating these rocks, therefore, depends upon which factors are considered of greatest validity in age assignment: the presence of distinctive genera whose uppermost range is elsewhere well established, the presence of equally distinctive genera whose lowermost range is well established, or consideration of the entire assemblage, which may require extending the ranges of both these "end-members." The last course seems best, and on this basis a Whiterock or Llanvirn age is indicated.

The early half of the Ordovician is characterized by provincial faunas, followed by increasing cosmopolitanism (Spjeldnaes, 1961, pp. 46–55; Whittington, 1966, pp. 697–698; Berry, 1967, pp. 420, 423). Two similar world-wide shelly provinces were recognized by both Spjeldnaes and Whittington, and further subdivisions of these were described by both authors. The degree of segregation that warrants classification into faunal provinces remains to be agreed upon. To divide the world conveniently into two parts at any time using any criteria seems overly simple; nevertheless, there seems to have been greater provincialism in marine faunas in the early half of the Ordovician than in the preceding part of the Cambrian and the later part of the Ordovician.

The contrast in geographic occurrence of some of the brachiopods is shown in Figure 2. The brachiopods

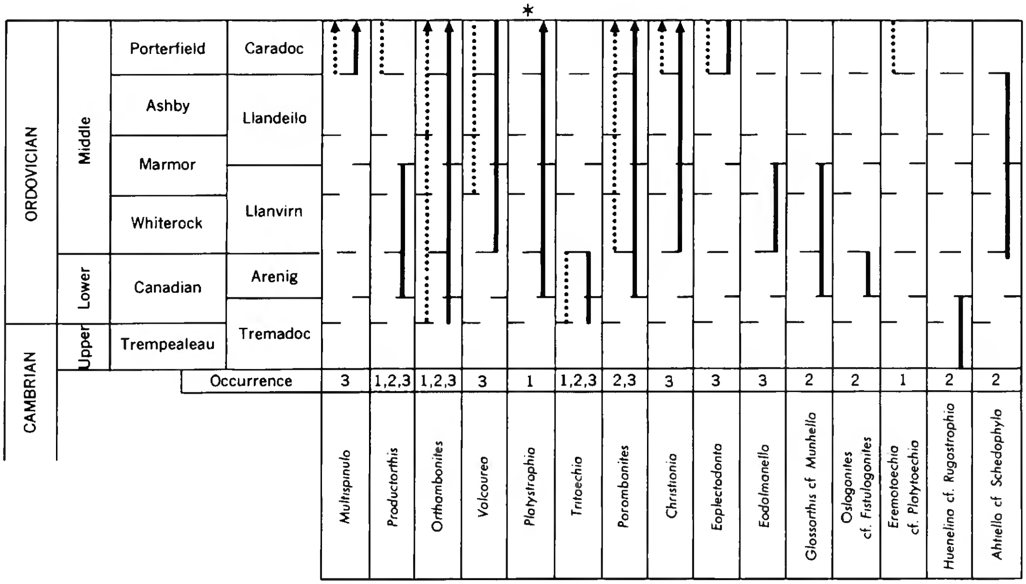

FIGURE 2.—Ranges of brachiopod genera that occur in the Shin Brook Formation and equivalent rocks in New Brunswick and Newfoundland, and genera most closely related to those known only from these rocks. Broken lines, North American ranges; solid lines, ranges outside of North America. Arrow indicates that range extends beyond limits of chart; asterisk indicates that range is entirely beyond limits of chart. Correlations after Whittington (1966, p. 700). Occurrences: 1, Shin Brook Formation, Maine; 2, New Brunswick localities; 3, New World Island, Newfoundland.

charted there include genera that are separated elsewhere not only by considerable stratigraphic intervals but also by geographical distances or provincial barriers not heretofore known to have been bridged. The trilobites from the same rocks represent a similar mixture (Whittington, 1966, pp. 709, 717). Thus, the fossils from the Shin Brook Formation and related rocks under discussion here blur the contrasts of the traditional faunal provinces.

In discussing the twofold clustering of early Caradocian brachiopod genera, Williams (in Moore, 1965, p. H241) suggested that the generic contrasts of the stocks of one cluster "are so different from their contemporaries that they must have had a long evolutionary history in an unidentified basin (or basins) which first became connected with the North American and European provinces during mid-Ordovician time."

The continental platforms and their margins now are so well known that there is little likelihood that such basins will be found on them. Continental areas and epeirogenic seas must have constituted then, as now, only a fraction of the earth's surface, perhaps only a minor fraction; the largest part was occupied by the oceans.

Much of the present boundary between continental and oceanic masses is characterized by active volcanism. By analogy with this kind of boundary, and because of its position near the edge of the present continent, the Shin Brook Formation and related rocks under discussion here may well be interpreted as a segment of the boundary between the true ocean and the continental margin; thus, their fossils may be a small sample of the fauna that evolved in truly oceanic waters. Islands in the open ocean are both isolated habitats of endemic organisms and stepping stones for migration. Because island flanks commonly slope steeply, habitats controlled by depth are telescoped, and deposits derived from the island flanks contain organisms from a wide range of environments.

The flanks of volcanic islands at the border of the oceans were the possible habitats of the root stocks of genera that found their way onto the continental platforms. Thus, one might expect island faunas to be more diversified than those of the platforms and to find on the islands both precursors and survivors of platform genera as well as genera that never became established on the continental platforms. The fossils of the Shin Brook Formation and related rocks are of special interest because they may be a small and incomplete sample of the oceanic realm.

Phylum BRACHIOPODA

Fistulogonites, new genus

Diagnosis.—A ventribiconvex clitambonitid having pitted costellae, lacking a cardinal process on the dorsal valve, and having a sessile pseudospondylium on the ventral valve.

Description.—Unequally convex shells, the ventral valve nearly pyramidal, three to four times deeper than the dorsal valve. Outline poorly known, probably semicircular, the maximum width at the slightly auriculate hingeline. Dorsal valve bears shallow sulcus, best defined in midpart of shell, that widens anteriorly so that anterior commissure is probably slightly sulcate. Ventral interarea high, about one-third the shell length, concave, apsacline. Delthyrium covered by arched pseudodeltidium that is closed, or possibly pierced at its apex by a tear-shaped foramen. Dorsal interarea relatively short, about one-third the length of that of the ventral interarea; notothyrium apparently unmodified, open. Ornament costellate, each costella bearing a row of very fine pits.

Dorsal interior has elevated notothyrial platform but no cardinal process; prominent median ridge extends forward from base of notothyrial platform to about midlength of valve. Brachiophore bases stout transverse blades that extend anterolaterally from margins of notothyrial platform without support; sockets poorly defined at the junction of the interarea with their posterolateral margins.

Ventral interior characterized by stout teeth underlain by thickenings along the inner margins of the delthyrium that converge near the floor of the valve to form a pseudospondylium whose anterior edge is slightly lifted above the floor of the valve. Posterior part of valve floor thickened to form a broad arch that disappears near midlength.

Discussion.—This monotypic genus is erected to contain the specimens assigned to *Fistulogonites novaterrensis*, new species, described below. It clearly belongs to the Clitambonitidina, but the presence or absence of pseudopunctae in these specimens cannot be determined. If this is a valid criterion for the distinction between the superfamilies Clitambonitacea and Gonambonitacea, the superfamilial assignment cannot be made at this time. The genus, however, possesses other features that are distinctive of genera assigned to the Gonambonitinae—features such as pitted costellae like those of *Estlandia* and a pseudospondylium like that of *Raunites.* The absence of a cardinal process suggests that the new genus is most closely related to *Oslogonites.*

Fistulogonites novaterrensis, new species

PLATE 1B

DESCRIPTION.—External and internal features of the species are the same as those of the genus described above, based on fragmentary and deformed internal and external molds of one dorsal valve and six ventral valves.

Costellae are angular, of varying width, wider than interspaces, spaced at about five per millimeter, and arise by branching at poorly defined successive generations. Pits very fine, less than 0.1 mm in diameter, deeper than wide, about 12 to 15 per millimeter. Growth lines at irregular intervals, considerably less conspicuous than radial ornament.

The measurements given below (in millimeters) are of preserved parts of specimens; the probable restored dimensions, if significantly different, are shown in parentheses:

GSC No., and part	*Length*	*Width*	*Thickness*
24776 (holotype): dorsal valve	4. 0	6. 0 (7. 2)	0. 8 (1. 0)
24777 (paratype): ventral exterior	8. 5	6. 5 (8. 5)	1. 5 (4. 5)
24778 (paratype): ventral exterior	5. 0	6. 3	3. 0 (4. 0)
24779 (paratype): ventral interior	6. 5	7. 2	2. 0 (3. 0)

OCCURRENCE.—Unnamed tuffaceous sandstone, Twillingate quadrangle, New World Island, Newfoundland, at the point on the geologic map of Williams (1963) indicated by *F* symbol, 0.5 mile northwest of Village Cove.

DISCUSSION.—The principal and unusual features of this species can be discerned despite the small number of specimens and their poor preservation. Although the species has features characteristic of gonambonitaceans, the absence of a species or genus with this combination of features indicates the necessity for a genus (herein erected) to contain it.

Congeners bearing a different density of costellae, or whose costellar pits are different in dimension or spacing probably will be placed in different species.

Munhella, new genus

DIAGNOSIS.—A dorsibiconvex costellate orthid having internal features similar to *Glossorthis.*

DESCRIPTION.—Dorsibiconvex to possibly convexoconcave shells known from a small number of incomplete and deformed specimens. Outline probably nearly semicircular, the maximum width at or near the hingeline. Ventral interarea short, apsacline; delthyrium open, unmodified. Dorsal interarea anacline, about one-third length of that of the ventral valve. Ornament costellate.

Ventral interior probably has stout teeth, short, erect, receding dental plates that project forward near the floor of the valve to form the posterolateral margins of the muscle field. Muscle field broadly triangular, the anterior margin broadly rounded, trilobate, and slightly elevated above the shell floor, the adductor scar depressed below the diductors and projecting slightly beyond them.

Dorsal interior has sockets floored by shallow excavations in shell tissue, bordered by divergent brachiophore bases. Notothyrial platform a thickening of shell that merges anteriorly with shell floor. Cardinal process thin, bladelike. Median ridge broad and rounded.

DISCUSSION.—This monotypic genus is erected to contain the specimens assigned to *Munhella cummingi,* new species, described below. It has all the features of the subfamily Orthinae, and in dorsal cardinalia, kind of ornament, and (probably) shape it is quite similar to Öpik's (1930, p. 82) genus *Glossorthis.* Its dorsibiconvex profile and differences in ventral muscle scars clearly set it apart from that genus. Although the outline and relative proportions of the ventral musculature are quite similar, that ventral musculature of *Glossorthis* rises anteriorly onto a medium septum, whereas that of *Munhella* has no median septum and is ankylosed to the shell floor.

Munhella cummingi, new species

PLATE 1A

DESCRIPTION.—External and internal features of the species are the same as those of the genus, described above, based on fragmentary and deformed internal and external molds of two articulated valves, eight dorsal valves, and ten ventral valves.

Shells large and shallow, wider than long. Dorsal valve has a broad shallow sulcus deepest near midlength, probably nearly extinguished at the anterior margin. Costellae angular, arise by branching and implantation in interspaces which are generally wider than costellae. Interspaces bear elevated growth lines. Costellae spaced at 7 to 10 per 5 mm around the anterior part of the valve, but finer and more crowded toward the cardinal extremities.

The measurements given below (in millimeters) are of preserved parts of specimens; probable restored dimensions are in parentheses:

GSC No., and part	*Length*	*Width*	*Thickness*
24781 (holotype):			
dorsal exterior	12.7	31.0	—
ventral exterior	17.0	27.0 (34.0)	—
internal mold	—	—	4.0
24782 (paratype):			
ventral interior	20.0	33.0	—
24783 (paratype):			
ventral exterior	18.2	29.5 (34.0)	—
internal mold	—	—	3.2
24784 (paratype):			
ventral exterior	18.2	31.0 (35.0)	—
24785 (paratype):			
dorsal interior	27.8	31.7	—

Occurrence.—Unnamed tuffaceous(?) siltstone within Unit 1, Napadogan quadrangle, York County, New Brunswick: Loc. *a,* at the point indicated by an *F* symbol on a tributary to Rocky Brook shown on map by Poole (1958), approximately 46°20′N, 66°56′W, includes collections made by Robb (1870, p. 190), L. M. Cumming, and the writer at or near the same point; and Loc. *b,* Middle Hayden Brook, 2,600 ft. northwest of its mouth, approximately 46°27′20″ N, 66°46′20″W.

Discussion.—Poor preservation prohibits observation of some features of this species, and some features and most dimensions have been modified by deformation. Deformation is particularly evident in the length-width ratios and in the outline of the shells, and it is confirmed by the appearance of the specimens. One specimen is nearly as wide as it is long, but most specimens are about one-third wider than long; original proportions probably lay somewhere between these extremes.

Relative depth of dorsal and ventral valves is consistent in all specimens examined, although this characteristic is exaggerated in some specimens by deformation. One specimen (Plate 1A, figures 7, 8) was deformed to the shape of a geniculated shell, a most unlikely form for an orthid.

Specimens assigned to this species from Robb's collections bear old labels identifying them as *Chonetes canadensis, Strophomena perplana,* and *Streptorhynchus*?, corresponding to names in the list attributed to Billings in Robb's report (1870, p. 190).

Rugostrophia, new genus

Diagnosis.—A costate huenellid having a pseudospondylium and lacking a cardinal process.

Description.—Dorsibiconvex shells, rounded in outline, the maximum width beyond midlength, and having deep ventral sulcus and correspondingly high dorsal fold so that the anterior commissure is strongly plicate. Ventral interarea apsacline, short, concave; delthyrium open. Dorsal interarea short, anacline to orthocline; notothyrium open. Shell surface ornamented by costae over entire surface, the costae strongest in the region of the fold and sulcus. Growth lines conspicuous in anterior part of shell, becoming rugose near the margins.

Ventral interior has short stubby teeth. Dental plates thick, erect, advancing to form lateral margins of pseudospondylium. Muscle field tripartite, the adductor scar elevated above the diductors and extending beyond them. Posterolateral shell floor has as many as five pairs of radial ridges.

Dorsal interior has brachiophore bases supported by shelflike plates that merge with the shell edge at the posterolateral extremities. Sockets broad and shallow. Notothyrial platform formed of thickened shell, wide, merges anteriorly with broad, low median ridge; cardinal process lacking. Adductor muscle scars deeply impressed, each nearly triangular, the posterior pair slightly larger than the anterior pair, more widely separated, and partly flanking them. Myophragm merges with sulcus at anterior termination of muscle scars at about midlength of shell.

Discussion.—This monotypic genus is erected to contain the specimens assigned to *Rugostrophia silvestris,* new species, described below. The simplicity of its internal features, especially the presence of a pseudospondylium and the absence of a cardinal process, together with its costate radial ornament, ally it with the more primitive huenellids, probably the Huenellinae. Of the costate genera assigned to that subfamily, it differs from *Huenella* in the lack of a cardinal process and from *Huenellina* in the lack of the lateral septa that characterize the dorsal valve of that genus; also, both of these genera have radial ornament of a kind quite different from that of *Rugostrophia*, new genus.

Rugostrophia silvestris, new species

FIGURE 3; PLATE 2B

DESCRIPTION.—External and internal features of the species are the same as those of the genus described above, based on fragmentary and deformed internal and external molds of 15 dorsal valves and 25 ventral valves.

Shells large and deep, articulated specimens probably nearly spherical; cardinal extremities rounded, hinge width about two-thirds maximum width; widest at about two-thirds length of shell. Costae subangular, flat topped, about twice as wide as interspaces, the both widening anteriorly, a few costae branching. Costae on fold and sulcus more conspicuous than those on flanks, about 10 per 5 mm at about 15 mm from beak. Growth lines confined to interspaces in posterior half of shell, becoming prominent toward the front, passing through a zone where radial and concentric ornament are about equal to form a reticulate pattern, grading forward to growth rugae and suppressed radial ornament of the anterior quarter of the valve. Lateral margins of shell thickened on interior.

The measurements listed below (in millimeters) are of preserved parts of specimens (probable restored dimension in parentheses):

GSC No., and part	*Length*	*Width*		*Depth*
		Hinge	*Maximum*	
24786 (holotype):				
ventral interior	23. 5	22. 0	31. 5	8. 0(10. 0)
24787 (paratype):				
dorsal interior	23. 5	23. 0	33. 0	14. 0
24788 (paratype):				
ventral interior	18. 5	20. 0	31. 5	8. 0

OCCURRENCE.—Unnamed tuffaceous siltstone, Napadogan quadrangle, York County, New Brunswick, at two places: Loc. *a*, tributary to Rocky Brook together with *Munhella cummingi*, new species, at the locality described for that species; and Loc. *b*, Middle Hayden Brook, 2,600 ft. northwest of its mouth, approximately 46°27′20″N, 66°46′20″ W (the same locality described for *M. cummingi*, new species).

DISCUSSION.—Despite deformation and incomplete preservation of the specimens, the following features were noted that cannot be matched with any known species or genus: the consistent absence of a cardinal process, the presence of a pseudospondylium entirely ankylosed to the shell floor, and the pronounced radial ornament.

Some of the features described are based upon visualization of a reconstructed shell (Figure 3) based on a composite, using what appeared to be the best preserved proportions and parts of specimens in the collection, and by drawing inferences from complementary structures. For example, the teeth have ap-

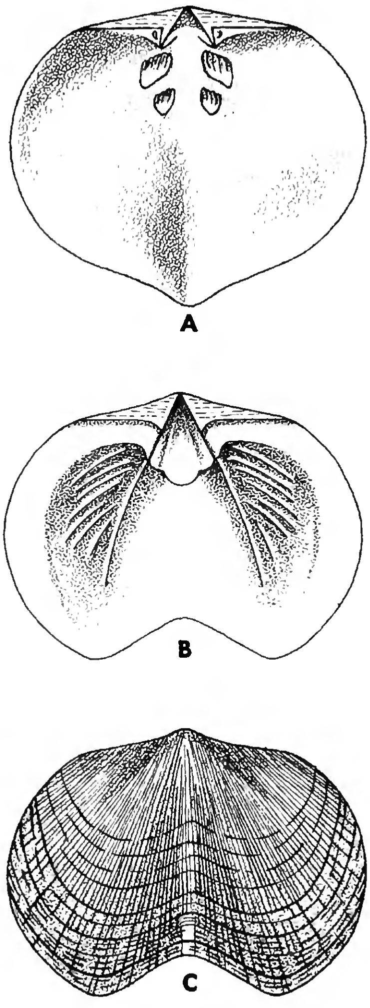

FIGURE 3.—*Rugostrophia sylvestris* new species. Reconstructions based on several specimens: A, dorsal interior; B, ventral interior; C, dorsal exterior. (Drawings by Mrs. R. C. Wigder; all approximately × 2.)

parently been sheared away from the holotype and are imperfectly preserved on all other specimens; nevertheless, it seems reasonable to postulate the presence of strong triangular teeth normal for syntrophids to fit the well-defined sockets of the dorsal valve. Similarly, the description of the external ornament is based on a composite of several incomplete external molds, all of which preserve costae in the fold or on the sulcus, but only one of which bears them on the flanks; those of the medial region are therefore thought to be considerably stronger than those of the flanks.

Schedophyla, new genus

DIAGNOSIS.—A convexoconcave, parvicostellate plectambonitid lacking dorsal median ridge.

DESCRIPTION.—Convexoconcave shells having thin body cavity, semicircular in outline, the cardinal extremities slightly extended. Ventral exterior has apsacline interarea, delthyrium covered at least in part by low-arched pseudodeltidium. Foramen not observed, probably lacking. Profile of ventral surface of low convexity in posterior half, flattening and becoming concave in anterior region. Dorsal exterior has short anacline interarea, notothyrium covered at least in part by chilidium; lateral profile of low, nearly uniform convexity bearing a shallow sulcus that disappears anteriorly. Radial ornament parvicostellate; concentric growth lines of varying prominence. Shell structure not determined.

Ventral interior has short stout teeth supported by short dental plates that descend to the floor of the valve to form the posterolateral margins of the muscle field. Muscle field relatively short, slightly to moderately raised above shell floor, cordate in outline, the rounded terminations of the diductor scars projecting slightly beyond that of the adductor scar. Pallial marks conspicuous, saccate, the vascula media originating at the anterior edges of the diductor muscle scars, and having paired lateral branches that enclose the genitalia and that give rise to one pair or more of secondary branches that bifurcate distally, and a pair of main branches that bifurcate distally.

Dorsal interior has slender, bladelike, divergent socket ridges that rise directly from the shell floor, defining shallow sockets and bordering the slightly raised notothyrial platform. Cardinal process bulbous, simple, apparently undifferentiated. Median ridge obscure or lacking; a pair of small submedian ridges extend to midlength, marking inner margins of adductor musculature. Mantle canal system not known.

DISCUSSION.—The monotypic genus is erected to contain the specimens assigned to *S. potteri*, new species, described below. Its orthoid cardinalia and its profile resemble those of *Valcourea*. Its assignment to that genus or related genera is prohibited, however, by its cordate ventral musculature, its parvicostellate ornament, and by pallial marks that are unlike those of the dinorthids. Confirmation of its assignment to the plectambonitaceans must await determination of the shell structure of *Schedophyla*.

Assuming that its shell is pseudopunctate, this genus possesses the essential characteristics of the Plectambonitidae and is most similar to *Ahtiella*. It lacks the

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PLATE 1.—*Munhella*, new genus, and *Fistulogonites*, new genus.

Part A.—*Munhella cummingi*, new species.
(PHOTOS BY R. H. MCKINNEY.)

Figures 1–6.—Holotype. 1, 2, Dorsal and ventral views of internal mold; 3, external mold of dorsal valve; 4, rubber replica of ventral internal mold; 5, rubber replica of dorsal external mold; 6, rubber replica of ventral external mold. (All views × 1.5) GSC 24781 (coll. GSC 40749, L. M. Cumming), from Napadogan quadrangle, York County, New Brunswick (Poole, 1958) at the point indicated by an "F" symbol on a tributary to Rocky Brook, approximately 46°20′ N, 66°56′ W.

Figures 7, 8.—Paratype. Dorsal and ventral views (× 1.5) of internal mold. GSC 24783 (R. B. Neuman coll.), from same locality as holotype.

Figure 9.—Paratype. Ventral external mold (× 1.5). GSC 24784 (R. B. Neuman coll.), from same locality as holotype.

Figures 10, 11.—Paratype. Dorsal internal mold and rubber replica (× 1.5). GSC 24785 (coll. GSC 3157, Charles Robb), from same locality as holotype; specimen bears label "*Strophomena*."

Figure 12.—Paratype. Ventral internal mold (× 1). GSC 24782 (coll. GSC 3157, Charles Robb), from same locality as holotype; specimen bears label "*Streptorhynchus*?"

Part B.—*Fistulogonites novaterrensis*, new species.
(PHOTOS BY C. F. BUDDENHAGEN IV.)

Figures 1, 2.—Holotype. Dorsal internal and external molds (× 4). Note absence of impression of cardinal process; specimen is too friable to permit making of replica. GSC 24776, from unnamed tuffaceous sandstone, Twillingate quadrangle, New World Island, Newfoundland, at the point on the geologic map of Williams (1963) indicated by an "F" symbol, one-half mile northwest of Village Cove.

Figures 3, 7.—Paratype. Ventral internal and external molds (× 6). Note rows of spines on impressions of costellae. GSC 24777, from same locality as holotype.

Figure 4.—Paratype. Ventral internal mold (× 4). GSC 24780, from same locality as holotype.

Figures 5, 6.—Paratype. Ventral internal mold and rubber replica (× 4). GSC 24779, from same locality as holotype.

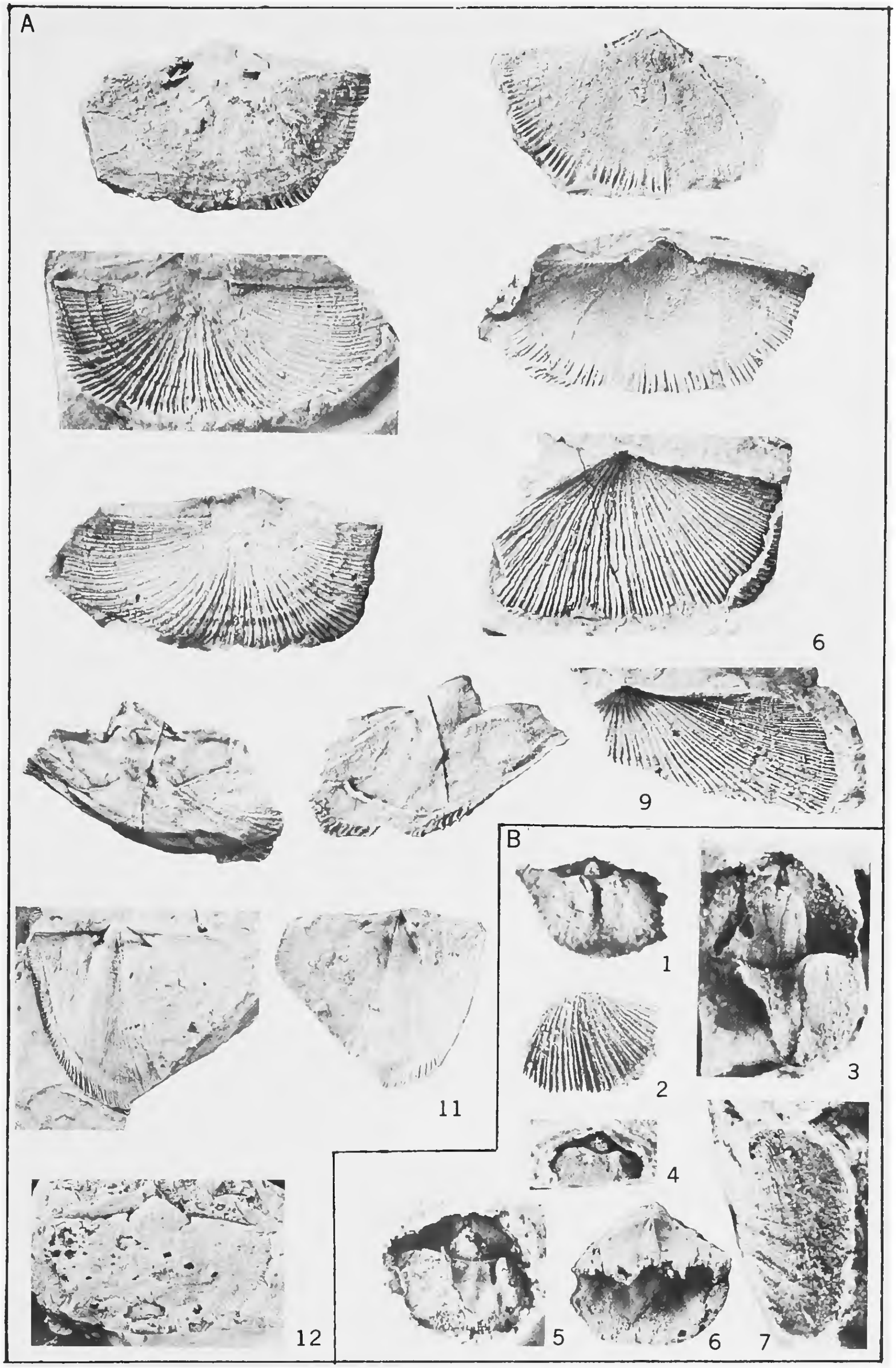


PLATE 1

TABLE 1.—*Measurements (in millimeters) of* Schedophyla potteri, *new species.*

GSC No., and part	*Length*	*Width*		*Depth*
		Hinge	*Midlength*	
24793 (holotype): dorsal interior	10.8	11.0 (17.0)	15.0	1.5
24794 (paratype): ventral interior	12.0	15.0 (18.0)	16.0	0.8
24795 (paratype): ventral interior	9.5 (10.5)	14.7	11.2 (12.5)	?
24796 (paratype)	10.5	13.8 (14.5)	13.5	0.7

dorsal median ridge of that genus, however, and its ornament is not rugose, as is that of the closely related genus *Inversella.*

Schedophyla potteri, new species

PLATE 2A

DESCRIPTION.—External and internal features of the species are the same as those of the genus described above, based on fragmentary and deformed internal and external molds of 10 dorsal valves and 23 ventral valves.

Profile of ventral valves varies with size and degree of deformation: shells less than 7 mm long, of low convexity; larger shells of low convexity in posterior part, becoming concave in anterior part, the degree of resupination variable, probably due in large measure to deformation. Dorsal valves consistently convex, but sulcus variably preserved, shallow, and confined to posterior two-thirds of shell where it includes about 6 major costellae.

Parvicostellate ornament consists of larger costellae spaced at about 10 per 5 mm and include about 5 finer ones at the anterior edge of shells about 10 mm long; growth lines prominent at irregular intervals on anterior third of shell.

The measurements given in Table 1 are of common large-sized specimens, including the holotype, but the collection includes specimens less than half the size of these. Probable restored dimensions of incomplete specimens are in parentheses.

OCCURRENCE.—Unnamed tuffaceous siltstone, Napadogan quadrangle, York County, New Brunswick, at Middle Hayden Brook, 2,600 ft. northwest of its mouth, approximately 46°27′20″N, 66°46′20″W—Loc. *b,* described above, for *Munhella cummingi,* new species, and *Rugostrophia silvestris,* new species.

PLATE 2.—*Schedophyla,* new genus, and *Rugostrophia,* new genus.

Part A.—*Schedolphyla potteri,* new species. All illustrated specimens from Napodagan quadrangle, York County, New Brunswick, west bank of Middle Hayden Brook, 2,600 feet northwest of its mouth, approximately 46°27′20″N, 60°46′20″W. (PHOTOS BY R. H. MCKINNEY; ALL × 2.)

Figures 1, 2, 5, 6.—Holotype, GSC 24793. 1, 2, Dorsal internal mold and rubber replica; 5, 6, external mold and replica.

Figures 3, 4.—Paratype, GSC 24794. Ventral interior and rubber replica.

Figures 7, 8.—Paratype, GSC 24795. Ventral interior and rubber replica.

Figures 9–11.—Paratype, GSC 24796. 9, 10, Interior and rubber replica; 11, external mold.

Part B.—*Rugostrophia sylvestris,* new species. (PHOTOS BY R. H. MCKINNEY.)

Figure 1.—Paratype, GSC 24789. Dorsal internal mold (× 1.5). Locality same as for specimens of *Schedophyla potteri* (Part A of this plate).

Figure 2.—Paratype, GSC 24790. Dorsal internal mold (× 1.5). Locality and collection same as for GSC 24783 (figures 7, 8 of Plate 1A).

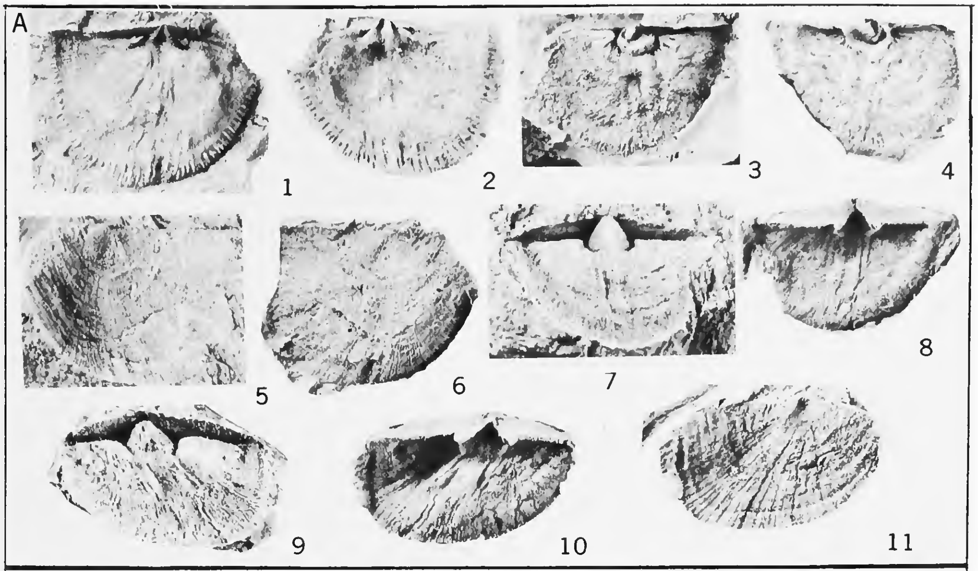
Figures 3, 4, 8.—Holotype, GSC 24786. Ventral internal mold, rubber replica, and rubber impression of posteromedial and right side of exterior (× 1.5). Locality and collection same as for GSC 24781 (figures 1–6 of Plate 1A).

Figures 5, 6.—Paratype, GSC 24791. Dorsal internal mold and rubber replica (× 1.5). Locality and collection same as for GSC 24783 (figures 7, 8 of Plate 1A).

Figures 7–9.—Paratype, GSC 24792. Replica of dorsal interior and internal mold from which it was made (× 1). Locality and collection same as for GSC 24781 (figures 1–6 of plate 1A).

Figure 10.—Paratype, GSC 24787. Rubber replica of exterior part of right side of dorsal valve (× 1.5). Replica reflects ornament but not convexity of external mold. Same locality and collection as GSC 24783 (figures 7, 8 of Plate 1A).

Figure 11.—Paratype, GSC 24788. Ventral internal mold (× 1.5). Same locality and collection as the holotype (figures 1, 2, 5, 6 of Part A of this plate).



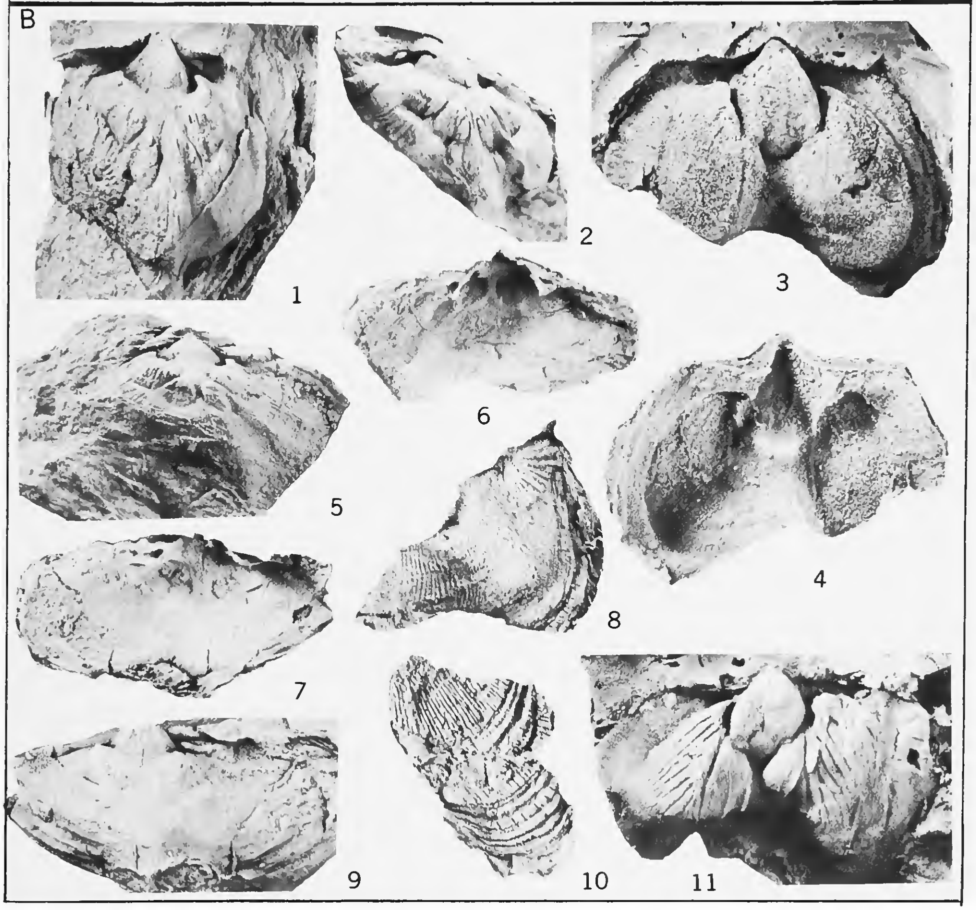


PLATE 2

DISCUSSION.—The shape, proportions, and details of ornament of the shells in this suite of specimens have been considerably modified by tectonic deformation. Although all ventral valves preserve the resupinate profile distinctive of the genus, the place of resupination and the degree of concavity of the anterior part of the shell vary widely. Such features as shell depth, outlines, length-width ratios, and the configuration of the dorsal sulcus also vary widely in response to deformation, as do the details of ornament, except in small parts of some specimens. Thus, species characteristics are known only in very general terms; a more precise species definition must await better preserved specimens. Nevertheless, the present material is sufficient to establish that these specimens possess a hitherto unknown combination of characteristics.

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Reuben James Ross, Jr.

A New Middle Ordovician Syntrophopsid Genus

ABSTRACT

The new genus *Cuparius,* a pitted syntrophopsid, is described from the Middle Ordovician *Orthidiella* and lower *Anomalorthis* zones of Nevada. The new genus is found also in Newfoundland and in the Mystic Conglomerate of Quebec.

In 1965, Dr. G. A. Cooper, in the company of the author and several other biostratigraphers, collected silicified brachiopods from an old locality south of Frenchman Flat on the Nevada Test Site. From the insoluble residue Cooper obtained rare specimens of pitted syntrophopsids which he very kindly transmitted to the author for description. The species represented by these silicified specimens occurs also as calcareous shells in the great bioherm at Meiklejohn Peak, Nevada (Ross, 1964, pp. C25–C26). Specimens from both places are the basis for the description that follows.

When Ulrich and Cooper (1938, p. 231) described the genus *Syntrophopsis* they called attention to two species that bore pitted exteriors like *Porambonites.* These species were classified with *Syntrophopsis* because brachiophore plates converge dorsally and because dental lamellae form a true spondylium. In *Porambonites,* the dental plates unite with the floor of the pedicle valve discretely, and brachiophore plates are parallel, without converging to form a septalium in the brachial valve; a spondylium can be simulated because of deposition of secondary material in mature shells of *Porambonites* (Schuchert and Cooper, 1932, p. 102).

The pitted surface and fine radial costellae distinguish a group of shells of early Middle Ordovician age which cannot otherwise be separated from *Syntrophopsis.* These species are named *Cuparius* in honor of Dr. Cooper, who first recognized that they represented a genus distinct from *Porambonites.*

In June 1968, with the assistance of Dr. Valdar Jaanusson, the author was able to examine topotype specimens of *Porambonites* at the Naturhistoriska Riksmuseet, Stockholm, as part of a research project under National Science Foundation Grant GA–4020.

Family SYNTROPHOPSIDAE Ulrich and Cooper, 1936

Cuparius, new genus

Syntrophopsis Ulrich and Cooper (part), 1938, p. 231.
Porambonites Pander (part), Ulrich and Cooper, 1938, pp. 242–243.
Porambonites Pander (part), Cooper, 1956, pp. 609–610.

DIAGNOSIS.—Shells transversely elliptical in outline, subequally biconvex in anterior profile. Brachial valve the deeper in lateral profile. Pedicle sulcus and brachial fold originate near midlength, variable in width and depth. Pedicle cardinal area of variable width, curved, apsacline; brachial cardinal area short, straight or very slightly curved, anacline. Surface marked by fine radial costellae and by fine pits. On surface, pits appear between costellae for most part, but decorticated calcareous shells show concentric rows of shallow pits crossing radial rows to form closely packed series of quincuncial patterns. Shell substance impunctate.

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Pedicle interior as in *Syntrophopsis,* except that median septum is reduced and does not extend forward in shell. Interior of brachial valve like *Syntrophopsis.*

TYPE-SPECIES.—*Cuparius cardilatus,* new species.

DISCUSSION.—This new genus includes the following previously described species:

Cuparius landmani (Ulrich and Cooper), 1938, p. 234. Boulder in Mystic Conglomerate, Quebec.

Cuparius vetusta (Ulrich and Cooper), 1938, p. 239. Boulder in Mystic Conglomerate, Quebec.

Cuparius umbonatus (Cooper), in Ulrich and Cooper, 1938, p. 242, pl. 53C, fig. 21.—Cooper, 1956, p. 609, pl. 107B, figs. 4–11. Antelope Valley Limestone, Ikes Canyon, Nevada.

Cuparius sp. 1 (Cooper), 1956, pp. 609, 610, pl. 108H, figs. 40–42. Antelope Valley Limestone, lower part of middle member associated with *Palliseria* in unit 8 of McAllister (1952, p. 11), Quartz Spring area, Nevada (Ross, 1967, pl. 11).

Cuparius sp. 2 (Cooper), 1956, p. 610, pl. 107A, figs. 1–3. Lower part of the Table Head Formation, at Table Point, Newfoundland.

Cuparius sp. 3 (Cooper), 1956, pp. 610, 611, pl. 106D. (Probably the same species as that described below from the *Orthidiella* zone, Ranger Mountains, Nevada.)

Another species, *Porambonites*? sp. 4 of Cooper (1956, p. 611), is known only from a shell exterior and comes from the late Middle Ordovician of Pennsylvania, presumably from strata younger than that of the other examples; it is excluded from this group until better known. According to Williams (1962, p. 230), *Porambonites acutiplicata* Reed resembles this shell from Pennsylvania and has dental plates that ally it with true *Porambonites,* not with *Syntrophopsis.*

The genus *Punctolira* has the same shell structure and ornamentation, the same kind of spondylium, and very similar brachiophore plates. It differs in having a rudimentary cardinal process.

Cuparius, new genus, may have special stratigraphic significance. It occurs in the *Orthidiella* zone of Nevada at the Nevada Test Site and at Meiklejohn Peak and is known in the same zone in the northern Monitor Range. It also is found in the lower part of the Table Head Formation of Newfoundland; recent correlations made by the present author show that the lower part of the Table Head is equivalent to the *Orthidiella* zone. The new genus also is known in the lower *Anomalorthis* zone in the Quartz Spring area of Nevada, and it probably is in the same zone at Ikes Canyon.

The few species that occur higher stratigraphically may belong to true *Porambonites* rather than to *Cuparius,* new genus.

Cuparius cardilatus, new species

PLATE 1: FIGURES 1–8

DESCRIPTION.—Shell of medium size for the genus; transversely elliptical; length of pedicle valve between three-fourths and eight-tenths of width. Hinge width equals seven-tenths to eight-tenths of greatest width. Valves equally convex in anterior profile; brachial valve the deeper in lateral profile. Greatest convexity of pedicle valve near beak. Brachial fold and pedicle sulcus initiated at or in front of middle of shell; width at anterior margin close to half greatest width of shell.

On outer surface very fine costellae separated by finer interspaces. At radius of 5 mm from brachial umbo, costellae spaced 5 per mm; at 10 mm radius spaced 6 per mm. Pits obvious in radial rows between costellae; however, decorticated specimens show pits closely spaced in quincuncial series, 6 per mm both radially and concentrically at radius of 10 mm from brachial umbo.

In interior of brachial valve there is one pair of lanceolate canal patterns (vascula media?) along lateral flexure of fold. A second lanceolate pair lies about one-quarter of distance from flexure to hinge line. A lobate mantle impression lies between this pair and hinge-line. A pair of small elliptical scars in front of notothyrial cavity may be adductor muscle scars. In pedicle valve one pair of canal patterns extends from front of spondylium onto tongue, diverging slightly. Flabellate canal patterns cover much of posterolateral part of shell. Median septum under spondylium low and short.

Measurements (in millimeters) of holotype: length of brachial valve, 12.5; length of pedicle valve, 13.6; width, 17.5; hinge width, 14.1; thickness, 9.7; length of fold, 5.2; anterior width of fold, 9.3; costellae at 5 mm, 5 per mm; costellae at 10 mm, 6 per mm; pits at 5 mm, 5 per mm; pits at 10 mm, 6–7 per mm.

TYPES.—Holotype, United States National Museum (USNM) 162818; paratypes USNM 162819–21.

OCCURRENCE.—The holotype and paratypes USNM 162819–20 were collected from Antelope Valley Limestone at same locality as United States Geological Survey (USGS) collection D719–CO (Ross, 1964, p. C20; 1967, pl. 11). Paratype USNM 162821, from USGS collection D1968–CO, was collected from

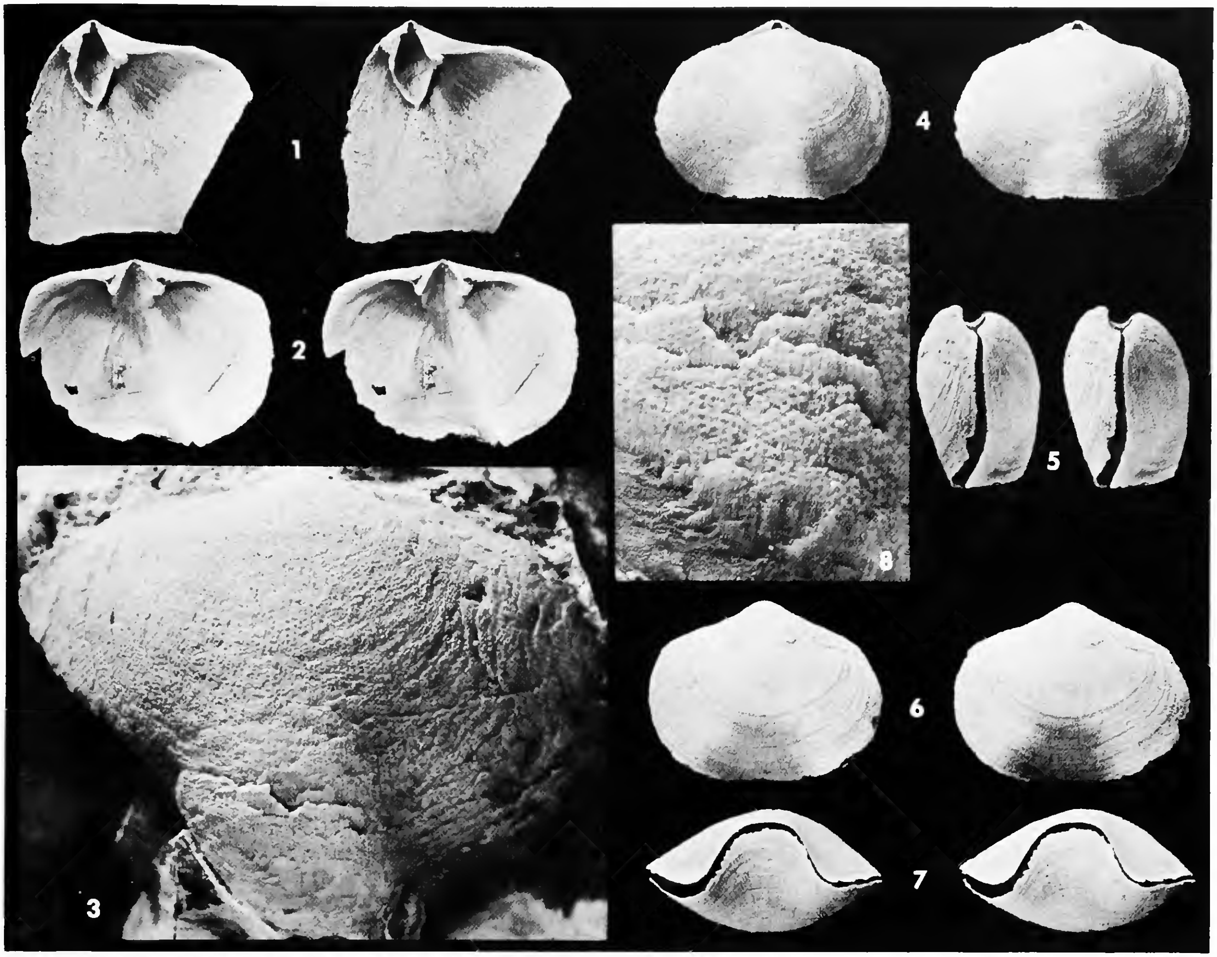

Plate 1.—*Cuparius cardilatus,* new species. 1, Paratype, pedicle interior, fragmentary specimen; USNM 162819 (USGS coll. D719–CO), Nevada Test Site; stereophotograph (× 1.9). 2, Paratype, brachial interior, damaged specimen; USNM 162820 (USGS coll. D719–CO), Nevada Test Site; stereophotograph (× 1.9). 3, Paratype, brachial valve, dorsal surface largely decorticated (× 4.6); USNM 162821 (USGS coll. D1968–CO), bioherm, Meiklejohn Peak. 4–7, Holotype, complete specimen, dorsal, right lateral, ventral, and anterior view; USNM 162818 (USGS coll. D719–CO), Nevada Test Site; stereophotographs (× 1.9). 8, Same specimen as figure 3, showing quincuncial packing of pits on small area on anterior part of fold (× 9.3).

Antelope Valley Limestone, in bioherm 167 feet above its base, Meiklejohn Peak (Ross, 1964, p. C26).

Discussion.—*Cuparius cardilatus,* new species, is readily distinguished from *C. landmani* (Ulrich and Cooper) by its greater hinge width. It is a larger species than *C. vetusta* (Ulrich and Cooper); *C. vetusta* seems to have a somewhat longer pedicle sulcus. *Cuparius umbonatus* (Cooper) is a wider and longer species and yet has a narrower hinge. The species designated *Porambonites*? sp. 1 by Cooper (1956, pp. 609, 610, pl. 108h) is about the same size but is much more coarsely pitted and seems to have a narrower hinge than *C. cardilatus,* new species; in both respects it resembles *C. umbonatus.* A Newfoundland species, *Porambonites*? sp. 2 of Cooper (1956, p. 610, pl. 107a), has a much narrower hinge.

The small specimens described as *Porambonites*? sp. 3 by Cooper (1956, pp. 610, 611, pl. 106d) probably are immature individuals of *C. cardilatus,* from about one-third to one-half grown.

From the calcareous specimens, it is obvious that the pitted structure of the shell is not limited to the external surface and that the shell substance is essentially fibrous. The shell structure should be the subject of study by electron microscope, using methods of Williams (1968).

Other shells found at about the same stratigraphic level (R. J. Ross, Jr., unpublished data) show no evidence of pitting; these have been assigned to *Syntrophopsis,* although they are above the expected stratigraphic range of that genus. The lack of pits cannot be attributed to silicification because calcareous specimens are found with the same characteristics.

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H. B. Whittington

A New Calymenid Trilobite from the Maquoketa Shale, Iowa

ABSTRACT

Parts of the exoskeleton, other than the thorax, of the trilobite species *Calymene mammillata* Hall, 1861, are redescribed from the original and new material. The latter comes from the cephalopod coquina beds in the Elgin Shaly Limestone Member, the lowest member of the Maquoketa Shale; this is probably the original locality. The Elgin Member is of Richmond, or possibly slightly older, age. The absence of buttresses from fixed cheek to glabellar lobes, the large basal glabellar lobe, papillation of the anterolateral angle of the glabella, and long, gently sloping preglabellar field with a lateral boss combine to distinguish the cranidium of *C. mammillata* from that of any known species. It is regarded as the type-species of a new genus, *Thelecalymene,* and as most closely related to *Gravicalymene,* species of which have been described recently from contemporaneous and older rocks of the midcontinent and New York State.

In 1936 Shirley discussed earlier work on calymenid trilobites and distinguished five new genera, basing his distinctions on characters of the glabella and adjacent fixed cheeks, and the preglabellar field (anterior border). He drew attention to the presence, in certain species, of papillation of particular glabellar lobes, and of corresponding buttresses projecting from the fixed cheek to meet such papillae, and he pointed out that these papillae and buttresses project over the axial furrow to form a bridge. He divided calymenids into two series, based on presence or absence of the papillate-buttressed structures; however, whether these series are separate lines of descent or whether phylogeny is complicated by parallel series has yet to be demonstrated. Difficulties have been encountered in using form of the preglabellar field—whether it is flat, ridged or rolled in sagittal profile—in the way Shirley used it, and care must be taken to distinguish the form as seen in internal molds from that of the external surface of the exoskeleton. Nevertheless, the criteria Shirley used have been applied to discriminate species and genera in British (Dean, 1962, 1963) and North American (Whittington, 1954; Stumm and Kauffman, 1958; Ross, 1967) Ordovician material. There has been little recent work on Silurian calymenids except for that of Tillman (1960) and Campbell (1967). Until more is known of exoskeletal characters of calymenids throughout their stratigraphical range, it will not be possible to delineate phylogenetic lines.

The species from Iowa described here exhibits a group of cranidial and pygidial characters which set it apart from any other; consequently, it is made the type of a new genus. The age cannot be given more precisely than within the upper part of the Cincinnatian Series, and relationships to other genera are uncertain, though species of *Gravicalymene* may be the most closely related.

The material from Iowa was collected in 1952 on a field trip undertaken with the advice of Dr. G. Arthur Cooper. It is a pleasure to acknowledge my indebtedness to him for many hours of companionship in the field, for his wise guidance during my studies of Ordovician rocks and fossils, and for his inspiring example as a practicing paleontologist. I am indebted also to Dr. Roger L. Batten, American Museum of Natural History (AMNH) for the loan of Hall's type mate-

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rial, and to the late Professor A. K. Miller for the loan of specimens in the geology department of University of Iowa (UI). The material was prepared and photographed in the Museum of Comparative Zoology, Harvard University (MCZ). Dr. V. Jaanusson, State Museum of Natural History, Stockholm (RM), kindly loaned type and other material of *Papillicalymene papillata,* on which Figures 1*e–h* are based.

Family CALYMENIDAE Burmeister, 1843

Thelecalymene, new genus

DIAGNOSIS.—Glabella bell-shaped in outline, three pairs of lateral lobes, anterolateral angle of frontal glabellar lobe papillate. No genal buttresses to lateral lobes 1–3p. Preglabellar field broad (sagittal and exsagittal), sloping forward and upward from furrow, low boss at lateral margin projects towards corner of frontal glabellar lobe. Eye lobe opposite lateral glabellar lobe 2p, broad low eye ridge; anterior, inner corner of cheek slightly buttressed towards corner of frontal glabellar lobe. Hypostome without swelling or ridge on anterior lobe of middle body, posterior lobe with median posterior indentation; outline of posterior border bilobed.

Pygidium with pleural region displaying deep pleural furrows which die out distally, leaving a border of width one-third that of the region; faint interpleural furrows. External surface of exoskeleton granulate, except in furrows.

TYPE-SPECIES.—*Calymene mammillata* Hall, 1861.

DISCUSSION.—The diagnosis presented above is intended to be read in conjunction with my diagnosis (Whittington, in Moore, 1959, pp. O450, O451) of the family, lines two to four of which should read "widest across occipital ring or pre-occipital (i.e., 1p) lateral lobes; may or may not project in front of genae."

Dean (1962, pp. 111–118; 1963, pp. 216–228) described, from the Ordovician of Britain, species of *Flexicalymene, Diacalymene,* and *Gravicalymene* and erected the genus *Onnicalymene,* distinguished from *Flexicalymene* essentially by the relatively posterior position of the eye lobe. Ross (1967, pp. B7–B17) has discussed *Flexicalymene* and *Gravicalymene* and described species of them from the Ordovician of Kentucky and Ohio. Species of *Flexicalymene* in Britain (Figure 1*i,j*) and North America (see also Whittington, 1954, pp. 147, 148; Stumm and Kauffman, 1958) have, as Ross (1967, p. B9) remarks, the axial furrow straight or slightly curved convexly outward, this curvature being related to the evenly graduated size of the lateral glabellar lobes. None of these lateral lobes is buttressed to the fixed cheek, the pleural region of the thorax is narrow (transverse) than the axis, and there is no smooth border on the pygidium. Of these characters, the lack of buttresses on the fixed cheek, is the only one that *Flexicalymene* has in common with *Thelecalymene.*

The type-species of *Diacalymene, D. diademata* (Figures 1*c,d,* herein and Whittington, in Moore, 1959, p. O450, figs. 353,2*a,b*) is from the Silurian, Wenlock, of Czechoslovakia. Lateral glabellar lobe 2p is opposed closely by a genal buttress, and the preglabellar field is strongly ridged, the posterior-facing slope having a low projection where it meets the anterior border opposite the axial furrow. Rostral suture is situated some distance down the anterior-facing slope of the field. The inner, anterior corner of the fixed cheek is inflated and projects slightly, but the anterior angle of the frontal glabellar lobe is not papillate. The inflated inner corner of the fixed cheek and the slight distal projection (not a buttress) on the preglabellar field are as in *Thelecalymene,* but the genal buttress opposite lobe 2p and the ridged preglabellar field distinguish *Diacalymene* from that genus. The pygidium of *Diacalymene* has a narrow smooth border, but includes only five axial rings and pleural ribs. Thus, while *Diacalymene* and *Thelecalymene* have some characters in common, the two are not closely related if genal buttresses opposed to lateral glabellar lobes are considered important characters in phylogeny.

In *Gravicalymene* (figure 1*k,l*) the glabella is like that of *Thelecalymene* in having a relatively large basal lobe, so that the outline of the lateral margin is curved concavely outward. There are no genal buttresses to lateral lobes 1–3p in either genus, but *Gravicalymene* does not have the outer angle of the frontal lobe papillate. The preglabellar field is strongly ridged in *Gravicalymene,* not gently upsloping medially as in *Thelecalymene.* In certain species of *Gravicalymene* (*G. hagani, Gravicalymene* sp. of Ross, 1967, pl. 3, figs. 1, 19) there is a slight development of a buttress on the outer part of the preglabellar field that resembles the much stronger boss in this position in *Thelecalymene.* The deep, trenchlike posterior border furrow in *Gravicalymene hagani* Ross, widest medially, is like

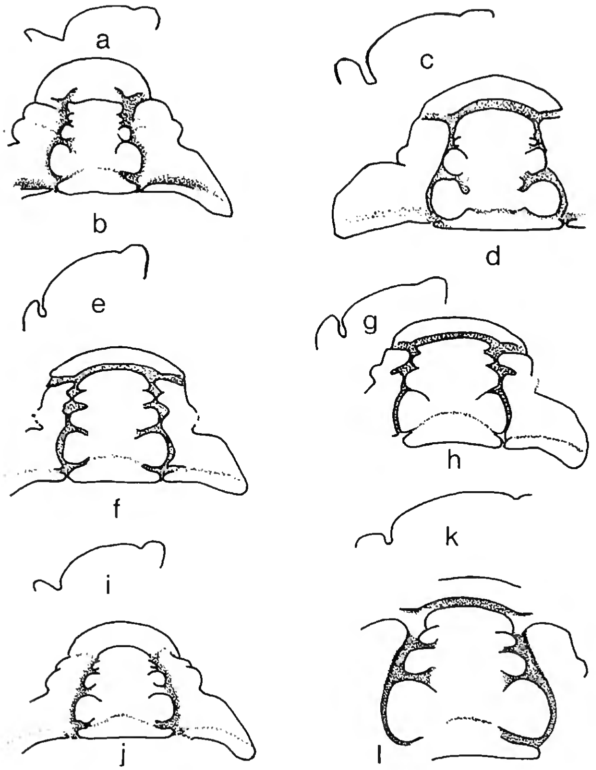

FIGURE 1.—Outlines of cranidia of type species of calymenid genera, sagittal profile and dorsal views: a, b, *Thelecalymene mammillata* (Hall, 1861), based on MCZ 8672/2 (see Plate 1: figures 1–4); c. d, *Diacalymene diademata* (Barrande, 1846), based on MCZ 8346, Wenlock age portion of Liteň Shale, St. Ivan, Prague district, Czechoslovakia; e, f, *Papillicalymene papillata* (Lindström, 1885), based on RM Ar 6208, Hemse Beds of Ludlow age (Martinsson, 1967), Östergarn, Gotland; g, h, *P. papillata,* based on RM Ar 27199, Hemse Beds of Ludlow age, Hammars, Östergarn, Gotland; i, j, *Flexicalymene* cf. *caractaci* (Salter, 1865), based on original of Whittington (1965, pl. 18, figs. 9, 10), Longvillian Stage, Caradoc Series, North Wales; k, l, *Gravicalymene convolva* Shirley, 1936, based on Sedgwick Museum A5877, Ashgill Series, Birdshill quarry, near Llandeilo, South Wales.

that in *Thelecalymene mammillata* (Hall). The pygidia of *Gravicalymene* from Kentucky (as described by Ross) appear to have one less pleural rib than in *T. mammillata,* and lack the distinct border; interpleural furrows are similar in being deeper proximally and distally. Only the pygidium described as *Gravicalymene*? sp. 5 by Ross (1967, p. B13, pl. 3, fig. 13) has a distinct border, but it has one less axial ring and pleural rib than *T. mammillata.* The cranidium described as *Gravicalymene* sp. 4 by Ross (1967, pp. B12, B13, pl. 3, figs. 14–17), from the same formation, may belong with this pygidium; it has a preglabellar field which is less strongly ridged than that of many species of *Gravicalymene,* and thus is more like that of *Thelecalymene.*

Among Ordovician calymenids, *Thelecalymene* is thus most like *Gravicalymene,* and is approximately contemporaneous with it in the lower part of the Maquoketa Shale (*G.* aff. *quadricapita* of Ross, 1967, pl. 4, figs. 14, 15). An Ordovician species that is like *Thelecalymene mammillata* in having the anterolateral angle of the frontal glabellar lobe buttressed from the inner, anterior corner of the fixed cheek is *Papillicalymene husseyi* Stumm and Kauffman (1958, pp. 957–959, pl. 123, fig. 18) from high Richmond strata of Michigan. This latter species has lateral glabellar lobes 2p and 3p opposed by low genal buttresses, and it shows a low projection at the outer edge of the preglabellar field; it differs from *T. mammillata* in having a deep preglabellar furrow and hence a strong flexure in the preglabellar field at the margin of this furrow, and the palpebral lobe may be situated slightly farther back. Stumm and Kauffman referred their species to *Papillicalymene* Shirley (1936, p. 396, fig. 1), of which the type-species, *Calymene papillata* Lindström, 1885, is from strata of Ludlow age in Gotland. Through the kindness of Dr. V. Jaanusson I have been able to examine the type and other material of this Swedish species, and it will be redescribed elsewhere. *P. papillata* (Figure 1*e–h*) has prominent genal buttresses opposed to lateral lobes 2p and 3p, the anterolateral margin of the frontal glabellar lobe papillate, and a deep and narrow preglabellar furrow, from the anterior margin of which the preglabellar field curves upward close to the frontal slope of the glabella before arching through 180° to descend vertically to the rostral suture. The frontal glabellar lobe may be opposed by a buttress from the inner corner of the fixed check (Figure 1*f*), or from the outer part of the preglabellar field (Figure 1*h*). The pygidium is like that of *T. mammillata,* but it has a much less conspicuous sixth pleural rib and a narrower (transverse) border. Thus, *Papillicalymene* is quite distinct from *Thelecalymene.* Stumm and Kauffman's species is based on a single, incomplete internal mold of the cranidium, and more material is needed to confirm its generic assignment, as those authors have recognized.

Thelecalymene mammillata (Hall, 1861)

FIGURE 1*a, b*; PLATE 1: FIGURES 1–7; PLATE 2: FIGURES 1–13.

Calymene mammillata Hall, 1861, pp. 50, 51; Hall, in Hall and Whitney, 1862, p. 432, figs. 1, 2; Walter, 1927, p. 239–241, pl. 19, figs. 1–3.

MATERIAL, GEOLOGICAL HORIZON, AND AGE.—AMNH 1408a–g, originals of Hall (1861); 1408a, holotype, incomplete cranidium, original of Hall (1862, fig. 1); 1408e, incomplete pygidium, original of Hall (1862, fig. 2) and a second pygidium on the same slab (Plate 2: FIGURES 7, 9, 19, 13) that has some of the exoskeleton attached and is not flattened; 1408b–d, three incomplete cranidia; and 1408f, g, incomplete pygidia; all are from "the shales above the Galena Limestone, Maquoketa Creek, 12 miles west of Dubuque, Iowa." UI 9069, 9077–8, originals of Walter (1927) from the same locality as Hall's specimens, and approximately from the well-known section, one-quarter mile southwest of Graf, Dubuque County, Iowa (Ladd, 1929, pp. 341–343). This section is in Ladd's graptolite zone of the Elgin Shaly Limestone Member, the lowest part of the Maquoketa Shale. When visiting this section in August 1952 I observed some 20 feet of dark gray shales, in the upper 6 feet of which were calcareous, sandy beds, 6–8 inches thick, with cephalopods (Miller and Youngquist, 1949). Dissociated exoskeletal parts of the calymenid (MCZ 8672) occur in the lower part of the cephalopod beds, and there also occur gastropods, bivalves, and rarer linguloid brachiopods. Hall's specimens are in similar calcareous sandstones and contain cephalopods and gastropods. These beds must be approximately Beds 11–16 of Thomas's section, quoted by Ladd (1929, pp. 342–343). The only other trilobite that I have seen from the Graf section is the cranidium of *Primaspis* cf. *crosotus* (Locke, 1843), a species from the Eden of the Cincinnati district; the specimens were collected by Mr. H. W. Tichenor. USNM 10263, from Maquoketa Creek, Iowa, presumably is from the same beds. Ladd (1929, pp. 384, 395) lists *"C". mammillata* only from his depauperate zone at the base of the Elgin Member, but evidently the species ranges higher, into Ladd's graptolite zone.

The Maquoketa Shale is regarded (Twenhofel, et al., 1954) as being of Richmond age; the characteristic form in Ladd's graptolite zone of the Elgin Member being apparently *Orthograptus truncatus peosta* (Hall). Professor W. B. N. Berry (personal communication, March 1968) has identified in collections from the Graf section this species and also *Orthograptus truncatus abbreviatus* (Elles and Wood), a form he considers confined to Richmond and younger strata. Glenister (1957) concluded from her study of conodonts that the Elgin Member in Iowa was Richmondian or possibly slightly older. Professor Walter C. Sweet (personal communication, 28 January 1968) states that the Elgin of Iowa has yielded a number of specimens of the conodont *Phagmodus undatus,* which he considers is probably of Eden age, though it may be younger. The "graptolite zone" of Ladd embraces beds, at scattered localities, containing abundant graptolites; my investigations showed that different species occurred at particular localities, and cast doubt on the view that the age of these beds at different localities lay within the same limited span of time. Thus, the age of the Elgin Member appears to be Upper Ordovician, possibly Richmond, possibly older.

DESCRIPTION.—Occipital ring widest (sagittal) medially, distally curving forward to merge, across the shallow axial furrow, with the inner, posterior corner of the cheek. Occipital furrow deepens behind basal glabellar lobe into transversely elongate apodemal pit. Basal (1p) lateral lobe oval in outline, inflated, separated by shallow longitudinal furrow from median lobe. The 2p lateral lobe similar in outline and inflation to 1p lobe, length (exsagittal) half that of 1p lobe; 3p lobe inflated, anterior angle of frontal glabellar lobe weakly to strongly papillate, the tip directed slightly upward and outward at some 45° to the sagittal line; anterior margin of frontal lobe curved convexly forward, the curvature varying according to the strength of the papillation of the lobe (compare figures 4 and 5 of Plate 1). Axial furrow a narrow, deep trench curving around the basal glabellar lobe, broadening progressively anteriorly, deep anterior pit opposite frontal lobe. Slope of frontal lobe of glabella is vertical adjacent to broad, shallow pre-

PLATE 1.—*Thelecalymene mammillata* (Hall). 1–4, Cranidium: anterior, left lateral, oblique, and dorsal views (× 3); MCZ 8672/2, Elgin Shaly Limestone Member, Maquoketa Shale, 0.25 mile southwest of Graf, Dubuque County, Iowa. 7, Dorsal view (× 6) of anterior portion of same specimen, showing details of external surface, glabellar lobes, and preglabellar field. 5, 6, Holotype, cranidium: dorsal and oblique views (× 3); AMNH 1408a, shales above the Galena Limestone, Maquoketa Creek, 12 miles west of Dubuque, Iowa (probably same locality and horizon as original of figures 1–4, 7). Original of Hall (1862, fig. 1).

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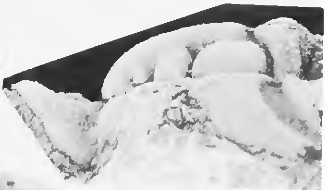

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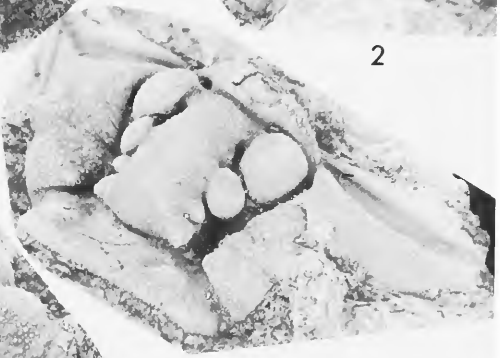

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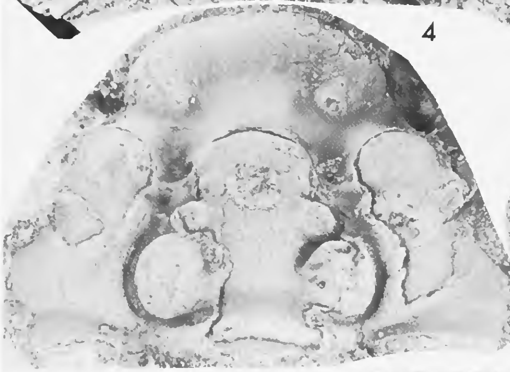

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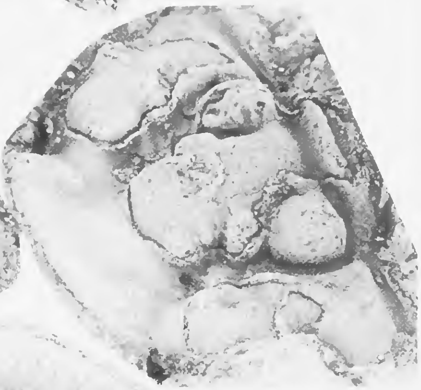

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PLATE 1

glabellar furrow, on anterior side of which a broad (sagittal and exsagittal) preglabellar field slopes gently upward to margin, where it is abruptly flexed to slope downward and inward for a short distance to the rostral suture (Plate 2: figure 12). In dorsal view margin of preglabellar field is curved so that field projects as a lip; a broad, low boss at the inner, lateral margin of this field. Cheek subquadrant in outline, moderately convex, the portion in front of the eye lobe inflated so that it projects slightly over the shallow border furrow; lateral border rounded, widening toward genal angle; posterior border widens progressively outward, posterior border furrow a steep-sided, flat-bottomed trench which is widest (exsagittal) medially. Eye lobe situated midway across cheek, the transverse line through midpoint runs through anterior portion of 2p lobe. Palpebral lobe with low, broad rim, continued across fixed cheek by broad, low, eye ridge, which runs down into axial furrow opposite lateral glabellar lobe 3p (Plate 1: figures 5, 7). Anterior branch of suture runs forward and slightly inward to reach margin well outside projected line of axial furrow; course of posterior branch angulate (Plate 1: figures 3, 4), the oblique angle situated a short distance out and back from the eye lobe, from whence the branch runs straight outward and backward to the rounded genal angle. Hypostome with median body gently convex, middle furrow deep at border furrow, extending inward and backward as a faint furrow; the two median furrows curve to meet and outline a faintly more convex, crescentic posterior lobe of the middle body; median depression in posterior margin of posterior lobe. Anterior border continuous with anterior wing, narrow and flexed to slope downward and forward, sutural margin curved convexly forward. Lateral border narrow, convex; posterior border broader, horizontal and bilobed in outline, a sagittal furrow bisecting the border.

Thorax unknown. Axis of pygidium composed of seven rings (Plate 2: figures 6, 9), this portion tapering evenly, and a prominent, parallel-sided, posterior portion which is bluntly rounded posteriorly. First six ring furrows complete, deepest distally, seventh furrow not so deepened and not reaching axial furrow, shallower and narrower (transverse) eighth furrow on posterior portion. Pleural regions curved down so that the outer part slopes steeply, but not vertically. Six deep pleural furrows (Plate 2: figure 13), which, together with the axial furrow along the margin of the seventh axial ring and posterior portion of the axis, define six prominent ribs. The pleural furrows die out on the outer portion to leave a border of width one-third that of the pleural region. Five interpleural furrows traverse the first five ribs, situated closer to the posterior than the anterior margin of the rib, and are deepest adjacent to the axial furrow, shallow medially, and deeper distally, where the first three extend on to the border. The sixth rib is unfurrowed.

External surface, except in furrows, bearing scattered granules varying in diameter; no regular arrangement of larger granules.

Discussion.—The relations between *Thelecalymene mammillata* and species of other genera are discussed above, and it is considered that *Thelecalymene* may be most closely related to *Gravicalymene,* though it has some characters in common with *Diacalymene.* A species of *Gravicalymene* is present in the lower part of the Maquoketa Shale (Ross, 1967, Plate 4: figures 14, 15), as is *Flexicalymene fayettensis* (Slocum, 1913; Ladd, 1929, p. 395; Whittington, 1954, p. 148), which appears to be a typical member of the genus. *"F." gracilis* (Slocum, 1913), from the highest member of the Maquoketa Shale (Ladd, 1929, p. 395), appears from Slocum's description to have the anterolateral margin of the frontal glabellar lobe closely approached by a buttress from the inner, anterior angle of the cheek. Such a structure is similar to that in the

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Plate 2.—*Thelecalymene mammillata* (Hall). 1, 5, Cranidium; dorsal and oblique views (× 2); AMNH 1408c, shales above the Galena Limestone, Maquoketa Creek, 12 miles west of Dubuque, Iowa (probably same locality and horizon as originals of figures 3 and 4 of this plate). 2, Glabella and part of left fixed cheek: dorsal view (× 2); AMNH 1408d, same locality as figures 1, 5 (above). 3, Incomplete hypostome: exterior view (× 3); MCZ 8672/1, Elgin Shaly Limestone Member, Maquoketa Shale, 0.25 mile southwest of Graf, Dubuque County, Iowa. 4, Free cheek: exterior view (× 3); MCZ 8672/3, same locality as figure 3 (above). 6, Pygidium: dorsal view (× 2); AMNH 1408e, same locality as figures 1, 5 (above). Original of Hall (1862, fig. 2). 7, 9, 10, Pygidium: right lateral, dorsal, and posterior views (× 2); on same slab as AMNH 1408e. 8, Pygidium: first axial ring and adjacent parts of pleural regions broken off, dorsal view (× 4.5); AMNH 1408g, same locality as figures 1, 5 (above). 11, Holotype cranidium: anterior view (× 2); AMNH 1408a (see also Plate 1: figures 5, 6). 12, Incomplete cranidium: anterior view, showing ventrally-facing portion of preglabellar field (× 2); AMNH 1408b, same locality as figures 1, 5 (above). 13, Oblique view (× 6) of same specimen as in figures 7, 9, 10 (above), showing details of external surface; first pleural furrow at extreme left, anterior band of first pleura broken off.


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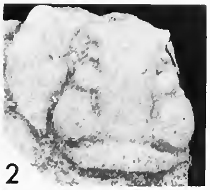
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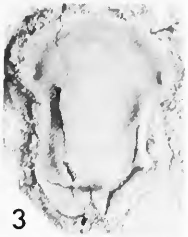
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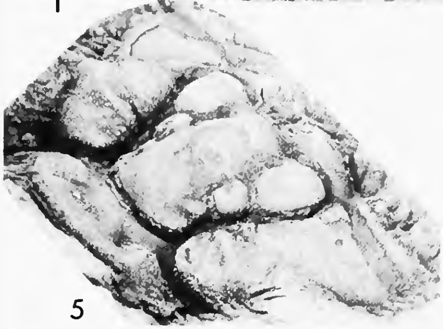
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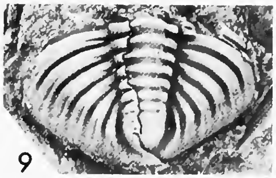
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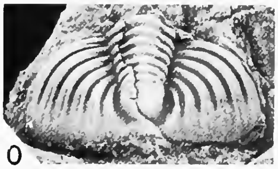
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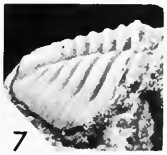
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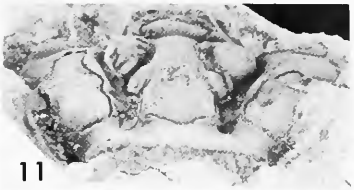
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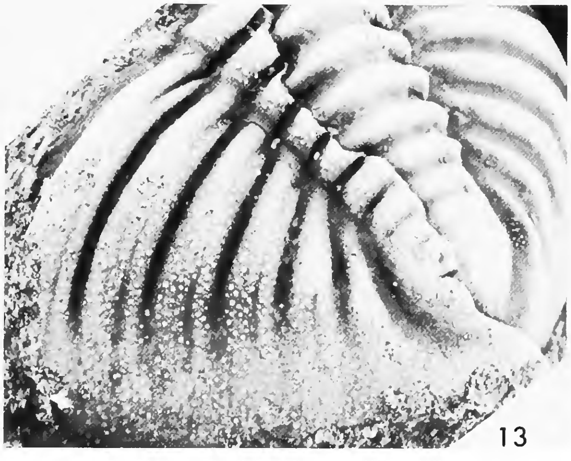
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PLATE 2

species *Papillicalymene husseyi* Stumm and Kauffman, 1958 (see above). However, Stumm and Kauffman (1958, p. 955), in discussing *"F." gracilis,* do not mention any buttress; evidently both *gracilis* and *husseyi* need further investigation.

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SILURIAN

Arturo J. Amos
and S. Noirat

A New Species of *Ancillotoechia* from the Zapla Formation, Northern Argentina

ABSTRACT

A new species of a trigonirhynchid brachiopod, *Ancillotoechia cooperensis,* is described from beds of probable Wenlockian age from the Province of Jujuy, Argentina. It is the first reported occurrence of the genus in the southern hemisphere.

The genus *Ancillotoechia* Havlícek (1959) is a trigonirhynchid brachiopod that McLaren (in Moore, 1965, p. H561) distinguished from similar genera—*Cupularostrum* Sartenaer (1961) and *Rostricellula* Ulrich and Cooper (1942)—because of its strong subrounded plications, covered septalium supported by a median septum in the brachial valve, and dental plates in the pedicle valve. Species of *Ancillotoechia* were described for the first time by Havlícek (1959) from the Bohemian Silurian: *A. ancillans* (Barrande) and *A. radvani* Havlícek from the lower beds of the Kopanina Limestones (Budňany) and *A. minerva* (Barrande) from the Liteň beds (Wenlock). Recently, a North American species from the St. Clair Limestone (Wenlockian), *Camarotoechia marginata* (Thomas), was included by Amsden (1968) in this genus.

The occurrence of *Ancillotoechia* in Argentina reported here is the first in the southern hemisphere. The specimens were collected in the northern part of the Sierra de Puesto Viejo near Las Chaquetas, or Chaqueta, east of San Juancito Chico, in the Province of Jujuy. Poorly preserved pelecypods were also found with the brachiopods.

The authors are indebted to Dr. R. Bellmann for the information given on the fossil locality and to Dr. C. Rayces for the loan of specimens of the Instituto de Geología y Minería (Jujuy).

Family TRIGONIRHYNCHIIDAE McLaren, 1965

Genus *Ancillotoechia* Havlícek, 1959

DIAGNOSIS.—Subcircular in outline with slightly divergent dental lamellae in the pedicle valve and a low median septum extending anteriorly as a low and delicate ridge in the brachial valve.

TYPE-SPECIES.—*Rhynchonella ancillans* Barrande, 1879.

Ancillotoechia cooperensis, new species

PLATE 1: FIGURES 1–14

DESCRIPTION.—The specimens are of medium size, subglobose with a subcircular outline. Maximum width at midlength of valves. Valves moderately convex. The ventral sulcus and brachial fold conspicuous anteriorly.

A few well-marked costae present in the sulcus, fold, and flanks. Anterior commissure uniplicate and serrated. No other ornamentation can be observed except delicate concentric growth lines. Shell structure unknown.

Pedicle exterior with moderately pointed umbo with apical angle of 118°. Sulcus well marked anteriorly, flanked by two well-rounded costae, with two costae originating at the umbo. In some specimens a third costa intercalates between the marginal and the sulcus

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costae near the posterior third of the valve. Flanks evenly convex with four costae, including the marginal.

Brachial exterior not so convex with fold less defined than corresponding sulcus, conspicuous at midlength with one costa. In some specimens a second costa intercalates between the marginal and the central costa. Flanks evenly convex with four costae including the marginal.

Pedicle interior with very short dental lamellae, dorsally divergent, leaving a large and deep umbonal cavity. Lateral cavities very small, usually filled with secondary growth. Teeth strong and subrounded.

Brachial interior with short septalium supported by a relatively short and thick septum. Septalium covered by small cardinal plate. Median septum extends anteriorly as a thin and low ridge to about midlength of valve. Short and strong crural processes directed ventrally.

Dimension of holotype and paratype (measurements in millimeters):

	Holotype (SJ 114d)	*Paratype* (SJ 114a)
Length of pedicle valve	14.5	11.6
Length of brachial valve	12.2	10.8
Thickness	10.0	7.9
Maximum width	14.9	11.3
Width of fold at commissure	6.2	2.1
Length/width ratio	0.97	1.0
Length/thickness ratio	1.45	1.46

MATERIAL.—Several steinkerns, external and internal impressions of ventral and brachial valves. Most of the specimens were found in ferruginous concretions.

LOCALITY.—Las Chaquetas, or Chaqueta, east of San Juancito Chico, Sierra de Puesto Viejo, Jujuy Province, Argentina.

TYPES.—Holotype, SJ 114d, and paratype, SJ 114a, in Instituto de Geología y Minería, Jujuy (IGM). Other specimens: SJ 113–17 (in IGM); MLP 10761–2 (in Museo de La Plata).

REMARKS.—This new species, in general, resembles the type of *Ancillotoechia ancillans* (Barrande), but it is subrounded and globose, with well-marked ribbing. Internally, the dental lamellae are slightly divergent, leaving a large umbonal cavity. Other described species are, however, very different in shape and ribbing. Internally, *A. marginata* (Thomas) from the St. Clair Limestone (Amsden, 1968) is similar, but externally is subtriangular in outline, with the surface covered by 4 or 5 costae in 3 mm.

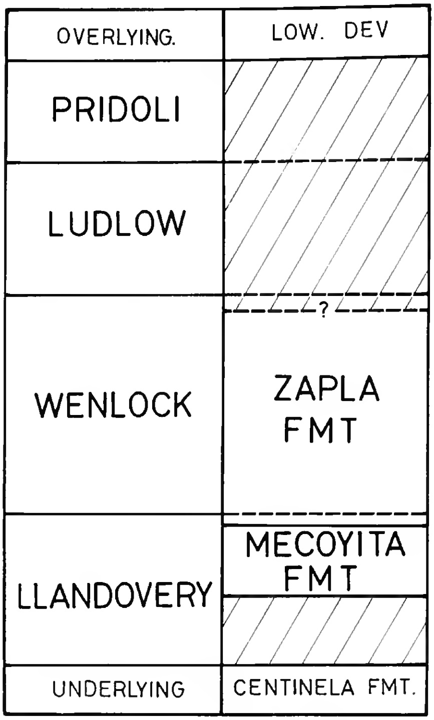

FIGURE 1.—Silurian stratigraphic sequence, northern Argentina.

Geologic Setting

Formations of Silurian age are exposed in northern Argentina along several sub-Andean ranges east of Jujuy City. Some exposures are also known near the Argentine-Bolivian border. Stratigraphically, the Silurian rocks lie unconformably on top of the Centinela Formation of Caradocian age (Harrington and Leanza, 1957, p. 8). The sequence starts with a marine glacial conglomerate, 30 meters thick, called Mecoyita Formation (Turner, 1960) or "Horizonte Glacial de Zapla." This formation was formerly considered the top of the Centinela Formation of Caradocian age by Harrington and Leanza (1957, p. 8), of Silurian age by Schlagintweit (1943). On top of the Mecoyita Formation lies the Zapla Formation, 640 meters thick, composed of dark gray to light blue, yellow and reddish shaly sandstones, and a ferruginous sandstone member about 5 to 25 meters thick near the base of the sequence. A paraconformity is evident between the Zapla Formation and the overlying Lower Devonian rocks (Figure 1).

Fossils were found in the Zapla Formation, collected during economic studies of high-grade iron ore found

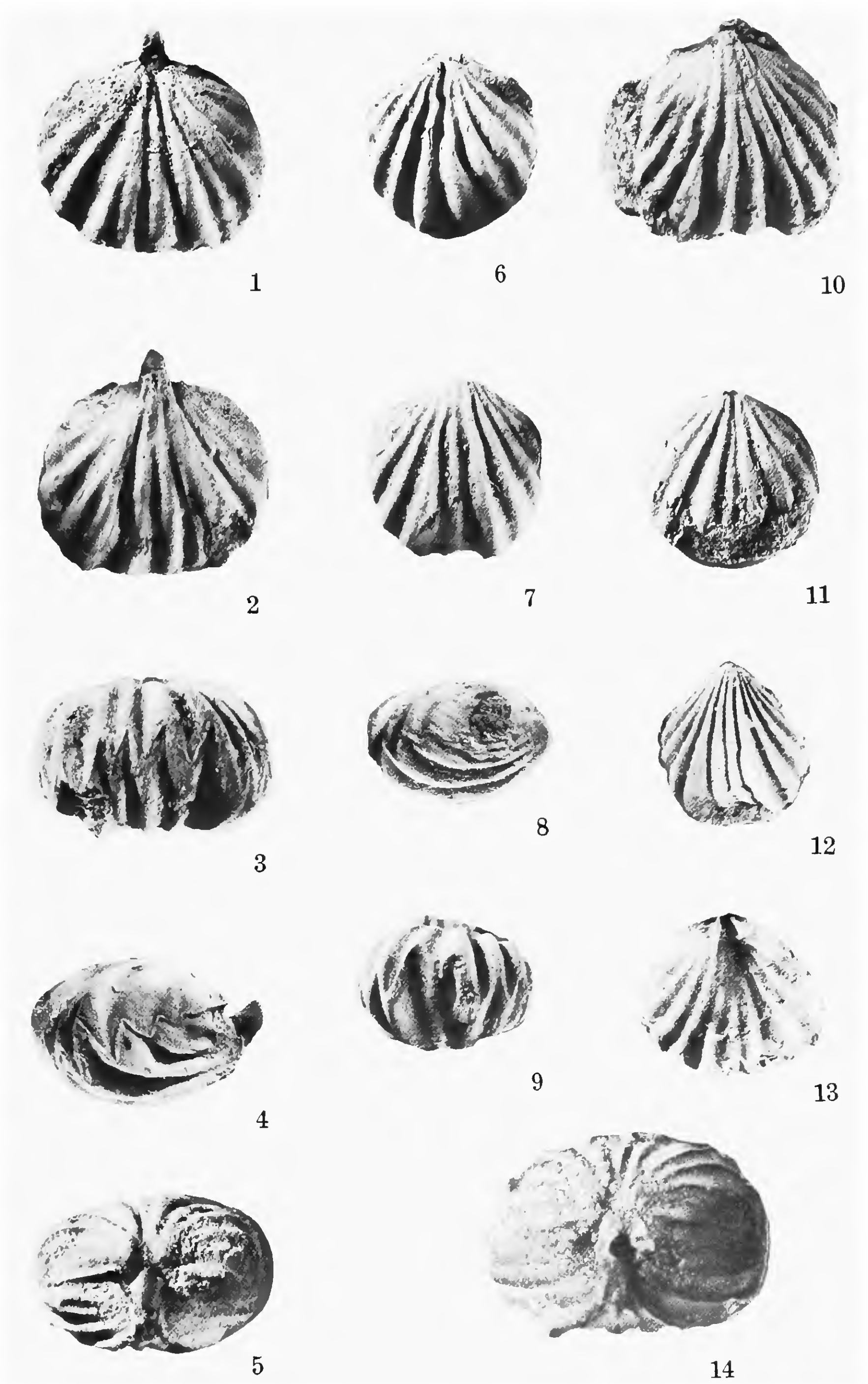

Plate 1.—*Ancillotoechia cooperensis,* new species. 1–5, Holotype, SJ 114d, (× 2): 1, brachial exterior; 2, pedicle exterior; 3, anterior commissure; 4, lateral view, 5, posterior view. 6–9, Paratype, SJ 114a (× 2): 6, brachial exterior; 7, pedicle exterior; 8, lateral view; 9, anterior commissure. 10–14, Other specimens: 10, pedicle exterior, SJ 115a; 11, brachial exterior, SJ 116a (× 2); 12, rubber mold of pedicle exterior, SJ 113c (× 2); 13, rubber mold of pedicle interior, MLP 10762 (× 2); 14, rubber mold of holotype, SJ 114d, posterior view (× 3).

in the ferruginous sandstone member. Fossils also were found during oil exploration in the sub-Andean ranges. However, no descriptions of the coelenterates, brachiopods, mollusks, trilobites, and graptolites have ever been made (Castellaro, 1966). Therefore, the age of the beds above the fossiliferous Ordovician was merely assumed or the age was assigned by comparison with known faunas of other parts of Argentina and Bolivia. For example, Angelelli (1946) mentioned the trilobite *Calymene* in his study of the Zapla ferruginous ore, and Cecioni (1953) mentioned finding a specimen of "*Homalonotus*." The *Calymene* was compared with *C. blumenbachi* by Harrington (1956), who also mentioned that the rocks of the Zapla area have yielded *Scotiella, Clarkeia,* and *Monograptus* cf. *priodon.*

The trilobites mentioned above are known to occur in formations from the Silurian up to the Middle Devonian in other parts of the world. The well-known Silurian guide fossil *Clarkeia antisiensis* (d'Orbigny) also has been mentioned in the geological literature of this area, but the authors were unable to verify this identification. This new species of *Ancillotoechia* is the first fossil ever to be described in Northern Argentina from the Silurian Period.

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Thomas W. Amsden

Triplesia alata Ulrich and Cooper

ABSTRACT

Ulrich and Cooper's description of *Triplesia alata,* 1936, was based on specimens from the "Brassfield" Limestone of Searcy County and the Batesville district of north-central Arkansas, but recent investigations indicate that the Batesville specimens are from the Cason Shale. This species is also present in the Blackgum Formation of eastern Oklahoma and in the Cochrane Formation of south-central Oklahoma. The strata bearing *Triplesia alata* are believed to be of early upper Llandoverian age (C1–2 zone) and slightly older than the Brassfield strata of Dayton, Ohio. This species has the typical, elongate, bifid triplesiid cardinal process with a hoodlike chilidium near its base. The chilidium fits into a shallow ventral delthyrium and the pseudodeltidium has a median ridge produced by a thickening of the shell. All known North American representatives of *Triplesia* sensu stricto are Llandoverian or older; Wenlockian species formerly assigned to this genus are now referred to *Placotriplesia.* The biostratigraphic distribution of these genera in European strata is uncertain.

Triplesia alata Ulrich and Cooper is distributed over a wide area in Arkansas and Oklahoma (Figure 1). It is present in strata of late Lower Silurian age (upper Llandoverian) and is thus one of the late representatives of the genus *Triplesia* sensu stricto. Miser (1922, p. 29, pl. 7a, figs. 1–3) first reported specimens from the "Brassfield" Limestone of the Batesville district in north-central Arkansas (referred to *Triplesia ortoni*). Later, Ulrich and Cooper (1936, p. 346, pl. 48, fig. 23, pl. 50, figs. 11, 14, 16, 17, 20, 21, 24) referred these shells to a new species, *Triplesia alata,* basing their description on specimens from the Batesville district, and from Searcy County, Arkansas. In 1960, I reported this species from the Cochrane Formation of the Arbuckle Mountains and Criner Hills in south-central Oklahoma (Amsden, 1960, p. 50), and later it was found in the Blackgum Formation of northeastern Oklahoma (Amsden and Rowland, 1965, pp. 15, 17, 21, 31, 93). The present study is based on specimens from the Searcy County and Batesville districts of Arkansas, including Ulrich and Cooper's type specimens, and on collections from the Blackgum and Cochrane Formations of Oklahoma. A study of these collections totaling over 100 specimens furnishes additional details on external and internal morphology and on the biostratigraphic and geographic distribution of this species. This study also supplies additional information on the morphology and biostratigraphic range of the subfamilies Triplesiinae and Placotriplesiinae.

I thank Dr. G. Arthur Cooper for the loan of the United States National Museum collections of *Triplesia alata* and *T. ortoni.* The repositories of the figured specimens are abbreviated as follows: United States National Museum, USNM; University of Oklahoma, OU.

Stratigraphic and Geographic Distribution

Ulrich and Cooper (1936, p. 346) based their description of *Triplesia alata* on specimens from the "Brassfield" Formation near Gilbert, Searcy County, Arkansas. These authors also noted that one specimen from the Brassfield at Soldiers Home, Dayton, Ohio, "has the characters of this species." The specimen which Ulrich and Cooper (1936, pl. 50, figs. 16, 17, 20, 21) illustrated from Cason Mine and which herein is designated the lectotype and refigured (Plate 2: figures 1–5) is the same specimen illustrated earlier by Miser (1922, pp. 28–29, pl. 7a, fig. 1) and reported to be from residual clays in the Montgomery Mine. The stratigraphic position of *T. alata* has been some-

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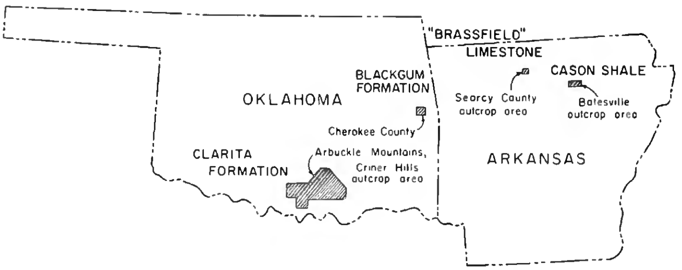

FIGURE 1.—Outcrop areas of the Cason Shale, "Brassfield" Limestone, Blackgum Formation and Cochrane Formation.

thing of a puzzle because at Cason Mine, and at most places in the Batesville district, the Cason Shale is directly overlain by typical St. Clair Limestone. The only megafossils heretofore reported from the Cason Shale are specimens of *Girvanella,* which Ulrich (in Miser, 1922, p. 28) assigned to an Upper Ordovician age. The overlying St. Clair Limestone is richly fossiliferous and yields many brachiopods, but includes no representative of this species, or of the genus *Triplesia* sensu stricto (Amsden, 1968, pp. 11, 12). It was, therefore, of considerable interest when, in September 1966, T. L. Rowland, O. A. Wise, Jr., and I visited Love Hollow Quarry and found a lens of limestone within the Cason Shale that yielded several specimens of *T. alata.* It now seems reasonable to assume that all of the specimens from the Batesville district originally came from some part of the Cason Shale (see Amsden, 1968, pp. 5–7). In the fall of 1967 I revisited Love Hollow and found that the limestone lens had been completely removed by quarry operations; however, its relationship to the Cason Shale and the overlying St. Clair Limestone has been illustrated (Amsden, 1968, fig. 5).

The Searcy County specimens are from the "Brassfield: Tomahawk Creek (?=Buffalo River), 6 miles east of St. Joe, ½ to 1 mile west of Gilbert" (Ulrich and Cooper, 1936, p. 346). I have not examined this limestone in the Gilbert area, but Maher and Lantz (1953) describe it as pink, crystalline limestone. In this region the "Brassfield" Limestone is reported to be underlain by the Cason Shale and overlain by the St. Clair Limestone. No representative of *T. alata* or of any form of the genus *Triplesia* has been reported from the St. Clair Limestone in the Gilbert area (Amsden, 1968, p. 9).

Triplesia alata is present in the upper ten feet of the Blackgum Formation at Blackgum Landing on the south shore of Lake Tenkiller (NW¼SW¼SE¼ sec. 32, T 14 N, R 22 E), Cherokee County, eastern Oklahoma (upper limestone member, stratigraphic section Ch2–D, Amsden and Rowland, 1965, p. 93). About 20 specimens have been found in the Blackgum Formation, where they are associated with *Microcardinalia protriplesiana* Amsden (1966, p. 1010).

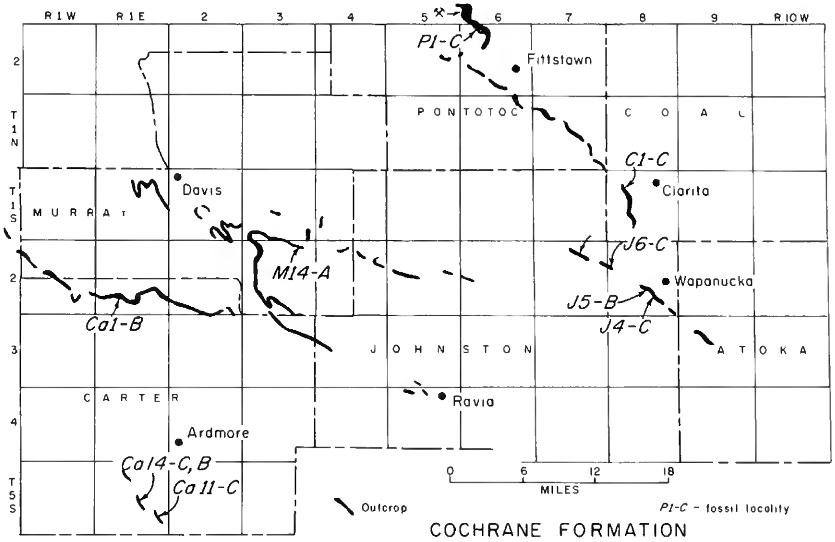

FIGURE 2.—Distribution of the Cochrane Formation in the Arbuckle Mountains and Criner Hills of Oklahoma. Numbers (P1–C, etc.) refer to collecting localities yielding specimens of *Triplesia alata* (see Amsden, 1960, appendix; modified from Amsden, 1960, fig. 15).

Triplesia alata is widely distributed in the Cochrane Formation of the Arbuckle Mountains and Criner Hills of south-central Oklahoma (Figure 2). About 100 specimens, many of which are articulated shells, have been collected from this formation at the following localities: C1–C (upper 5 ft.); Ca1–B (8 ft. above base); Ca11–C; Ca14–C, B; J4–C (upper 2 ft.); J5–B (5 ft. below top); M14–A; P1–C. Descriptions of these localities may be found in Amsden (1960, appendix). *Triplesia alata* also has been collected from loose blocks of Cochrane at the Ideal Cement Quarry (SE¼ sec 36, T 3 N, R 5 E), Pontotoc County, Oklahoma, and in Johnston County (SW¼ sec. 2, T 2 S, R 7 E), Oklahoma. The Cochrane has a maximum thickness in the Arbuckle Mountains-Criner Hills region of about 60 feet, and *T. alata* appears to range through most of the formation.

Age of the *Triplesia alata* Beds

The brachiopod fauna associated with the strata bearing *Triplesia alata* is small. The Cason Shale limestone lens at Love Hollow Quarry in the Batesville district does include representatives of *Plectodonta, Meristina, Streptis,* and a few others, but based on present knowledge none furnishes critical age data. Undoubtedly the most significant association is the presence of *Microcardinalia protriplesiana* in the beds of the Blackgum Formation bearing *Triplesia alata* in eastern Oklahoma. In 1966 I described this species and discussed its age in terms of the stricklandiid phylogenetic studies of Williams and of Boucot and Ehlers (Amsden, 1966, pp. 1010–1015, fig. 1). The structure of the dorsal apparatus of *Microcardinalia protriplesiana* is similar to that of *Stricklandia lens progressa* Williams from Llandovery strata in the C1–2 zone, suggesting a correlation with the early upper Llandoverian. On the other hand, *Microcardinalia triplesiana* (Foerste) from the Brassfield Formation at Soldiers Home, Dayton, Ohio, has a different dorsal structure; and, on the basis of these presumed phylogenetic differences, I concluded that Foerste's species was distinctly younger than *M. protriplesiana* and assigned it to zone C4–5. Carlson and Boucot (1967, p. 1122) have questioned this age relationship, pointing out, quite correctly, that *M. triplesiana* and *M. protriplesiana* have never been found in stratigraphic juxtaposition. The Brassfield at Soldiers Home also yields specimens of *Triplesia ortoni* (Meek), a species which is easily distinguished from *T. alata*. On the basis of this evidence it is here suggested that the beds bearing *T. alata* are correlative with one another, and are older than the *T. ortoni*

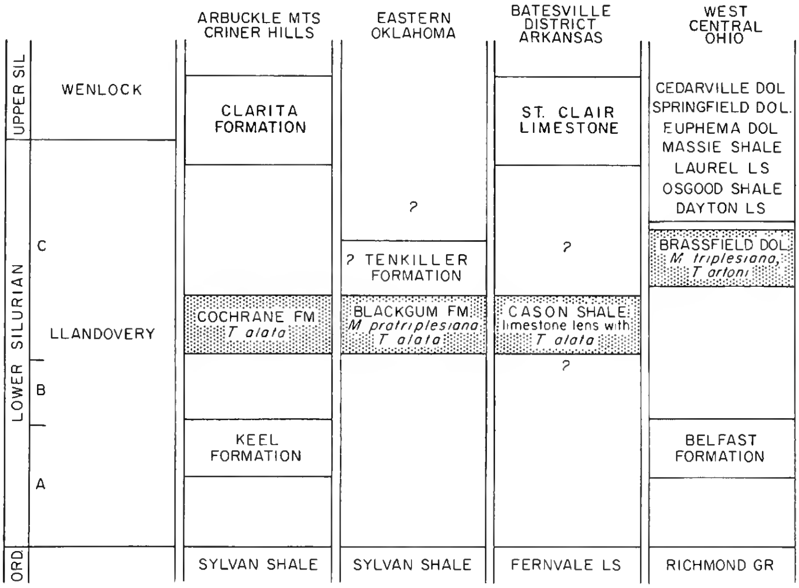

Figure 3.—Suggested correlation of the *Triplesia*-bearing beds (dotted) in Oklahoma, Arkansas, and western Ohio, and the brachiopod-bearing strata (toned) of the St. Clair Limestone and Clarita Formation. The ages of the other strata shown are not given detailed consideration in the present report.

beds as shown in Figure 3. *Microcardinalia protriplesiana* is found only in the Blackgum Formation, and its correlation with the Cochrane Formation and Cason Limestone lens is based almost entirely on the presence of *Triplesia alata*, there being little corroborative brachiopod evidence. It is emphasized that this correlation is proposed only for the beds of the Cason Shale bearing *T. alata* and that the other parts of this stratigraphic unit may have a different age.

Rexroad (1967, pp. 12–14) has pointed out that there is a discrepancy between the age of the Brassfield Formation as determined by conodont correlations with the standard British section and the age based on brachiopod correlations. According to that author the Brassfield conodonts in the Cincinnati Arch region—and this includes the Brassfield at Soldiers Home, Dayton, Ohio (Rexroad, 1967, locality 15, p. 19), represent the upper part of Walliser's Bereich I zone. This part of the Bereich I zone, which includes the *Monograptus cyphus, M. gregarius, M. convolutus* graptolite zones, falls almost entirely within the middle Llandovery zone B. In contrast, *M. triplesiana* from the Brassfield at Dayton indicates a correlation with upper Llandoverian zone C4–5, and even *M. protriplesiana*, which is the oldest *Microcardinalia* zone now recognized in Ohio, Arkansas, Oklahoma, and Nebraska, falls in the upper Llandoverian zone C1–2 and is younger than Bereich I.

The genus *Triplesia*, based on *T. extans* (Emmons) from the Middle Ordovician, generally has been defined to include species ranging into the Wenlockian. I suspect, however, that most if not all of the Wenlockian species referred to *Triplesia* actually are representatives of *Placotriplesia* (Amsden, 1968, p. 40) and, at least in eastern North America, *Triplesia* sensu stricto appears to be confined to Llandoverian and older strata (see discussion under Triplesiinae and Placotriplesiinae).

Internal and External Morphology

As Ulrich and Cooper (1936, p. 346) have given a detailed description of the external characters of *Triplesia alata*, only a few points, concerned mainly with the effect of growth on relative shell proportions, need be discussed here. Immature specimens of *T. alata*, i.e., shells under ten millimeters long, have an erect ventral beak which stands well above the brachial umbo. The fold and sulcus on these small individuals are shallow and poorly defined, and the width is only slightly greater than the length (length/width ratio about 0.80; see Figure 4). With increased size the dorsal umbo becomes swollen so that it stands as high or higher than the pedicle beak, and the ventral sulcus and dorsal fold develop into strong, well-defined shell features. The lateral component of growth at this later stage of development was much stronger than the anterior component, so that large specimens are markedly transverse; the length/width ratio among specimens over 15 millimeters long generally falls between 0.65 and 0.70 (Figure 4). All shells are essentially smooth, although a few of the largest individuals may show faint plications. Specimens from the Cason Shale (limestone lens) near Batesville, the "Brassfield" Limestone of Searcy County, and the Blackgum and Cochrane Formations of Oklahoma appear to be similar in all respects.

Triplesia alata has the characteristic, prominent triplesiid cardinal process (Figure 5; Plate 1: figures 2–4). This process has a long shaft which bifurcates, producing two rodlike myophores extending into the posterior part of the ventral valve. Each myophore is partially cleft, probably to give the diductor muscles a better point of attachment. The base of the cardinal process is much thickened and expanded laterally to produce a stout structure out of which the sockets are excavated. A small collarlike or hoodlike structure is present on the dorsal side of the cardinal process near the base. The ventral interarea is well developed, and the stout teeth are supported on long dental plates. The pseudodeltidium is marked by a thickening of the shell wall which produces a ridge on the external and internal side of the interarea; this ridge is clearly a part of the interarea, as the growth lines of the latter pass without interruption through the pseudodeltidium (Figure 5; Plate 1: figure 1). Near the front margin the pseudodeltidium is notched back (i.e., posteriorly) to make a delthyrial opening into which the cardinal process collar fits (Figures 5c, 6). Presumably the collar corresponds to the chilidium, although this structure in the triplesiids is small because of the extravagantly developed cardinal process. The adductor muscles make four moderately deep scars in the brachial valve (Plate 2: figure 3). The pedicle muscle scars have not been observed in *T. alata*, but they probably are similar to those in *T. ortoni* (Plate 2: figure 12).

Triplesia alata is most similar to *Triplesia anticostiensis* Twenhofel (1914, p. 26; 1928, p. 198, pl. 18, figs. 1–5) from the lower part of the Jupiter Forma-

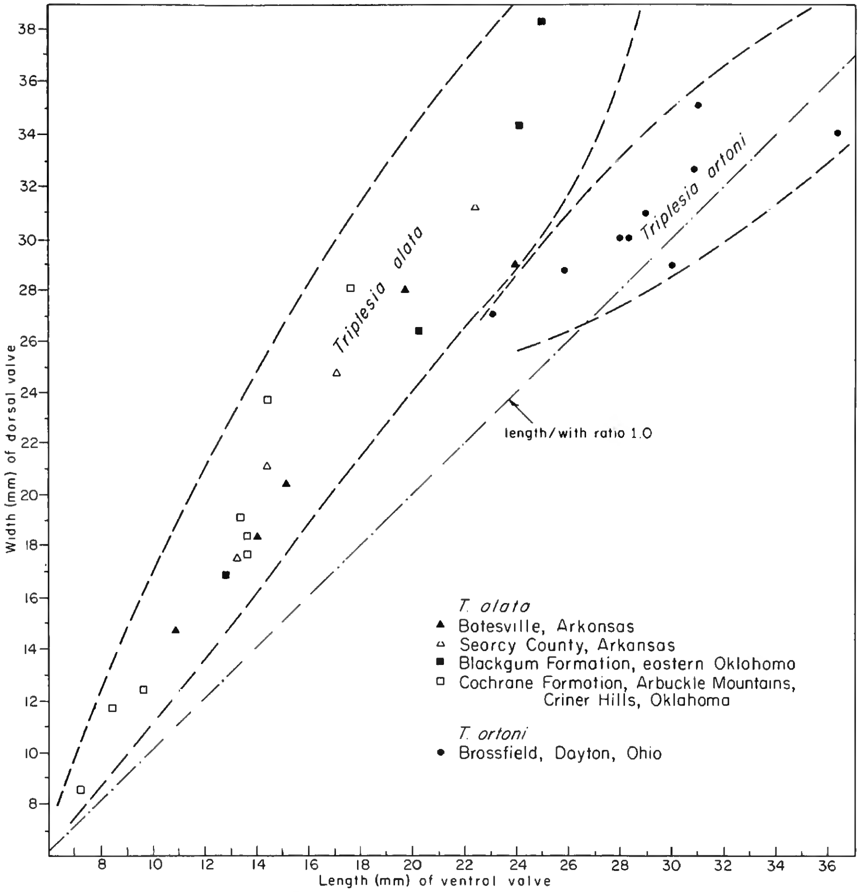

FIGURE 4.—Comparison of the length-width relationship (dorsal valve) of *Triplesia alata* Ulrich and Cooper, from the Cason Shale and "Brassfield" Limestone of Arkansas and the Cochrane and Blackgum Formations of Oklahoma, with *Triplesia ortoni* (Meek), from the Brassfield Formation at Soldiers Home, Dayton, Ohio.

tion (late Llandovery) on Anticosti Island. *T. anticostiensis* originally was described as a subspecies of *Triplesia insularis* (Eichwald), but the European species has a much different external form and *T. anticostiensis* would appear to be no more closely related to it than to *T. alata* or *T. ortoni*. Both *T. anticostiensis* and *T. alata* have a strongly transverse shell with broad, well-defined brachial fold and pedicle sulcus; however, the Anticosti species has a much more swollen brachial umbo, and the cardinal margins are rounded and lack the "ears" of *T. alata*. Also, *T. alata* is similar to *Triplesia ortoni* (see Plate 2: figures 6–17; also, Meek, 1872, p. 280; Hall and Clarke, 1892, pl. 11c, figs. 21, 28, 32, 34, 35) from the Brassfield Formation, Soldiers Home, Dayton, Ohio, but the two species can be readily distinguished by differences in outline and shape. As noted by Ulrich and Cooper, the cardinal extremities in *T. alata* are flattened and drawn out into "ears," whereas in *T. ortoni* this part of the shell is rounded. Moreover, mature shells of *T. alata* have a decidedly transverse outline with a length/width ratio ranging from about 0.7 to 0.8 while *T. ortoni* has a more-elongate outline with a length/width ratio ranging from about 0.9 to 1.0 (Figure 4). Finally, the fold and sulcus of *T. alata* are well-defined structures with steep margins, whereas in *T. ortoni* these are more rounded with less sharply delineated lateral margins.

The internal characters of *Triplesia alata* and *T. ortoni* are similar. The United States National Museum collections include two excellent dorsal interiors of *T. ortoni* with nearly complete cardinal processes. One of these shows the cardinal process hood (Plate 2: figures 15–17); the other shows the cleft extremities

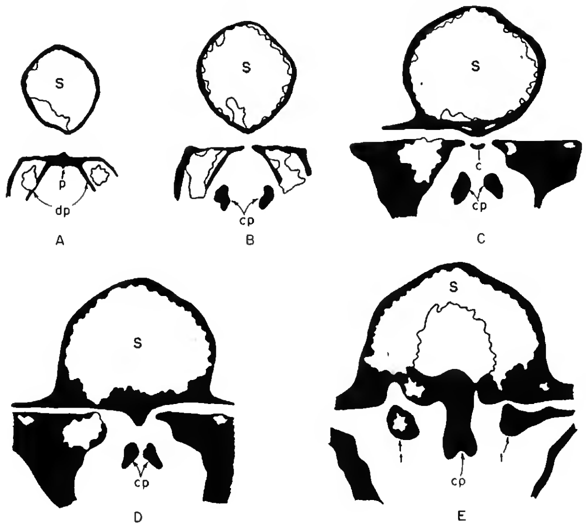

FIGURE 5.—Transverse serial sections (× 3.7) of *Triplesia alata* Ulrich and Cooper, Blackgum Formation, Blackgum Landing, Lake Tenkiller, SE¼SW¼, sec. 32, T 14 N, R. 22 E (stratigraphic section Ch2–D, Amsden and Rowland, 1965, p. 93). Ventral valve incomplete; toned areas (S) represent portions obscured by silicification; cp, cardinal process; dp, dental plate; c, collar; p, pseudodeltidial ridge; t, tooth. Portions of peels A, D, E are illustrated on Plate 2: figures 1, 2, 4. Distance (mm) from posterior tip of ventral beak: A, 0.5; B, 1.6; C, 1.9; D, 2.1; E, 2.2. Peels, OU 5681.

of the cardinal process and the basal portion of the process including the sockets (Plate 2: figures 13, 14, 16). The United States National Museum collections also include a ventral valve showing the pseudodeltidium and the muscle scars (Plate 2: figure 12).

Subfamilies Triplesiinae and Placotriplesiinae

In 1968, I proposed the new genus *Placotriplesia* for smooth triplesiids with a ventral sulcus and dorsal fold and with a flat pseudodeltidium which lacked a median ridge (Amsden, 1968, p. 40). Prior to this it had been assumed that all triplesiids have a pseudodeltidium with a median ridge or fold, and the family had been so diagnosed (Wright, 1963, p. 741). The discovery of shells with a flat pseudodeltidium made it necessary to emend the family Triplesiidae, subfamily Triplesiinae, and genus *Triplesia* and to introduce a new subfamily, the Placotriplesiinae. The present study of *Triplesia alata* and *T. ortoni* furnishes some additional details on the distinction between the subfamilies Triplesiinae and Placotriplesiinae. In the subfamily Triplesiinae, as exemplified by *T. alata* and *T. ortoni,* the delthyrium is almost completely closed by a pseudodeltidium (Figure 6). This structure is commonly described as having a median fold, but in *T. alata* it consists of a thickening of the shell wall to produce a ridge. This pseudodeltidial ridge does not extend forward until it is flush with the leading edge of the ventral interarea; instead, it is recessed posteriorly to produce a small delthyrial opening into which the cardinal process collar fits. The function of the ridge is conjectural, although it may represent a strengthening of the shell at a point of weakness associated with the articulation. It should be noted that there is no break in the growth layers of the shell as they pass through the pseudodeltidium, and if the ridge were not present there would be no evidence for any pseudodeltidium. The ventral interior of *T. ortoni* (see Plate 2: figures 12, 14) is interesting because it has a small pit, just posterior to the muscle scars, which probably enters a small canal leading through the thickened shell wall to the pedicle opening. No such structure has been observed in *T. alata,* although the preservation of the specimens under study is such that it seems unlikely this would have been preserved.

The subfamily Triplesiinae ranges from the Middle Ordovician (Llanvirn) to the Upper Silurian (Wenlockian). The geographic and stratigraphic distribution of representatives of this subfamily, and, in fact, of all the Triplesiidae, is erratic, but at the present time 14 species representing seven genera and subgenera are known from Silurian strata in North America:

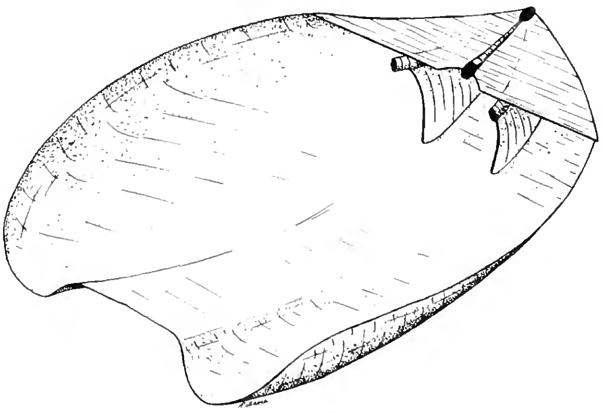

FIGURE 6.—Pedicle valve of *Triplesia alata* showing structure of the palintrope, delthyrium, pseudodeltidium, teeth, and dental plates.

WENLOCKIAN

Oxoplecia? niagarensis (Hall and Clarke); "Niagaran"dolomites near Milwaukee, Wisconsin
O. infrequens Ulrich and Cooper: St. Clair Limestone
Streptis glomerata Ulrich and Cooper: St. Clair Limestone
Brachymimulus americanus Ulrich and Cooper: St. Clair Limstone, Clarita Formation
?B. elongatus Ulrich and Cooper: St. Clair Limestone
Onychotreta (*Onychotreta*) *mesleri* Ulrich and Cooper: St. Clair Limestone
O. (*O.*) *multiplicata* Ulrich and Cooper: St. Clair Limestone, Clarita Formation
O. (*O.*) *angustata* Ulrich and Cooper: St. Clair Limestone
O. (*O.*) *miseri* Ulrich and Cooper: St. Clair Limestone
Onychotreta (*Eilotreta*) *lenta* (Thomas): St. Clair Limestone
Onychotreta (*Lissotreta*) *plicata* Ulrich and Cooper: St. Clair Limestone

LLANDOVERIAN

Triplesia ortoni (Meek): Brassfield Formation
T. anticostiensis Twenhofel: Jupiter Formation
T. alata Ulrich and Cooper: Cason Shale (limestone lens)

The Placotriplesiinae do not possess a pseudodeltidium ridge or fold. Serial sections (Figures 7, 8) show no evidence of any internal or external thickening of the shell wall at this point, and the interarea of well-preserved specimens (Plate 2: figure 18) reveals no structure of this kind. In fact, it is not possible to determine the position of the dental plates from the exterior, and the pseudodeltidium is in no way distinguished from the pedicle interarea, other than its arbitrary designation as that part of the shell between the dental plates. The cardinal process is strongly developed and appears similar to that of the other representatives of the Triplesiidae; however, it is not known whether it has a collar, or if there was any delthyrial opening developed near the front edge of the pseudodeltidium. Almost all information pertaining to this subfamily is based on *Placotriplesia praecipta,* which has such a small shell that these structures, if present, would be minute.

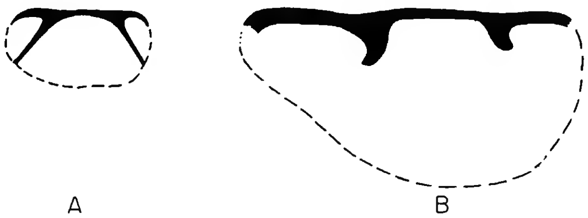

FIGURE 7.—Transverse serial sections (× 11) of pedicle valve of *Placotriplesia praecipta* (Ulrich and Cooper). Clarita Formation, Chimneyhill Creek, NE¼SE¼ sec. 5, T 2 N, R 6 E, Pontotoc County, Oklahoma (stratigraphic section P1–F; Amsden, 1960, p. 268). Distance (mm) from posterior tip of pedicle beak: A, 0.3; B, 0.6. Peels, OU 5699.

The subfamily Placotriplesiinae presently is known only from strata of Wenlockian age. North American species include *Placotriplesia praecipta* (Ulrich and Cooper) and *P. juvenis* (Ulrich and Cooper) from the St. Clair Limestone of Arkansas and the Clairita Formation, Fitzhugh Member, of Oklahoma, and *P. waldronensis* (Miller and Dyer) and *P. rostellata* (Ulrich and Cooper) from the Waldron Shale. (An examination of specimens from the Waldron Shale and the St. Clair Limestone, including Ulrich and Cooper's type specimens of *P. juvenis* and *P. rostellata* confirms the absence of a median ridge on the pseudodeltidium). The youngest known North American representatives of *Triplesia* sensu stricto are from strata of late Llandovery age, as shown in Figure 9. The distribution of *Placotriplesia* and *Triplesia* in European strata is uncertain. Barrande (1879, pl. 9, figs. 3, 6) illustrated two smooth triplesiids which could be representatives of *Placotriplesia: Mimulus moera* and *M. contrarius.* Unfortunately, Barrande's illustrations do not show clearly the structure of the interarea, and the species should be restudied. Davidson's (1871, p. 273, pl. 37, figs. 8–15; 1883, p. 143, pl. 9, figs. 17–22) description and illustrations of *Triplesia insularis* (Eichwald) indicate a median ridge on the pseudodeltidium. According to Davidson, this species ranges into upper Llandoverian strata in Wales and the Welsh borderland. *Triplesia glabra* Williams (1951, p. 104, pl. 5, figs. 9–11) from upper Llandovery strata (C–1) has a median pseudodeltidial ridge, and *T. woodlandensis* Reed (1905, p. 910, pl. 20, figs. 8–16) from Llandoverian strata in the Girvan district probably has a median ridge (see Reed, 1905, pl. 20, fig. 10a). *Triplesia wenlockensis* Davidson (1883, p. 144, pl. 8, fig. 23) has a pseudodeltidial ridge, but apparently there

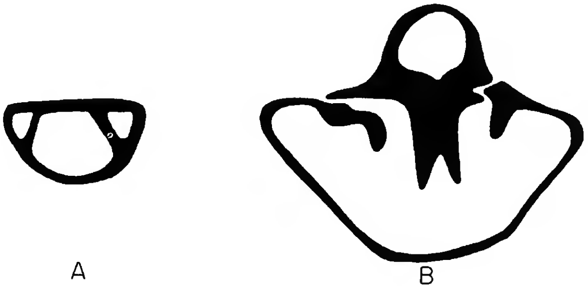

FIGURE 8.—Transverse serial peels (× 12) of *Placotriplesia praecipta,* St. Clair Limestone, Cason Mine, Batesville district, Arkansas. Distance from posterior tip of pedicle beak: A, 0.3 mm; B, 0.6 mm. Peels, OU 5698.

is some question concerning the Wenlockian age of this species. Further study of British and Czechoslovakian species is needed to determine if the genus *Placotriplesia* is actually represented and to determine the precise range of *Triplesia* sensu stricto. To my knowledge no representatives of the Triplesiidae have been reported from Silurian rocks on the island of Gotland.

A recently published article by W. W. Craig (1969) summarizes information on conodont zonation in the Batesville district, Arkansas. It is difficult on the basis of the biostratigraphic and lithostratigraphic data now available to precisely correlate these conodont zones with the brachiopod faunas of the Batesville district, but presumably the *Triplesia alata* beds are at least in part equivalent to Craig's pelmatozoan limestone representing the "*celloni*-zone (W) and upper Bereich I (W)." According to Craig (1969, p. 1625), "The conodonts of the Cason pelmatozoan biosparite are closely comparable to those of the Brassfield Limestone of the Cincinnati Arch region (Rexroad, 1967; Nicoll and Rexroad, 1968) and it seems likely that it was this unit that produced the macrofossils that were identified by Ulrich (*in* Miser, 1922, p. 29) as belonging to species common to the Brassfield Limestone."

As noted in the preceding discussion, the present study indicates that the *T. alata* beds of the Batesville district are slightly older than the *T. ortoni* beds of the Dayton region; moreover, the brachiopod faunas suggest that both the *T ortoni* and *T. alata* faunas should be assigned to the upper Llandovery Zone C, whereas Rexroad correlates the conodont faunas of the Brassfield of Dayton with the upper Bereich I zone, which he assigns to the middle Llandovery Zone B. The brachiopod fauna of the St. Clair Limestone that I recently described (Amsden, 1968) falls largely, perhaps entirely, within Craig's "*sagitta* zone," al-

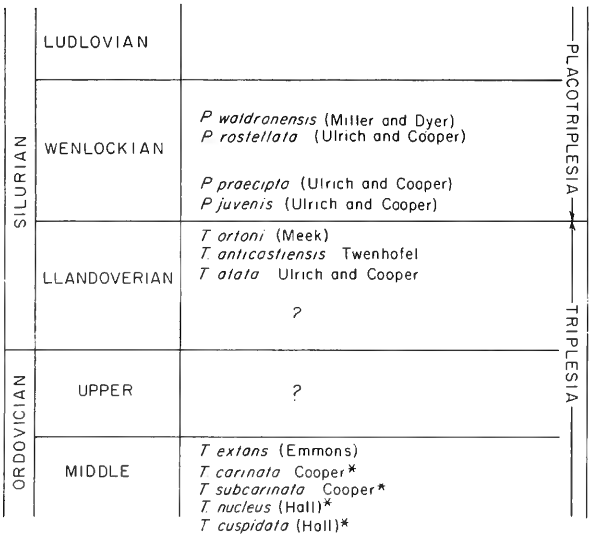

FIGURE 9.—Distribution of North American species of *Triplesia* and *Placotriplesia*. The structure of the pseudodeltidium on species marked with an asterisk has not been determined.

PLATE 1: figures 1–4, 13–15, 21.—*Triplesia alata* Ulrich and Cooper, Blackgum Formation, upper limestone member, south shore of Lake Tenkiller, SE¼SW¼, sec. 32, T 14 N, R 22 E, Cherokee County, Oklahoma (loc. Ch2–D, Amsden and Rowland, 1965, p. 93). 1–4, Transverse serial sections (see Figure 5 for other illustrations of this series): 1, part of pedicle palintrope showing dental plates and pseudeltidial ridge (× 12), 0.9 mm in front of beak; 2, brachial cardinalia showing bifid tips of cardinal process (× 8) at 1.9 mm; 3, brachial cardinalia (× 8) at 2.1 mm; 4, brachial cardinalia (× 8) at 2.2 mm., OU 5681. 13, Posterior view of a nearly complete articulated shell (× 1), OU 5688. 14, Brachial view of a large specimen (× 1), OU 5689. 15, Pedicle view (× 1), OU 5690. 21, Brachial view (× 1), OU 5691.

Figures 5–10, 12.—*Triplesia alata* Ulrich and Cooper, Cochrane Formation, Arbuckle Mountain-Criner Hills region, Carter County, southcentral Oklahoma. Specimen in figure 5 is from Rock Crossing, NE¼SE¼, sec. 35, T 5 S, R 1 E (loc. Ca11–C. Amsden, 1960, p. 208); specimens in figures 6–10, 12 are from Henryhouse Creek, SE¼ sec. 30, T 2 S, R 1 E (eight feet above base of the formation). 5, Brachial valve (× 1), OU 5682; 6, 7, lateral view (× 2) and posterior view (× 1) of an incomplete shell, OU 5683; 8, anterior view (× 1), OU 5684; 9, pedicle view (× 1), OU 5685; 10, lateral view (× 2) of a small shell, OU 5686; 12, pedicle view (× 1), OU 5687.

Figures 11, 16–20.—*Triplesia alata* Ulrich and Cooper, Cason Shale, limestone lens, Love Hollow quarry, SW¼ sec 4, T 14 N, R 8 W, Batesville district, Izzard County, Arkansas (see Amsden, 1968, p. 6); all views natural size. 11, pedicle view of small shell, OU 5692; 16, pedicle view, OU 5693; 17, brachial view, OU 5694; 18, pedicle view, OU 5695; 19, pedicle view of a large specimen, OU 5697; 20, brachial view, OU 5696.

Figures 22–25.—*Triplesia alata* Ulrich and Cooper, United States National Museum specimens from the "Brassfield" Limestone, Searcy County, Arkansas; all views natural size. Specimen in figure 22 is from Tomahawk Creek, six miles east of St. Joe; specimens in figures 23–25 are from one-half to one mile west of Gilbert. 22, brachial view of USNM 91874 (figured by Ulrich and Cooper, 1936, pl. 50, fig. 11); 23, pedicle view of USNM 91873, an unfigured paratype; 24, pedicle view of USNM 91873a (figured by Ulrich and Cooper, 1936, pl. 50, fig. 24); 25, brachial view of USNM 91873 (shell figured by Ulrich and Cooper, 1950, pl. 50, fig. 14).

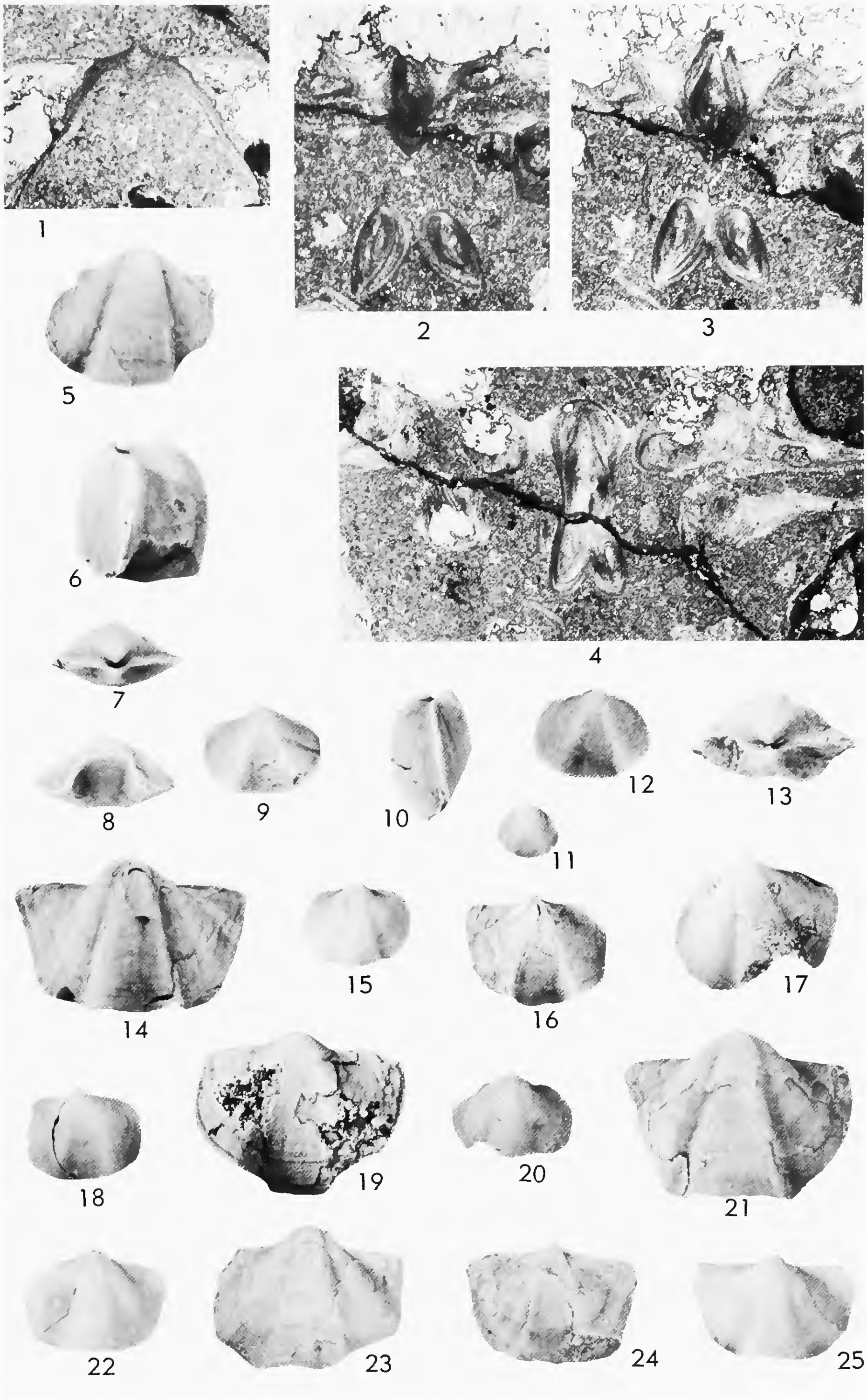

PLATE 1

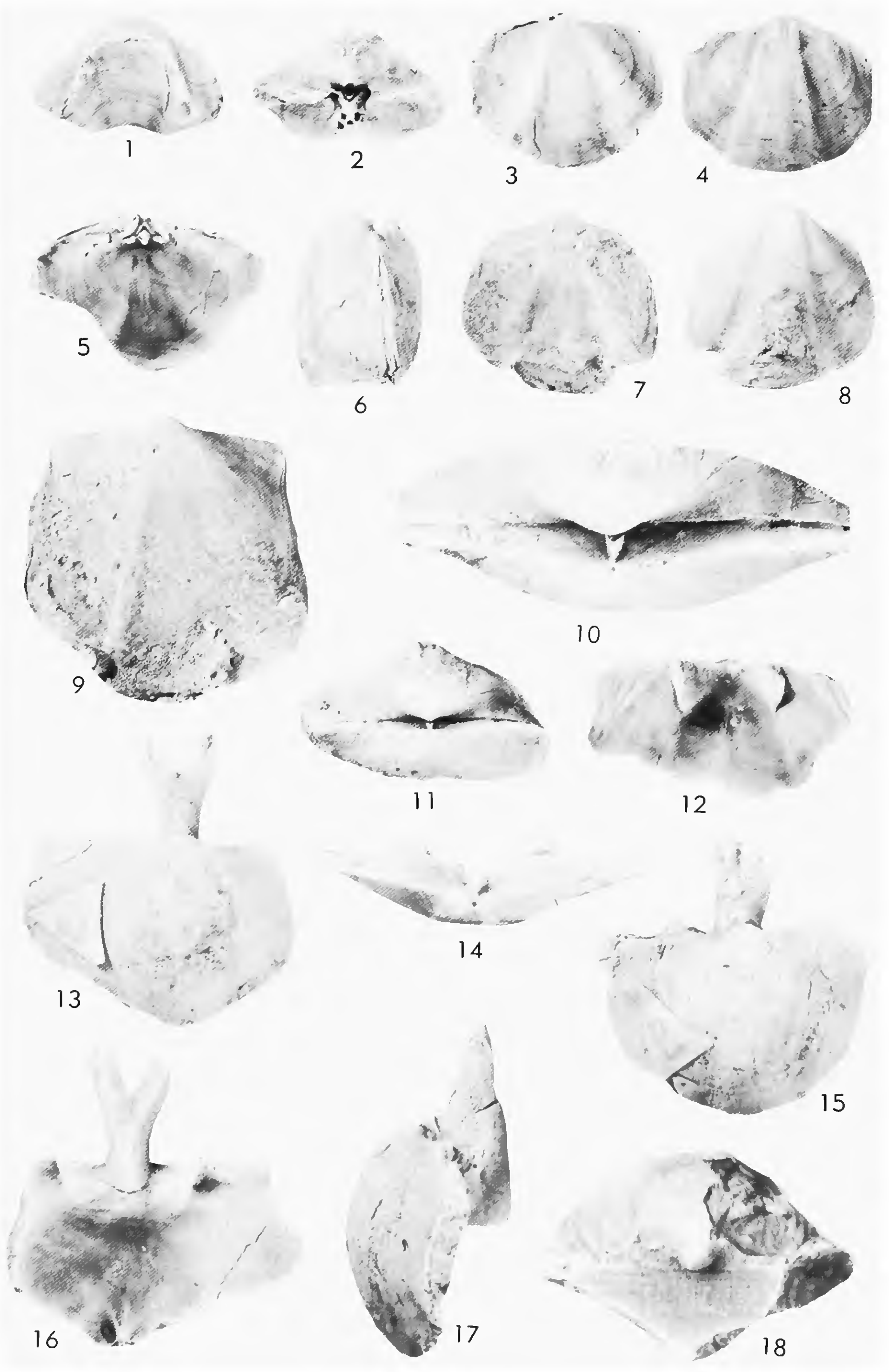

PLATE 2

though there could be some overlap on the underlying "*amorphognathoides*" and overlying "*siluricus*" conodont zones.

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PLATE 2: figures 1–5.—*Triplesia alata* Ulrich and Cooper. "Brassfield Formation" (probably from the Cason Shale), Cason Mine (?Montgomery Mine), Batesville district, Arkansas. This steinkern was illustrated by Miser (1922, pl. 7, fig. 1) as *Triplesia ortoni* from the Montgomery Mine; it was re-illustrated by Ulrich and Cooper (1936, pl. 50, figs. 16, 17, 20, 21), who assigned it to their new species *T. alata* and cited the locality as Cason Mine, USNM 91872. This specimen is here designated as the lectotype. Views are natural size. 1–4, anterior, posterior, pedicle, and brachial views; 5, rubber cast of the brachial valve showing muscle scars and incomplete cardinal process.

Figures 6–17.—*Triplesia ortoni* (Meek), Brassfield Formation, Soldiers Home, Dayton, Ohio. 6–8, Lateral, pedicle, and brachial views (× 1). USNM 85136a (figured in Shimer and Shrock, 1944, pl. 117, figs. 19–21); 9–11, pedicle (× 1.3), posterior (× 2), and posterior (× 1) views of a large shell, USNM 85136b; 12, 14, interior (× 2) and posterior (× 3) views of an incomplete pedicle valve, USNM 91871b (figured by Ulrich and Cooper, 1936, pl. 48, fig. 32); 13, 16, exterior and interior views (× 3) of the cardinal process, USNM 91871; 15, 17, external and lateral views of a dorsal cardinalia showing collar or chilidium, USNM 9187a (illustrated by Ulrich and Cooper, 1936, pl. 48, figs. 34, 35).

Figure 18.—*Placotriplesia praecipta* (Ulrich and Cooper), Clarita Formation, Fitzhugh Member, Chimneyhill Creek, NE¼SE¼ sec 5, T 2 N, R 6 E, Pontotoc County, Oklahoma. Posterior view (× 7) showing palintrope with no evidence of pseudodeltidium. (This is specimen OU 6368, illustrated in Amsden, 1968, pl. 18, fig. 3k.)

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Arthur J. Boucot

Aenigmastrophia, New Genus, a Difficult Silurian Brachiopod

ABSTRACT

A new genus of strophic shell, collected from Late Silurian (Ludlow) age beds in northern California and north-central Nevada, is described. The familial affinities of this shell are reviewed, and it is concluded that it cannot be placed in any presently defined family category. The limited material precludes additional work on the problem at this time.

During the summer of 1964 I visited several Late Silurian and Early Devonian fossil localities—discovered by Mr. Rodney Gregg, Gazelle, California, a former field assistant for Dr. Francis Wells of the United States Geological Survey—in the area between Gazelle and Callahan in the Klamath Mountains of northern California. At one of these localities—United States National Museum (USNM) locality 11162—a number of blocks of sandstone rich in plicate pentamerinids (*Kirkidium* sp.) were collected. During the preparation of these blocks, which had a total weight of about 100 pounds, there were obtained two specimens of a large, completely unfamiliar, strophic shell. Informal consultation with colleagues during the next few years produced no substantial suggestions as to the affinities of these two specimens, which were relegated to a drawer of unidentified brachiopods.

During the summer of 1965, in collaboration with Dr. Michael Murphy, of the University of California at Riverside, I began an extensive program of fossil collecting from the Roberts Mountains Formation in several areas on the north and west sides of the Roberts Mountains of Eureka County, Nevada. The subsequent processing of many tons of Silurian limestone containing silicified brachiopods produced (during sorting by Dr. J. G. Johnson) three specimens from USNM localities 13257 and 13237 that were identical, in most respects, to the two unfamiliar specimens collected earlier with Mr. Gregg in the Klamath Mountains.

The Klamath Mountain locality is difficult to date other than as Late Wenlock to Ludlow age. The fossils obtained from this locality are as follows: *Kirkidium* sp. (flat type), *Atrypella* cf. *A. prunum, Atrypa "recticularis," Howellella* sp., and tetracorals (sent to Dr. C. W. Merriam for study).

The occurrence of *Atrypella* in association with *Kirkidium* is suggestive of a Ludlow rather than a Pridoli age. *Kirkidium* does not normally range above the Ludlow—with the exception of a few spots in the Old World—and is unknown in proved Pridoli age beds in North America. The Klamath Mountain locality cannot, at present, be tied into the occurrences in the Peyton Ranch Limestone Member of the Gazelle Formation (which is exposed a few miles to the east) because of lack of mapping in this region. Relatively detailed mapping of the area of Silurian rocks exposed to the west of Gazelle during the summer of 1963 did not turn up any fossiliferous sandstone of the kind yielding fossils from Gregg's locality, which is a few miles farther west. All of the shelly fossils in the Gazelle area have been collected from either the Peyton Ranch Limestone Member or calcareous shales occurring no more than a few meters below the base of the limestone. It is possible that Gregg's locality represents a

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lateral equivalent of the Gazelle Formation, which includes a variety of rock types, but it also it possible that the locality represents a higher horizon than is preserved in the Gazelle area. The Peyton Ranch Limestone Member appears to be the highest Silurian unit preserved in that area.

The age of the Roberts Mountains Formation occurrence (USNM loc. 13257) is known with far more certainty. The new genus occurs with *Ptychopleurella* sp., *Dolerorthis* sp., *Dalejina* sp., *Isorthis* sp., *Kirkidium* sp. (both small fine-ribbed and large fine-ribbed), *Cymbidium* sp. (coarsely plicate and finely plicate forms), *Gypidula* sp., orthotetacid brachiopod, *Atrypa* sp., *Atrypella* sp., *Spirigerina* cf. *S. marginalis, Gracianella crista, Nucleospira* sp., *Howellella?* sp., and *Alaskospira* sp.—an association of undoubted Ludlow age. The second Roberts Mountains collection (USNM loc. 13237) has yielded the following forms: *Ptychopleurella* sp., *Dolerorthis* sp., long-lobed *Dicoelosia* sp., *Isorthis?* sp., *Pentamerifera* sp., *Conchidium* aff. *bilocularis, Conchidium* sp., *Severella* aff. *magnificaformis, Gypidula* sp. (both smooth and plicate forms), *Clorinda* sp., aff. *Gacella* sp., *Ferganella* sp., *Atrypa* sp., *Atrypella* sp., *Dubaria* sp., *Gracianella lissumbra, G. plicumbra, Nucleospira* sp., *Protathyris?* sp., *Hedeina* aff. *balchaschensis,* and *Alaskospira?* sp.—which, taken together, indicate a Ludlow age.

Superfamily and Family Uncertain

Aenigmastrophia, new genus

PLATE 1: FIGURES 1–15

DIAGNOSIS.—The unique features of this genus are a combination of gently concavoconvex cross section, laterally elongate strophic outline, and a relatively smooth exterior associated with a laterally directed, narrow pair of cardinal process lobes [1] flanking a variably developed ridgelike median septum in the brachial valve and a raised pedicle callist area in the posterior portion of the pedicle valve flanked by a pair of elongate, anterolaterally directed hinge-teeth.

TYPE-SPECIES.—*Aenigmastrophia cooperi,* new species.

REMARKS.—It is natural to attempt a comparison of *Aenigmastrophia* with other strophic shells. The genera of the Stropheodontidae are effectively removed from consideration by the absence of a denticulate hinge-line, a differently organized pedicle valve interior insofar as the muscle field is concerned, and the differing organization of the cardinalia and muscle field in the brachial valve. The absence of well-impressed muscle fields in either valve is one of the distinctive features of this novel genus. The isogrammids, as represented by *Isogramma* itself, at first glance possibly would appear to be allied, but the absence of the critical trapezoidal-shaped attachment scar on the umbo of the pedicle valve as well as the differing form of the cardinalia make this comparison unlikely in view of our present knowledge. The complex internal structures of the leptaenids find no counterpart in this genus except in regards to the presence of cardinal process lobes in the brachial valve. It is probable that pseudopunctae are present in *Aenigmastrophia* owing to the pustulose nature of the interior of one of the better-preserved specimens from Nevada. The genera of the Chonetacea are effectively removed from comparison because of their different cardinalia and pedicle valve interior, and also by the absence of spines or spine bases in *Aenigmastrophia.* The interiors of both valves in this peculiar new genus differ so greatly from what we know of Middle Devonian productids that a comparison of this Late Silurian form does not appear profitable despite the strophic nature of both; the lack of spines is another defect as well. The plectambonitids of the Silurian possess little similarity to this unique shell except for the strophic outline and concavoconvex profile. The orthotetacids have a completely different layout of their internal structures

PLATE 1: figures 1–10.—*Aenigmastrophia cooperi,* new species. 1–6, Holotype, a brachial valve, USNM 160179 (USNM loc. 13257): 1, dorsal view; 2, internal view; 3, anterior view; 4, posterior view; 5, side view; 6, side view of valve tilted to show cardinal process lobe. 7–10, Paratype, a pedicle valve, USNM 160180: 7, dorsal view; 8, internal view; 9, side view; 10, posterior view. (All views × 4.)

Figures 11–15.—*Aenigmastrophia greggi,* new species. 11, 13, 15, Holotype, a brachial valve, USNM 160182 (USNM loc. 11162): 11, rubber replica of interior; 13, impression of interior; 15, impression of exterior. 12, 14, Paratype, a pedicle valve, USNM 160183: 12, a rubber replica of interior; 14, impression of interior. (All views natural size.)

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[1] The designation of these structures is difficult. In other strophic shells, paired projections that have been inferred to have served as lophophore supports are termed "cardinal process lobes," but lateral to the cardinal process lobes there may occur additional paired projections termed socket ridges. The position of the projections in the herein-described shells is akin to that of socket ridges, but their function is inferred to be similar to that of cardinal process lobes.

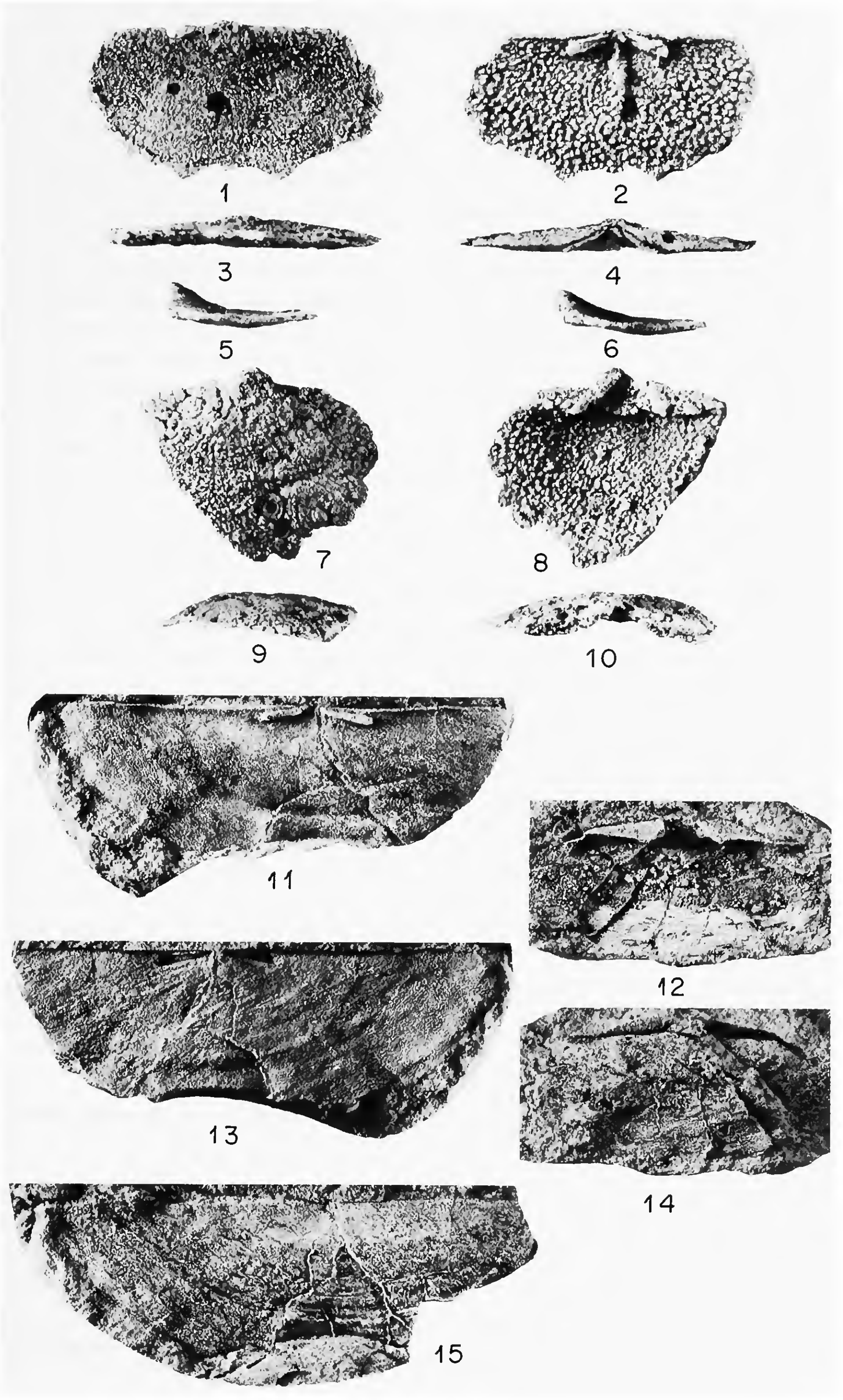

PLATE 1

which, combined with a prominent radial ornamentation in all forms, removes them from effective consideration. All-in-all, there appears no recourse at the present time but to confess ignorance of this puzzling taxon's familial affinities. The extreme rarity of the material does not assist the matter. The small specimens from the Roberts Mountains Formation are so similar to the rather large specimens from the Klamath Mountains that future ontogenetic studies on better collections probably will not afford many clues about familial affinity. In summary, the best that can be done is to suspect that the new genus belongs to the general group of pseudopunctate, flat-to-concavoconvex strophic shells so widespread in the Middle Paleozoic.

Aenigmastrophia cooperi, new species

PLATE 1: FIGURES 1–10

DESCRIPTION.—The exterior of both valves is relatively smooth except for the presence of weak, concentric growth lines. The shells are laterally elongate in form, with the length being about one-half the width. The position of maximum width coincides with the straight hinge-line. The brachial valve is gently concave and the pedicle valve is gently convex. The interarea of the brachial valve is relatively short and orthocline; that of the pedicle valve about twice as long and apsacline. The delthyrium of the pedicle valve includes an angle of about 90° and does not appear to be modified by deltidial structures, although, in view of the small nature of the sample, this conclusion may be premature. The notothyrial region includes an angle of more than 120° and is unmodified by chilidial structures. The teeth of the pedicle valve and the cardinal process lobes of the brachial valve both project to the exterior margin along the hinge-line. The plane of commissure appears to be planar. The anterior margins of both valves are evenly rounded, as are the lateral margins.

The interior of the brachial valve is relatively smooth except for minute pustules, which may reflect the presence of pseudopunctae. The cardinalia consist of a pair of laterally directed cardinal process lobes originating almost at the apex of the notothyrial region and expanding in size laterally. They include an angle of about 140° anteriorly. Narrow, posteriorly directed hinge-sockets are included in the region between the interarea and the cardinal process lobes. These sockets are very narrow and expand distally hardly at all. In small specimens a rounded median septum extends from the base of the notothyrial cavity to about the midlength, but in large specimens this septum is restricted to the posterior fraction of the valve and is a relatively insignificant structure. The anterior edge of the interarea is raised up over the interior of the valve as a low ridge, which gradually weakens in a lateral direction.

The interior of the pedicle valve is quite undistinguished and apparently smooth. The impress of a muscle field has not been discerned. In the delthyrial region, a pedicle callist is raised up off the floor of the valve. The hinge teeth consist of a pair of anterolaterally directed ridges, including an angle of about 90°. The interarea extends somewhat anteriorly over the posterior portion of the interior as a narrow, low platform, but the poorly preserved nature of the material precludes any comment about its distal relationships.

HOLOTYPE.—USNM 160179, from USNM loc. 13257, Roberts Mountains Formation, 672 feet above the base of the Formation, along a line of section east-northeast from a point 250 feet south and 3,699 feet west of hill 9219, west flank of Roberts Creek Mountain, Eureka County, Nevada.

MATERIAL.—Figured specimens: USNM 160179 (holotype), 160180. Unfigured specimen: USNM 160181, from E37–5, USNM loc. 13237, Roberts Mountains Formation, Birch Creek area, elevation 6,520 feet, 550 feet south and 4,450 feet west of southeast corner of Sec. 22, T 24 N, R 50 E, northern Roberts Mountains, Eureka County, Nevada; collected by M. A. Murphy in 1966.

REMARKS.—*Aenigmastrophia cooperi,* new species, is distinguished by its small size and relatively strong median septum in the brachial valve.

Aenigmastrophia greggi, new species

PLATE 1: FIGURES 11–15

HOLOTYPE.—USNM 160182, from USNM loc. 11162, unnamed Ludlow age sandstone, in middle of section 10, about one-half mile west of Mountain House Valley of East Fork of Scott River, China Mountain quadrangle, Siskiyou County, California.

MATERIAL.—The holotype and the paratype, USNM 160183.

REMARKS.—*Aenigmastrophia greggi,* new species, is similar to *A. cooperi,* new species, except for its large size and relatively weak median septum in the brachial valve.

DEVONIAN

Jean M. Berdan

Some Ostracodes from the Schoharie Formation (Lower Devonian) of New York

ABSTRACT

Ostracodes are reported from the Schoharie Formation for the first time. Descriptions and illustrations are given of three new genera and species—*Schohariella grandis, Parabingeria cooperi,* and *Vietor josephinae*—and of a new species of *Phanassymetria* Roth, *P. collilupana. Tubulibairdia punctulata* (Ulrich) is redescribed and figured, and related species are discussed. Three forms left in open taxonomy also are described and illustrated. None of these ostracodes occurs in the Camden Chert, which is correlated with the Schoharie on the basis of megafossils. Two of them, however, are similar to ostracodes described by Jones (1890) from drift boulders of the "Corniferous Limestone" near Canandaigua, New York. This similarity raises the possibility that Jones's material may have been derived from the Bois Blanc Formation (the Schoharie equivalent in western New York) rather than the Onondaga Limestone as hitherto supposed.

Hitherto, ostracodes have not been reported from the Lower Devonian Schoharie Formation in New York, and it therefore seems desirable to describe these forms, even though only one locality has been sampled and few species are present. These descriptions are particularly appropriate in a volume dedicated to Dr. G. Arthur Cooper because of his outstanding contributions to the study of the Devonian of New York.

The name Schoharie was first used by Vanuxem (1840, p. 378) for the "Schoharie layers," which were described as being rich in fossils. Later, Vanuxem (1842, p. 131) used the term "Schoharie grit," with the subheading "Shell grit." Mather (1843, p. 340), reporting on the geology of the type area, also called the formation the "Schoharie grit" and described it as being "a fine-grained calcareous grit rock, containing a great number of fossils . . . . The carbonate of lime gradually disappears from the rock where it is exposed to the weather, and the remaining mass is a rather porous and spongy fine-grained tough sandstone." The formation as originally conceived was thin and poorly exposed. Mather (1843, p. 340) stated that he had seen the formation in place at only two localities, one on "the mountain one or one and a half mile west and northwest of Schoharie," in Schoharie County, and the other on "the mountain one-half to one mile west and northwest of Clarksville," Albany County. Grabau (1906, pp. 180–181) indicated only two exposures in the Schoharie Valley, and he estimated the thickness of the Schoharie Grit in this area as being five or six feet. Ruedemann (1930, pp. 60–62), on the basis of nine outcrops, found the maximum thickness in the Albany area to be between six and eight feet.

Goldring and Flower (1942) restudied the stratigraphy of the Schoharie and Esopus Formations and named a new formation—underlying the Schoharie and overlying the Esopus—the Sharon Springs Formation, later renamed the Carlisle Center Formation (Goldring and Flower, 1944, p. 340). Johnsen and Southard (1962, p. A8) considered the Carlisle Cen-

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ter to be a member of the Schoharie and renamed the Schoharie Grit of previous authors the Rickard Hill Member of the Schoharie Formation. As understood by Johnsen and Southard (1962, p. A7), the Schoharie Formation is a complex of lithologic facies which extends from Herkimer County, New York, to Monroe County, Pennsylvania, and which reaches a thickness of more than 200 feet. Their Rickard Hill Member, which is the most fossiliferous part of the formation, extends from East Springfield, New York, to southern Albany County, New York. The ostracodes described in this paper are all from their Rickard Hill Member of the Schoharie (or the Schoharie Grit of former usage).

The nature of the contact of the Schoharie Formation with the overlying Onondaga Limestone has been reviewed by Oliver (1967, pp. A1, A2), who concludes that there is a sharp faunal break between the two formations. The lower contact of the Carlisle Center Member of the Schoharie as used by Johnsen and Southard (1962) with the underlying Esopus Formation is gradational. The contact is placed by Johnsen and Southard (1962, p. A8) at the lowest beds that are sufficiently calcareous to effervesce in cold dilute hydrochloric acid.

Cooper (1942) and Boucot and Johnson (1968, pp. B1–B4) have discussed the correlation of the Schoharie with other North American formations. Boucot and Johnson (1968, pp. B1, B3) consider the Schoharie to be early Emsian in age, in terms of the standard sequence in the Rhineland.

Most major groups of megafossils from the Schoharie Grit were described by Hall (1867, 1879, 1884, 1885; in Hall and Simpson, 1887; in Hall and Clarke, 1888) in his series of monographs on the paleontology of New York. Some of the groups have undergone considerable revision by later paleontologists, but as yet no microfossils, except conodonts (Klapper and Ziegler, 1967), have been described from the Schoharie Formation in New York. Generally, however, the ostracodes described from the Camden Chert of western Tennessee—which is correlated with the Schoharie on the basis of brachiopods by Cooper and others (1942, pp. 1748, 1779–1780) and by Boucot and Johnson (1968, p. B3)—have been considered representative of the ostracodes of Schoharie age.

Thirty-eight species of ostracodes were described from the Camden Chert by Bassler (1941) and Swain (1953). The Camden assemblage is dominated by bolliids (six species or subspecies of *Bollia*) and thlipsurids (five species of *Strepulites,* three species each of *Thlipsurella* and *Thlipsurina,* and one species each of *Stibus* and *Thlipsura*) but is lacking in beyrichiaceans. In generic composition the Camden assemblage resembles the ostracodes described from the Onondaga Formation of Pennsylvania by Swartz and Swain (1941), as suggested by Bassler (1941, p. 22) and Swain (1953, pp. 259–261), although the assemblage in Pennsylvania includes one beyrichiacean. In contrast, ostracodes from the Schoharie include two large beyrichiaceans, and bolliids and thlipsurids are scarce or lacking. In fact, the Schoharie assemblage described below has no species in common with the Camden assemblage.

The differences between the Camden and Schoharie ostracode assemblages may be due to differences in age, facies, or faunal provinces, or perhaps to all three. With regard to difference in age, Bassler (1941, p. 22) implied that the ostracodes he described came from near the base of the Camden, but Cooper (in Swain, 1953, p. 258) has noted: "No definite horizon can be stated for the specimens because they came from pure white clay found on the floor of the quarry. They evidently came from somewhere in the quarry wall, but I never located any of the material in place." In view of the uncertainty as to the exact stratigraphic position of the ostracode fauna within the Camden, and the possibility suggested by Swain (1953, p. 259) that the assemblage is mixed, it is conceivable that the Camden ostracodes are not precisely contemporaneous with those of the Schoharie and may be slightly younger.

With regard to difference in facies, although Boucot and Johnson (1968, fig. 2) include both formations in a limestone and chert belt on their generalized lithofacies map, the ostracodes from the Camden apparently came from a very fine-grained sediment indicative of a low-energy environment whereas the Schoharie beds from which the ostracodes are described are primarily a sand composed of quartz and calcite grains with calcareous cement, which suggests a high-energy environment.

With regard to difference in faunal province, the described ostracode faunas from the Lower Paleozoic of the Mississippi Valley area appear to differ from ostracode faunas of those formations in the Appalachian area that are dated as contemporaneous on the basis of other groups of fossils. Whether this faunal difference is due to lithologic facies or to some less tangible factor such as temperature or depth is yet to be determined. Benton County, Tennessee, where the Camden ostracodes were collected, is about 900 miles from Albany County, New York, and some differences might be expected.

The possibility exists that the difference between the Camden and Schoharie ostracode assemblages may be more apparent than real. Future collecting from other parts of the Schoharie Formation may show more elements in common than are now known.

Although no ostracodes have as yet been described from the Schoharie Formation, Jones (1890) described six species of ostracodes from the "Chert of the Corniferous Limestone" in Ontario County, New York. These ostracodes have been considered to come from the Onondaga Limestone (Bassler and Kellett, 1934, p. 75; Warthin, 1937) and, if so, are the only described ostracodes from the Onondaga of New York. The specimens, which are deposited in the New York State Museum, are molds and casts preserved in yellow buff-weathering rotted chert, and the accompanying labels indicate that they come from "Onondaga Ls., (drift), Canandaigua, Ontario County, N.Y." In 1964 I tried to find this assemblage in place in the Onondaga in the vicinity of Canandaigua, but without success. However, two of the species described by Jones, "*Eurychilina reticulata*" and "*Moorea kirkbyi*," resemble species from the Schoharie described in this paper. In addition, Oliver (1967, p. A7, fig. 2) has indicated that an outcrop of the Bois Blanc Formation, which is the equivalent of the Schoharie in western New York, occurs in the Phelps 7½-minute quadrangle, north and east of Canandaigua. Because the ostracodes described by Jones came from a boulder of glacial drift, there is a possibility that they actually may be from the Bois Blanc Formation rather than the Onondaga. As yet no ostracodes are known from the Bois Blanc, but the ostracodes that I have collected from the Onondaga do not include Jones's species. Further study of the assemblages of both formations is necessary before any firm conclusions can be drawn.

The original sample of Schoharie from which ostracodes were studied is a part of a collection made by G. A. Cooper for megafossils. The label with the ostracode sample reads "Schoharie, 1¾ mi. NNW of Clarksville, New York, G. A. Cooper, 1938, loc. 119f." This locality was described by Goldring and Flower (1942, p. 679) as follows: "Above New Salem along the Wolf Hill highway, one-quarter of a mile east of the New Scotland town quarry in the Onondaga limestone, the Schoharie is exposed in the woods above a road cut in the Esopus and Sharon Springs formations. Here only the upper part of the Schoharie grit is present, measuring two feet six inches, exposing the *pelops* bed, the upper layers and the Onondaga contact."

This locality was examined specifically for ostracodes in 1964 and 1968, when two additional collections for the United States Geological Survey (USGS) were made—USGS 7267–SD and USGS 8211–SD. The first of these (USGS 7267–SD) was taken from loose blocks apparently quarried by some previous paleontologist; the second (USGS 8211–SD) was collected in place about ten inches below the contact of the Schoharie with the Onondaga. The locality is overgrown, but about two feet of Schoharie is still exposed. The contact with the Onondaga is clear and appears to be somewhat irregular; the Schoharie just beneath the contact is a brown-weathering leached sandstone packed with brachiopods and other fossils. This bed is six or seven inches thick, and is underlain by ten inches to a foot of very hard, steel-gray, sandy limestone with fewer fossils; it was from this bed that the ostracodes in USGS 8211–SD were obtained. The locality is on the Clarksville 7½-minute topographic quadrangle, on the west side of Wolf Hill Road (New York Route 85), in the woods above the road, 1,500 feet south of benchmark 781 and 900 feet north of the point where a gas pipeline crosses the road.

The ostracodes described in this paper are few in both number of species and number of individuals. This is due in part to the siliceous character of the Schoharie matrix, which renders both collection and preparation of the material extremely difficult. The original sample containing ostracodes from Dr. Cooper's collection is small; it consists of pieces of rock which just fill a 3-inch by 4-inch tray. The two additional collections made by me specifically for ostracodes are larger but together do not represent more than half a standard 3-inch-deep drawer, or about 924 cubic inches of rock. Ostracodes are not abundant in the matrix, and one collection in particular, USGS 7267–SD, yielded very few specimens for the amount of rock processed. The matrix consists of sand grains, of both quartz and calcite, in a calcareous cement and includes aggregates of crystalline pyrite. The most abundant groups of fossils associated with the ostracodes are trilobites, brachiopods, and corals, which are randomly oriented in the rock and are in many instances fragmentary, especially the trilobites.

The ostracode specimens are calcareous and were prepared by the use of a vibratool and needle on broken pieces of rock. In some instances preparation is facilitated by heating the rock and quenching it in cold water; this technique was used on some of the material, but as it tended to make the shells spall off, some of the material was prepared without heating and quenching.

Because of the character of the matrix it is difficult to obtain unbroken specimens. In addition to the species described below, fragmentary ostracodes that are too poorly preserved to illustrate have been found. These fragments indicate the presence in the fauna of a beyrichiopsid; a bolliid; one or more species of hollinids, possibly including *Parabolbina*; a bairdiocyprid; a condracyprid; and a form resembling *Baschkirina* Rozhdestvenskaja, 1959. It is obvious that the ostracodes described in this paper represent only a small part of the total assemblage in the Schoharie Formation.

The classification used in this paper is based on the Treatise on Invertebrate Paleontology, Part Q, Ostracoda (Moore, 1961) except for the Beyrichiidae, which is taken from Martinsson (1962, 1963).

The type specimens are in the United States National Museum (USNM).

All photographs were taken by Robert H. McKinney and printed by Haruo E. Mochizuki, both of the United States Geological Survey.

Order PALAEOCOPA Henningsmoen, 1953

Superfamily BEYRICHIACEA Matthew, 1886

Family CRASPEDOBOLBINIDAE Martinsson, 1962

?Subfamily CRASPEDOBOLBININAE Martinsson, 1962

Schohariella, new genus

DIAGNOSIS.—Unisulcate to nonsulcate craspedobolbininids with broad, complete, tubulous velum, drop-shaped external muscle spot; crumina ventral, bluntly acuminate in lateral outline, protrudes markedly above velum. Dolonoid scar obscure, ventral in position. No torus.

TYPE-SPECIES.—*Schohariella grandis*, new species.

DISCUSSION.—This new genus is questionably placed in the Craspedobolbininae because of an obscure groove interpreted to be the trace of a dolonoid scar at the most ventral part of the crumina. In addition, it resembles the craspedobolbinine genera *Apatobolbina* and *Leptobolbina* in being essentially nonsulcate and having a prominent external muscle spot. *Schohariella* may be distinguished from these genera by the form of its crumina and by its broad, complete, tubulous velum. *Hyrsinobolbina* Martinsson, 1962, has a broad complete velum but is decidedly unisulcate and has a globular crumina. The genus *Schohariella* differs from typical treposelline genera in its broad tubulous velum and lack of the treposelline "bridge" at the contact of the crumina with the velum. It differs from described amphitoxotidine genera in essential lack of sulcation and in the character of the subcruminal field.

No tecnomorphs of *Schohariella grandis* have been found in the collections of the Schoharie Formation from Wolf Hill. The tecnomorphic specimen described by Jones (1890, p. 535, pl. 20, figs. 13a, 13b) as "*Eurychilina reticulata* Ulrich"—later renamed *Treposella reticulosa* by Warthin (1937, card 20)—appears, however, to belong to *Schohariella.* The material figured by Jones consists of an internal mold and external cast of the same tecnomorphic specimen, and is deposited in the New York State Museum (NYSM 4452). A latex cast of the original of Jones' specimen (Jones, 1890, pl. 20, fig. 13b) is illustrated herein as figure 24 of Plate 1, which shows the broad velum and drop-shaped muscle spot of *Schohariella.* The surface reticulation is coarser and the muscle spot is less well defined, however, than in *Schohariella grandis,* and it seems probable that the two specimens are not conspecific. As previously noted, *Schohariella reticulosa* was reported to have come from the Onondaga Limestone, but there is a possibility that it came from float from the Bois Blanc Formation, which is the Schoharie equivalent in western New York.

The name *Schohariella* is derived from a latinized diminutive of Schoharie, the formation in which the type-species occurs.

Schohariella grandis, new species

PLATE 1: FIGURES 25, 26

DESCRIPTION.—The lateral outline is semielliptical and amplete. A low, indistinct median lobe is bounded posteriorly by a very shallow median sulcus occupied by a slightly raised drop-shaped muscle spot. The posterior lobe is very slightly cuspate and is swollen in profile above the median and anterior lobes. A narrow, shallow fissus extends about two-thirds of the length of the valve beneath the muscle spot and the median lobe. The surface of the domicilium is finely punctate, except for the muscle spot. The velum is broad, tubulous, and radially striate with superimposed, very fine, concentric filae. It extends from the posterior cardinal angle around the free margin of the valve and apparently to the anterior cardinal angle, although as the anterior angle is broken it is difficult to be certain of this. The crumina is protuberant, bluntly triangular with broad base against the domicilium, and very faintly striatopunctate. In end view the crumina protrudes laterally as a linguiform extension at nearly a 45° angle to the plane of the valve. In ventral view the velum meets the crumina at about half its height but does not cross it. There is a probable dolonoid scar at the ventral edge of the crumina.

Holotype measurements (in millimeters): length including the velum, 3.40, not including the velum, 2.25; height including the crumina, 1.9, to the base of the crumina, 1.2.

MATERIAL.—The holotype only.

HOLOTYPE.—USNM 163663.

DISCUSSION.—Although only one specimen of this species has been found, it seems to be sufficiently distinctive to warrant description. It differs from *Schohariella reticulosa* (Warthin) not only in having the finer, less distinct reticulation and the more distinct muscle spot mentioned above but also in having a more conspicuous median lobe and fissus—the latter being almost lacking in *S. reticulosa.* Some of these differences might be due to the difference in the type of preservation, or might be sexual, as the only specimen of *S. grandis* is a heteromorph and the only specimen of *S. reticulosa* is a tecnomorph. It seems unlikely, however, that all the differences are due to either of these factors, and therefore the two species are considered distinct.

The specific name is indicative of the large size of the holotype.

Family BEYRICHIIDAE Matthew, 1886

Subfamily BEYRICHIINAE Matthew, 1886

Parabingeria, new genus

DIAGNOSIS.—Unisulcate to weakly bisulcate beyrichiid ostracodes; anterior and posterior lobes with cuspidal crest; median lobe set below hinge-line; distinct velar ridge; nearly horizontal zygal ridge extending onto posterior lobe, bounded ventrally by weak fissus. Crumina anteroventral, not distinctly set off from domicilium, inflating and obliterating velar ridge.

TYPE-SPECIES.—*Parabingeria cooperi,* new species.

DISCUSSION.—This genus closely resembles *Bingeria* Martinsson, 1962, from the Tofta Beds (Middle Silurian) of Gotland. However, *Bingeria* lacks the horizontal zygal ridge and subjacent fissus extending onto the posterior lobe and also has a more distinctly delimited crumina. *Arikloedenia* Adamczak, 1968, from the Middle Devonian of Poland is more distinctly bisulcate and lacks the distinct velar ridge, fissus, and zygal ridge of *Parabingeria.* The zygal ridge and fissus suggest some species of *Beyrichia* (*Simplicibeyrichia*) Martinsson, 1962, but in that subgenus the crumina is more distinctly developed and spines or pustules are present on the valves.

The name is derived from the Greek prefix *para* (near) and from *Bingeria,* indicating the similarity of this genus to *Bingeria.*

Parabingeria cooperi, new species

PLATE 1: FIGURES 27–30

DESCRIPTION.—The lateral outline is amplete and subelliptical. The anterior and posterior margins are smoothly curved; the ventral margin is nearly straight on tecnomorphs; the dorsal margin is slightly sinuate to straight; and the dorsal and ventral margins are subparallel. The anterior and median lobes are fused; the anterior lobe has a low cuspidal crest. The posterior lobe has a distinct cuspidal crest at the posterior angle. The median sulcus is distinct, curved anteriorly, and extends about two-thirds of the distance from the hinge to the ventral margin. A zygal ridge extends posteriorly from the median lobe, beneath the median sulcus, to the middle of the posterior lobe. A shallow fissus occurs beneath the zygal ridge. The velar ridge is distinctly separated from the domicilium, reflexed away from the contact margin of the valves; it is continuous around the free margin on tecnomorphs, and it is occupied by crumina and is obliterated anteroventrally on heteromorphs. The crumina is an indistinct swelling of the domicilium, anteroventral in position. The surface of the valves is smooth except for widely spaced, shallow punctae which are more numerous and deeper on the crumina.

The holotype, a heteromorphic right valve, is 3.3 mm in length and 2.2 mm in height. Two paratypes, a right and a left tecnomorphic valve, are 3.3 mm in length and 2.1 mm in height and 2.8 mm in length and 1.7 mm in height, respectively.

Material.—One complete right and one broken left heteromorphic valve, one complete and two broken right tecnomorphic valves, and one complete left tecnomorphic valve, all from G. A. Cooper collection 119f; also, two broken specimens in collection USGS 8211–SD.

Types.—Holotype, USNM 163660; paratypes, USNM 163661—2.

Discussion.—*Parabingeria cooperi* appears superficially similar to other large subquadrate beyrichiaceans from the Lower Devonian of North America, such as *Kloedenia? newbrunswickensis* Copeland, 1962, and *"Beyrichia" occidentalis* Walcott, 1884, from the Dalhousie beds and the Nevada Limestone, respectively. However, *P. cooperi* differs from both these species in being essentially unisulcate and in having a conspicuous velar ridge. The zygal ridge and fissus also are distinctive. Heteromorphs of the other taxa are not as yet known.

The beyrichiacean described by Jones (1890, p. 538, pl. 21, fig. 1) as *"Beyrichia kloedeni* M'Coy var." is a heteromorphic right valve with a prominent median lobe and a conspicuous crumina sharply delimited from the domicilium and thus is distinctly different from *Parabingeria cooperi.* Swartz and Swain (1941, p. 428) suggested that Jones's specimen might be a female of their *Kloedenia rectangularis,* which species also differs from *Parabingeria* in having a more prominent median lobe.

The specific name is given in honor of Dr. G. Arthur Cooper, who collected the specimens described.

Suborder KLOEDENELLICOPINA Scott, 1961

Superfamily PARAPARCHITACEA Scott, 1959

Family PARAPARCHITIDAE Scott, 1959

Genus *Neoaparchites* Bouček, 1936

Neoaparchites sp. aff. *N. mesleri* (Bassler, 1941)

Plate 1: figures 11–13

Description.—The lateral outline is elliptical and preplete. The hinge is less than half the length of the shell and very slightly incised. The greatest thickness is in the posterior third and dorsal half of the shell. The right valve slightly overlaps the left around the free margin. The shell surface is smooth.

A carapace measures 1.4 mm in length, 1.1 mm in height, and 0.7 mm in width.

Discussion.—One broken carapace (USNM 163664), found in collection USGS 8211–SD, appears to belong in *Neoaparchites* as diagnosed by Bouček (1936, p. 39), and Krandievs'ky (1963, pp. 17–18). This specimen has been compared to *"Paraparchites" mesleri* Bassler but it differs from that species in being preplete instead of amplete in lateral outline. *"Paraparchites" mesleri* is represented only by single valves, so the overlap is not clear, but it probably should also be assigned to *Neoaparchites.* Similar species are *Aparchites mesleriformis* Polenova, 1960, *Aparchites rozhdestvenskajae* Polenova, 1968, and *Antiparaparchites primaevus* Kesling, 1958; however, judging from the illustrations of those species, especially the last, they may belong in *Pseudoaparchites* Krandievs'ky, 1963, because of the character of the overlap.

Order PODOCOPIDA Muller, 1894

Suborder PODOCOPINA Sars, 1866

Superfamily BAIRDIACEA Sars, 1888

Family BAIRDIIDAE Sars, 1888

Genus *Bairdiacypris* Bradfield, 1935

Bairdiacypris? sp.

Plate 1: figures 20–23.

Description.—The lateral outline is reniform. The dorsal margin is curved; the anterior margin is evenly but sharply curved; the ventral margin is concave; and the posterior margin is bluntly acuminate. The maximum length is below midheight; the maximum width is in the posterior half; and the maximum height is in the anterior half of the carapace. The left valve overlaps the right around the free margins and overreaches the right along the dorsal margin. The hinge is short, straight, and slightly incised. The shell surface is smooth. The muscle scar is not known.

The figured specimen measures 0.85 mm in length and 0.40 mm in height and width.

Material.—Only the figured specimen (USNM 163665), a complete carapace.

Discussion.—The single specimen is tentatively assigned to *Bairdiacypris* because of the character of the overlap and outline. Although it appears similar to some specimens of *Camdenidea* Swain, 1953, the posterior is not as acuminate and the ends are not compressed as they are in that genus. It differs from specimens of *Silus* Polenova, 1968, in having a more acuminate posterior and in having the maximum height anterior.

Suborder METACOPINA Sylvester-Bradley, 1961

Superfamily HEALDEACEA Harlton, 1933

Family PACHYDOMELLIDAE Berdan and Sohn, 1961

Vietor, new genus

Diagnosis.—Pachydomellid ostracodes with flattened venter and conspicuous groove near and parallel to ventral margin on the right valve; left valve without groove.

Type-species.—*Vietor josephinae,* new species.

Discussion.—This new genus resembles other pachydomellid genera in being distinctly inequivalved and asymmetrical, with left over right overlap, a short incised hinge, and a thick shell that has conspicuous tubules which do not open to the exterior of the shell but may be seen when the shell is wetted. However, other genera of this family that develop longitudinal grooves have them situated close and parallel to the hinge-line instead of near the ventral margin as in the genus described.

The generic name is taken from the Latin *vietor,* one who makes baskets of osier to be covered with leather—the Roman equivalent of one who makes barrels, a cooper.

Vietor josephinae, new species

Plate 1: figures 1–5

Description.—The lateral outline is subovoid, and the ventral and dorsal outlines are irregularly elliptical. The left valve is larger than the right, overlapping it around the free margins but not overreaching it along the hinge. The left valve has a slight anterodorsal sag or depression, and the ventral surface is flattened so that it makes an acute angle with the lateral slope of the valve. The right valve has a more pronounced anterodorsal sag, posterior to which is a posterodorsal bulge which is bounded ventrally by a cleft or groove parallel to and just above the ventral angulation. This groove extends from near the posterior margin to about one-third of the length from the anterior margin. The ventral surface of the right valve is flattened and angulated like that of the left valve. The shell surface is smooth. Tubules may be seen on wetted specimens, especially on the ventral surfaces, where they appear to be more numerous and larger than those on the rest of the shell.

Measurements, in millimeters, of holotype (from coll. USGS 8211–SD): length 1.35, height 0.75, width 0.85. Two paratypes from the same collection measure, respectively, 1.4 and 1.35 mm in length; both measure 0.75 mm in height and 0.85 mm in width.

Material.—Three carapaces (including the holotype) from collection USGS 8211–SD and one carapace from collection USGS 7267–SD.

Types.—Holotype, USNM 163666; paratypes, USNM 163667–9.

Discussion.—This species is somewhat more abundant than would appear from the number of specimens listed above, for several additional specimens were seen in the matrix but broke in the course of preparation.

The species is named in honor of Mrs. G. A. Cooper.

Genus *Phanassymetria* Roth, 1929

Phanassymetria collilupana, new species

Plate 1: figures 6–10

Description.—The lateral outline is subtrapezoidal. The anterior margin is bluntly rounded; the ventral and dorsal margins are nearly straight and subparallel; and the posterior margin is rounded to obtusely angulate. The left valve overlaps the right around the free margins and has an indistinct longitudinal groove parallel to and just below the dorsal margin, which defines a sharp, angular ridge along the dorsum. The right valve has a similar groove restricted to the posterior half of the valve. The ventral surface of both valves is flattened. There is a low longitudinal ridge on the posterior half of the right valve at the junction of the ventral and lateral surfaces.

The ventral and dorsal outlines are subpyriform. In dorsal view the two dorsal ridges enclose a drop-shaped depression, which is open posteriorly and in which the hinge is incised. The width is greater than the height. The shell surface is smooth. Tubules are visible on wetted specimens and appear to be evenly distributed in both valves.

The holotype measures 1.4 mm in length, 0.8 mm in height, and 1.1 mm in width.

MATERIAL.—One carapace (the holotype), one right valve, and one left valve, all from collection USGS 8211-SD.

TYPES.—Holotype, USNM 163670; paratypes, USNM 163670a, b.

DISCUSSION.—This species appears to be intermediate between *Phanassymetria* Roth, 1929, and *Pachydomella* Ulrich, 1891, in some respects. It lacks the angular cross section of *Phanassymetria triserrata* Roth, the type species of the genus, but differs from *Pachydomella tumida* Ulrich in having a dorsal ridge on the right valve. It differs from the types of both these genera in having dorsal grooves on both valves instead of on the left valve only. Sohn (1961, p. 76) considered the most important criterion for distinguishing *Phanassymetria* from *Pachydomella* to be a longitudinal ridge below midheight on one or both valves of *Phanassymetria,* this feature not being present in *Pachydomella.* Accordingly, this new species is assigned to *Phanassymetria.* This is the first species of the genus reported outside the Midcontinent region.

The specific name is based on the Latin *collis* (hill) and *lupus* (wolf) with the suffix *ana* (denoting place) to indicate that the species is found near Wolf Hill Road.

Genus *Tubulibairdia* Swartz, 1936

Tubulibairdia punctulata (Ulrich, 1891)

PLATE 1, FIGURES 14–18

Bythocypris punctulata Ulrich, 1891, p. 196, pl. 17, figs. 2a-c.

Microcheilinella punctulata (Ulrich).—Bassler and Kellett, 1934, p. 412.

Tubulibairdia punctulata (Ulrich).—Sohn, 1961, p. 75, pl. 5, figs. 7, 10, 11, 14–17.

DESCRIPTION.—The lateral outline is subovate; the dorsal outline is ovate; and the anterior outline is indented subcircular. The greatest height and the greatest width are posterior to the midpoint of the carapace, and the greatest length is below the midpoint. The left valve overlaps the right around the free margins, especially on the ventral margin where a flap, or lappet, protrudes over the right valve in the anterior half of the carapace so that the ventral commissure is sinuate. The left valve is ovate in lateral outline and overreaches the right valve dorsally. The right valve is smaller than the left and subtrapezoidal in lateral outline. The hinge is straight, half or slightly more than half the greatest length of the carapace, and deeply incised. The shell surface is smooth or has extremely fine longitudinal striations. Tubules that are visible on lightly calcined specimens appear to be evenly distributed through the shell except for the muscle scar and overlapping parts of the ventral margin. The muscle scar is circular and located at or slightly below midheight on the left valve and at midheight on the right valve. It is composed of radiating muscle flecks.

Measurements (in millimeters) of the two figured specimens: USNM 163671 (Plate 1: figures 14–17), length 1.40; height 0.80, width 0.95; USNM 163672 (Plate 1: figure 18), length 1.60, height 0.95, width 1.10. The measurements of six other complete carapaces are as follows:

USNM Specimen	*Length*	*Height*	*Width*
163673	1. 75	1. 10	1. 15
163674	1. 70	1. 05	1. 15
163675	1. 65	1. 00	1. 10
163676	1. 60	1. 00	1. 10
163677	1. 60	1. 00	1. 10
163678	1. 45	0. 85	0. 90

MATERIAL.—Eight complete carapaces (USNM 163671–78), nine broken carapaces (USNM 163678a), and six separate valves (USNM 163678b).

DISCUSSION.—Although the genus is easily recognizable, species of *Tubulibairdia* are difficult to discriminate because they have few reliable distinctive characteristics. The most obvious difference between many of them is size, but size alone is hardly a reliable specific character in ostracodes. The specimens from the Schoharie are here assigned to *T. punctulata* (Ulrich) because, although they average slightly larger in size than typical *T. punctulata,* they seem to agree with that species in other respects. With regard to the size of the species, it should be noted that Ulrich (1891, p. 196) gave the dimensions of *T. punctulata* as 1.93 mm in length, 1.15 mm in height, and 1.14 mm in thickness. However, none of the specimens in the type lot (USNM 41823) attains this size. The holotype, figured by Sohn (1961, pl. 5, figs. 14–17), is 1.25 mm long, 0.75 mm high, and 0.85 mm wide; and the paratype figured by Sohn (1961, pl. 5, figs. 10, 11) is 1.50 mm long, 0.90 mm high, and 0.95 mm wide; a topotype from the Falls of the Ohio is 1.30 mm long, 0.80 mm high, and 0.85 mm wide. It must be assumed that either the specimen measured by Ulrich was not included in the type lot or that the measurements were in error.

In addition to *T. punctulata,* nine other taxa of *Tubulibairdia* have been described from North America. *T. tubulifera* Swartz, 1936, the type-species of the genus, was based on molds and casts, and not all of its dimensions can be determined. The holotype of *T. tubulifera* (USNM 94195), from the Shriver Chert of Curtin, Pennsylvania, is represented by an internal and an external mold of a left valve which measures 1.30 mm in length and 0.85 mm in height. According to Swartz (1936, p. 581), an average left valve measures 1.40 mm in length and 0.98 mm in height, and an average right valve measures 1.40 mm in length and 0.88 mm in height. These dimensions are comparable to those of *T. punctulata,* but a latex squeeze of the external impression of the holotype of *T. tubulifera* shows a high dorsal surface—which indicates that the valve was more umbonate than that of *T. punctulata*—and a weak longitudinal groove or sag parallel to and just below the dorsum. This weak sag is not comparable to the well-developed subdorsal groove of *Pachydomella tumida* Ulrich, 1891, which is the characteristic feature of the genus *Pachydomella* Ulrich, 1891.

Tubulibairdia simplex (Roth, 1929), as described by Lundin (1968, pp. 70–72), may also have a slight subdorsal groove like that of *T. tubulifera.* The following measurements (in millimeters) of the holotype (USNM 80646) of *T. simplex* are given by Lundin (1968, p. 71): length, 1.45; height, 0.88; and width, 0.80. Lundin's (1968, fig. 32) size-dispersion diagram shows, however, that *T. simplex* may attain considerably larger dimensions. That species differs from the holotype of *T. tubulifera.* in being more acuminate posteriorly.

Two species, *Tubulibairdia paucitubulis* Swartz and Swain, 1941, and *T. multitubulis* Swartz and Swain, 1941, from the Onondaga beds of Pennsylvania were described only from internal molds in shale. Swain (1953, p. 282) considered the smaller of these, *T. paucitubulis* (length, 0.82 mm; height, 0.45 mm), to be juvenile specimens of *T. multitubulis,* which is based on one broken internal mold that is 1.45 mm in length and 0.78 mm in height (Swartz and Swain, 1941, p. 446). *T. multitubulis* is unrecognizable by present criteria and will remain so until topotypic material is found and studied. Swain (1953, p. 280) considered *Tubulibairdia* to be a junior synonym of *Pachydomella* Ulrich, 1891, and assigned specimens from the Camden Chert to *Pachydomella multitubulis.* The Camden specimens lack the prominent subdorsal groove of true *Pachydomella* (compare *P. dorsoclefta* Swain, 1953, also from the Camden) and are here considered to belong to *Tubulibairdia.* These Camden specimens, which are more acuminate posteriorly than most other species of *Tubulibairdia,* may represent a new species.

Of the remaining five taxa assigned to *Tubulibairdia* in North America, *T. longula* (Ulrich and Bassler), 1913, from the Keyser Limestone in Maryland and *Tubulibairdia* sp. cf. *T. longula* (Ulrich and Bassler) described by Lundin (1965, pp. 65, 66) from the Henryhouse Shale of Oklahoma both appear to be somewhat smaller than the species previously discussed. The following measurements of *T. longula* are given by Ulrich and Bassler (1913, p. 542): length 1.15 mm, height 0.60 mm, and width 0.70 mm. The left valve of the holotype (USNM 53289) proportionately is not as high as that of the other species, so the specimen appears to be longer. Lundin (1965, p. 65) gave measurements of 1.20 mm in length, 0.72 mm in height, and 0.75 mm in width for the average of his adult specimens, although his diagram (Lundin, 1965, p. 66, fig. 37) shows two specimens attaining a length of 1.30 mm.

Tubulibairdia decaturi (Wilson, 1935) from the Birdsong Shale of Tennessee and *T. windomensis* Swartz and Oriel, 1948, from the Windom Member of the Moscow Shale of New York are both considerably smaller than any of the other species. Wilson (1935, p. 646) gave the measurements of *T. decaturi* as 0.62 mm in length, 0.36 mm in height, and 0.37 mm in width. The holotype (USNM 112905) is a small, corroded complete carapace, but single valves and fragments of *Tubulibairdia* in other collections from the Birdsong suggest that the species may attain larger dimensions. It will be necessary to study a large suite of specimens before the species can be adequately defined.

Swartz and Oriel (1948, p. 563) gave the following dimensions for *Tubulibairdia windomensis*: length 0.89 mm, height 0.62 mm, and width 0.65 mm. This species differs from all others of the genus in being finely punctate and in having the greatest height of the carapace anterior rather than median or posterior in position. The latter character suggests that the species may be based on juvenile instars rather than on adult specimens and raises the possibility that the punctation may be a juvenile characteristic.

Of all the North American species of *Tubulibairdia*, *T. chaleurensis* Copeland, 1962, is most similar to *T. punctulata*, and at one time it was thought that the specimens from the Schoharie might belong to *T. chaleurensis*. Copeland (1962, p. 48) gave measurements for one carapace as 1.70 mm in length, 1.10 mm in height, and 1.10 mm in width—dimensions which are comparable to those of the larger specimens here assigned to *T. punctulata*. Copeland (1962, p. 48), however, stated that the left valve overlaps the right "except anteriorly." In this respect *T. chaleurensis* differs from *T. punctulata*, in which the left valve overlaps the right around the entire free margin, including the anterior part. The Schoharie specimens agree with *T. punctulata* in this character.

Sohn (1961, pp. 75, 76) placed seven European species in *Tubulibairdia*, of which three were only questionably so assigned. One of these, *Cythere corbuloides* Jones and Holl, 1869 (the type-species of *Daleiella* Bouček, 1937), while probably a pachydomellid, may not belong in *Tubulibairdia*. Of the other six species, all but *Tubulibairdia? fecunda* (Přibyl and Šnajdr, 1950) are smaller than *T. punctulata*, and in *T.? fecunda* the hinge is not parallel to the ventral margin, as it is in most species of *Tubulibairdia*. Becker (1965, p. 178) has placed *Microcheilinella seminalis* Kummerow, 1953, in *Tubulibairdia*, but this is a very small species. In addition, *Microcheilinella regularis* Polenova, 1968, may also belong to *Tubulibairdia*, but this species also is smaller than *T. punctulata*. In summary, the species of *Tubulibairdia* require further study, but until this is done the specimens from the Schoharie are believed to be most correctly identified with *T. punctulata*.

Tubulibairdia punctulata is the most abundant ostracode species represented in the Schoharie Formation; and it has been found in all three of the collections studied.

Superfamily QUASILLITACEA Coryell and Malkin, 1936

Family BUFINIDAE Sohn and Stover, 1961

Genus *Parabufina* Smith, 1956

Parabufina? sp.

PLATE 1: FIGURE 19

DESCRIPTION.—The lateral outline is elliptical and amplete; dorsal and ventral margins are smoothly

PLATE 1.—*Vietor josephinae*, new species. Figures 1–5, views of holotype, USNM 163666, from coll. USGS 8211–SD: 1, right lateral, showing groove parallel to ventral margin; 2, left lateral; 3, dorsal, showing incised hinge-line; 4, ventral, showing flattened venter; 5, anterior. (All views × 15.)

Phanassymetria collilupana, new species. Figures 6–10, views of holotype, USNM 163670, from coll. USGS 8211–SD: 6, right lateral; 7, left lateral; 8, anterior, showing grooves on both valves below dorsum which set off angular ridges; 9, dorsal, showing hinge-line incised and enclosed by ridges; 10, ventral, left valve broken. (All views × 15.)

Neoaparchites sp. aff. *N. mesleri* (Bassler). Figures 11–13, views of USNM 163664, from coll. USGS 8211–SD: 11, right lateral; 12, left lateral; 13, dorsal. (All views × 15.)

Tubulibairdia punctulata (Ulrich). Figures 14–17, views of USNM 163671, from G. A. Cooper loc. 119f: 14, dorsal, showing incised hinge-line; 15, anterior (projections on anterior margin are adventitious); 16, ventral, showing lappet on left valve; 17, right lateral, showing overlap. Figure 18, left lateral view of USNM 163672, also from G. A. Cooper loc. 119f. (All views × 15.)

Parabufina? sp. Figure 19, USNM 163679, from collection USGS 8211–SD (× 15.)

Bairdiacypris? sp. Figures 20–23, views of USNM 163665, from collection USGS 8211–SD: 20, left lateral; 21, right lateral; 22, dorsal (anterior end toward top); 23, ventral (anterior end toward top). (All views × 15.)

Schohariella reticulosa (Warthin). Figure 24, view (×15) of latex cast of impression of a tecnomorphic right valve (NYSM 4452) from "Onondaga limestone (drift), Canandaigua, N.Y."

Schohariella grandis, new species. Figures 25, 26, views of holotype, USNM 163663, from G. A. Cooper loc. 119f: 25, lateral view of heteromorphic right valve (× 15); 26, ventral view of same specimen (× 30) after preparation, showing indistinct dolonoid (?) scar near contact margin; matrix not removed from right side.

Parabingeria cooperi, new species. Figures 27–30, views of USNM 163660–62, all from G. A. Cooper loc. 119f: 27, lateral view of tecnomorphic left valve (USNM) 163661), showing velar ridge, fissus and zygal ridge, and scattered punctae; 28, ventral view of heteromorphic right valve (holotype, USNM 163660), showing inflation of velar bend by crumina; 29, lateral view of heteromorphic right valve (holotype, USNM 163660); 30, lateral view of tecnomorphic right valve (USNM 163662, showing cuspate syllobium. (All views × 15.)

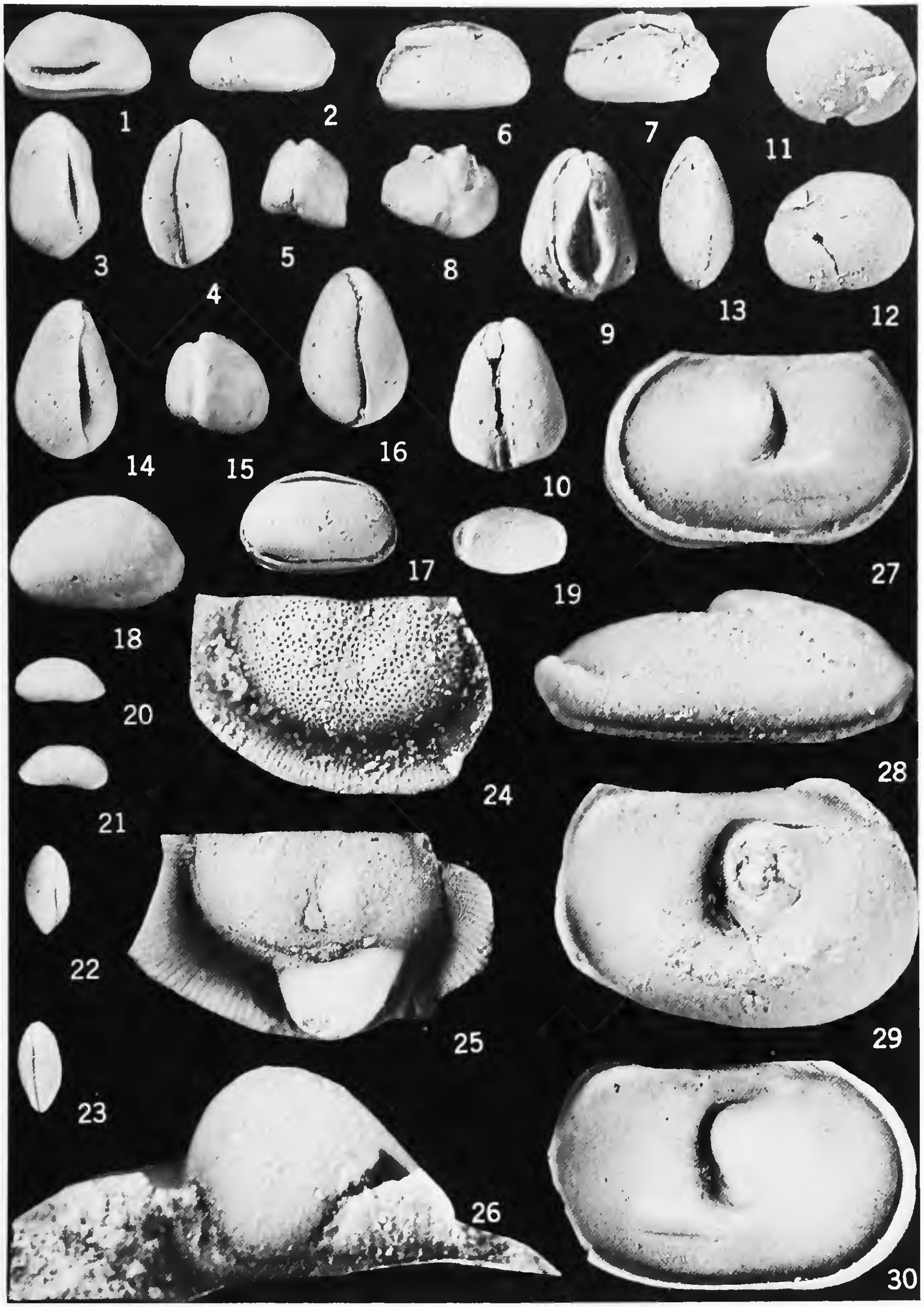
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PLATE 1

curved; and anterior and posterior margins are more sharply curved. A vertical outward-facing ridge is present at either end of the valve. The shell surface is smooth or minutely punctate.

One valve measures 1.05 mm in length and 0.55 mm in height.

MATERIAL.—One valve, from collection USGS 8211–SD.

DISCUSSION.—A single specimen (USNM 163679) of a right(?) valve was obtained for study; it is illustrated and described here to demonstrate the presence of this group of ostracodes in the Schoharie fauna. This specimen agrees with the generic description of *Parabufina* given by Smith (1965, pp. 6, 7) but lacks the spinelets on the anterior and posterior margins present on some specimens from the Ludlowville Formation. The genus *Parabufina* was placed in synonymy with *Bufina* Coryell and Malkin, 1936, by Sohn and Stover (in Moore, 1961, p. Q375), but it is here considered a valid genus.

The single specimen resembles, to some extent, the form described and illustrated by Jones (1890, p. 542, pl. 20, figs. 9a,b, 10a,b,) as *Moorea kirkbyi* from the "Corniferous chert" (Onondaga Limestone), although the vertical ridges of *M. kirkbyi* are more arcuate and the dorsal margin is straighter. Jones (1890, p. 542) described two specimens which he stated were "an inner and an outer cast." The internal cast that is deposited at the New York State Museum (NYSM 4592, new number; NYSM 13760/1, old number) is probably the original of Jones's figure 10, as his figure 9 is shown to be partly broken on the dorsal margin. Warthin (1945, index card) has suggested that this internal cast is unrecognizable but that it probably is of an *Octonaria* or *Strepulites.* However, in view of the two vertical ridges, it seems more likely that it belongs in the genus *Parabufina.*

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Dzieduszyckia in Nevada

ABSTRACT

The rare bisulcate Famennian rhynchonelloid brachiopod *Dzieduszyckia,* a homeomorph of the Triassic genus *Halorella,* occurs in barite of the Slaven Chert of Nevada. The rocks are western facies Devonian and the occurrence in them of *Dzieduszyckia* is the first reported for North America. Previously known occurrences of *Dzieduszyckia* are in Eurasia and North Africa. The presence of *Dzieduszyckia* implies that Slaven strata are, at least in part, of Famennian age, and other fossils suggest that they may range in age from Siegenian to Famennian.

One of the rarest of the cosmopolitan Late Devonian shelly invertebrates of the world is the brachiopod *Dzieduszyckia.* Previously recognized only in Poland, Morocco, and several localities in the Union of Soviet Socialist Republics (Biernat, 1967, p. 146), it is here recorded from Nevada. The Nevada occurrences have been the source of problems in affinities and age relations (Gilluly and Gates, 1965, pp. 40, 41) since their discovery, as have also those from Old World localities (Biernat, 1967). The object of this note is to diminish these problems.

Dzieduszyckia is a medium-size, strongly costate, laterally elongate, biconvex, strongly bisulcate shell, which, like *Halorella,* is asymmetrical about the median axis in degree of convexity and strength of ribbing. Unlike *Halorella,* however, which has only an inconspicuous median septum, it possesses a prominent median septum in the brachial valve; and, contrary to Siemiradzki (1909), it does not have spiralia. Its affinities have been reviewed critically by Biernat (1967), and we concur in her assignment of the genus to the Rhynchonelloidea. To discriminate unerringly between the Late Devonian *Dzieduszyckia* and its Triassic rhynchonelloid homeomorph *Halorella,* however, still can be a problem where preservation is poor.

We are grateful to the following for help with this study: G. A. Cooper, United States National Museum (USNM), for the loan of reference specimens of *Dzieduszyckia* from the Famennian of Morocco and from the Union of Soviet Socialist Republics and of *Halorella* from the Triassic of Europe; Henri Termier, University of Paris, for specimens of *Dzieduszyckia* from the Famennian of Morocco; D. V. Nalivkin, Academy of Sciences of the Union of Soviet Socialist Republics, for the gift (to J. G. Johnson) of the specimen of *D. baschkirica* herein illustrated (Plate 1: figures 1–5); N. J. Silberling and Mackenzie Gordon, Jr., for directing our attention to the problem, and to Silberling also for advice about field relations; James Gilluly for help in the field and advice about field relations; Nelson Shupe for photography of the specimens; J. G. Johnson for assistance in the laboratory; and Roman Kozlowski for informative correspondence relating to his and Gertruda Biernat's work on Polish *Dzieduszyckia.*

Occurrences in Nevada

The Nevada occurrences of *Dzieduszyckia* have been described by Silberling (in Gilluly and Gates, 1965, p. 40) as coming from four localities within the Shoshone Range, Lander County, in and adjacent to the Mount Lewis quadrangle. We have on hand seven lots of fossils, including thirty-four specimens, of which

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six lots, and perhaps all seven, are from the same four localities. Although poor, the preservation of the material is strikingly unusual in that it consists of imprints of the interior and exterior of the shell in gray barite. No shell-material is preserved. Gilluly and Gates (1965) consider that the barite deposits of the Shoshone range have a replacement origin. It is not known exactly how the imprints of *Dzieduszyckia* happened to be preserved, but one explanation could be that the shell material was dissolved away before replacement of the matrix.

The fossils were collected mainly by geologists of the United States Geological Survey (USGS) between 1950 and 1963. Later, a collection made by H. E. Wheeler in 1938 was discovered in the Stanford collections. Locality information for some of the collections is not available in detail, but the unique preservation precludes reasonable doubt as to its provenance. In the following list of known occurrences the letter "M" before the numeral indicates that the collection is located in the United States Geological Survey laboratories at Menlo Park, California.

1. USGS Green loc. M–135. Carico Claim. Greystone barite mine, NE¼ sec 26, T 28 N, R 45 E, Mt. Lewis (1/62,500) quadrangle, Nevada. *Dzieduszyckia* in dark crystalline limestone on strike with barite in easternmost quarry. Collected in 1957 by K. B. Ketner, N. J. Silberling, and James Gilluly.
2. Stanford University loc. 36430. Valley View barite mine, west side of Shoshone Range, north of Hilltop, north of Mt. Lewis quadrangle, approximately 17 miles southeast of Battle Mountain, Nevada. Collected in 1938 by H. E. Wheeler.
3. USGS Green locs. M–134 and 25023. Mound Springs barite quarries, 2 miles east and 1 mile south of NW corner T 28 N, R 44 E, Mt. Moses quadrangle, Nevada. Collected in 1957 by K. B. Ketner (his loc. 410); also by M. R. Mudge, Olcott Gates, and H. R. Gould; and again, in 1960, by Gordon Estes.
4. USGS Green loc. 25453, Hilltop, east of Mound Springs. T 28 N, R 45 E, Sonoma Range quadrangle, Nevada. Collected in 1950 by P. E. Cloud, Jr.
5. Carico barite prospect, Carico Lake, Shoshone Range, Lander County, Nevada. Perhaps the Carico claim at Greystone mine or perhaps another "Carico" claim south of the Mt. Lewis quadrangle. Specimen given to Ralph Roberts, United States Geological Survey, by an acquaintance in Battle Mountain.

Problems of Identification and Age

Despite its importance for regional geologic history, the taxonomy both of the Shoshone Range *Dzieduszyckia* and of similar forms from other continents has been confused. This confusion started with the description of the genus by Siemiradzki (1909), who mixed in with the spire-free type lot from the Devonian of the Kadzielnia quarry at Kielce, Poland, a spire-bearing shell from the Carboniferous of Maas, Belgium (Biernat, 1967, p. 136), and described the genus as a spire-bearer. The specimens from Morocco originally were assigned to the spire-free Triassic genus *Halorella* by Termier and Termier (1936, 1948) without reservation, although they were well aware of the age anomaly. In 1949, however, at the suggestion of G. A. Cooper, the Termiers considered the possibility of affinities with *Dzieduszyckia.* They decided to retain the name *Halorella* for the Moroccan shells but to call attention to the need for a general revision of the Paleozoic rhynchonelloids.

The first specimen from Nevada to come to our attention was one collected by Cloud in company with James Gilluly in 1950. This specimen (Plate 1: figure 13) is only a fragmentary impression of the anterior of a valve, and it was retained only because megafossils were so rare in the Slaven Chert. Since the beds were thought to be of upper Paleozoic age, this specimen was referred for study to Mackenzie Gordon, Jr., who made the perceptive suggestion that it was very like the Triassic genus *Halorella* (internal report of USGS). Such an identification, however, would have been inconsistent with the field evidence and with the Middle Devonian age later suggested on the basis of conodonts by W. H. Hass and ostracodes by Jean Ber-

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PLATE 1: figures 1–5.—*Dzieduszyckia baschkirica* (Tschernyschew), western part of Terek River area, southern Ural Mountains, Upper Devonian (D_3^2); brachial, pedicle, and anterior, posterior, and lateral views (× 1) of a steinkern, USNM 160193A.

Figures 6–17.—*Dzieduszyckia* sp., Slaven Chert, Shoshone Range, Nevada. All illustrated specimens except those of figures 8 and 13 are from USGS Green loc. M–134 (=25023). 6, Internal impression of a pedicle valve (× 2), USNM 160185; 7, 9, 12, pedicle and lateral and anterior views (× 1) of a steinkern, USNM 160186; 8, internal impression of a brachial valve (× 1.5), USNM 16087, from unnumbered locality at Carico Lake (No. 5 in list of occurrences); 10, partial external impression (× 1), USNM 160188; 11, exterior of a pedicle valve (× 1), USNM 160189; 13, partial external impression (× 1) of first Nevada specimen studied, USNM 160190, from USGS Green loc. 25453; 14, impression of a brachial valve (× 1), USNM 160191; 15, internal impression of a brachial valve (× 2), USNM 160192; 16, internal impression of a brachial valve (× 1), USNM 160193; 17, internal impression of a brachial valve (× 1), USNM 160184.

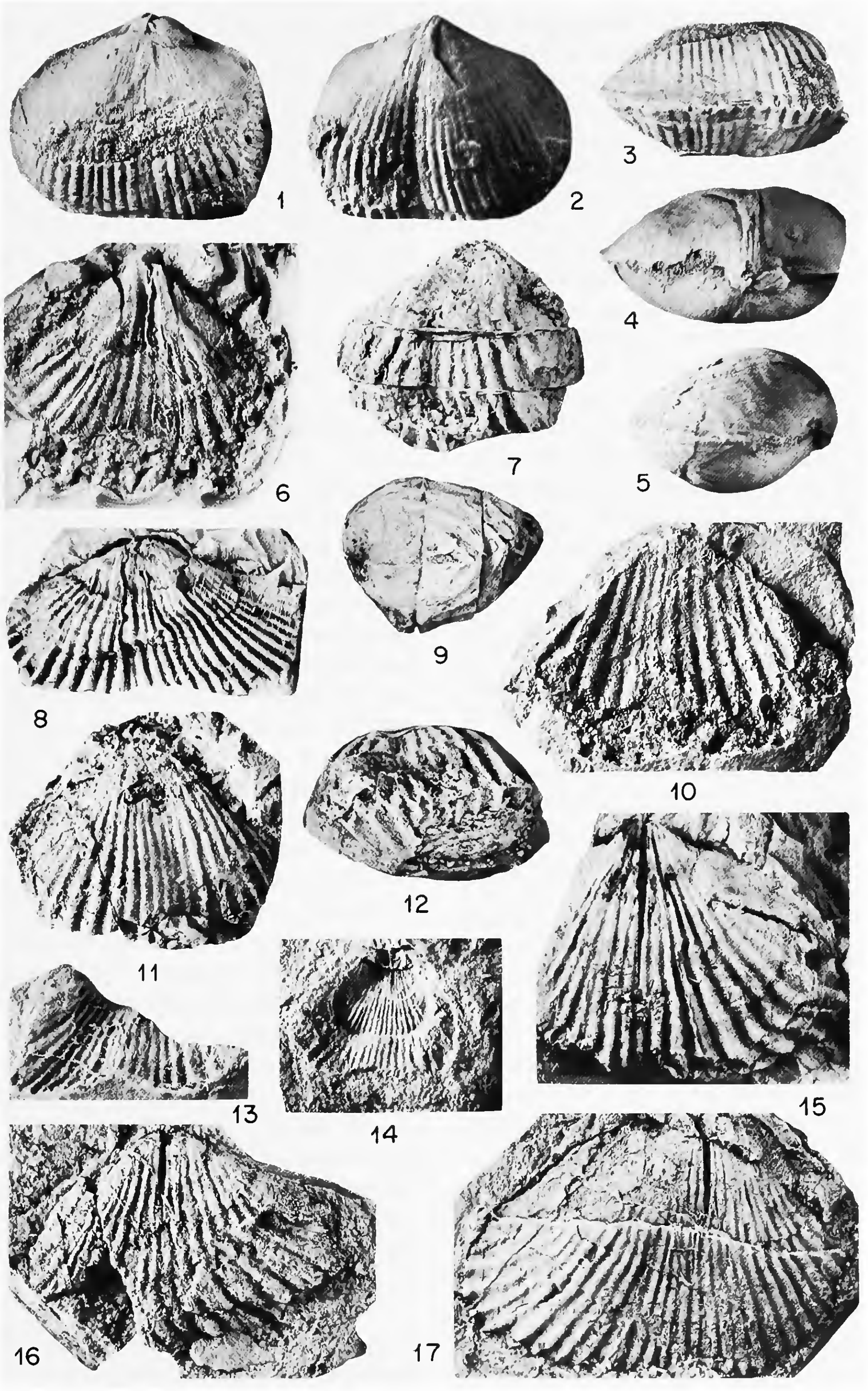

PLATE 1

dan (Gilluly and Gates 1965, p. 40)—unless *Halorella* had a much longer range than was believed likely.

Norman Silberling, therefore, became interested in the problem as a student of the Triassic, and he summarized the stratigraphic and paleontologic evidence available to December 1957 in an internal (USGS) report of which the critical parts later were published by Gilluly and Gates (1965, pp. 40–41). Silberling advised caution in choosing between a Triassic age, as favored by an assignment of the brachiopods to *Halorella,* and a Devonian age, as suggested by the microfossils of the Slaven Chert. Moreover, he already suspected that the brachiopods might be most similar to forms of "*Halorella*" described from the Upper Devonian of North Africa by Termier (1936).

Following up on Silberling's suggestion, Cloud (internal report, USGS, 23 September 1958; and in Gilluly and Gates, 1965, p. 41) compared the Slaven Chert brachiopods then available with both Triassic *Halorella* and similar Moroccan Famennian rhynchonelloids assigned to *H. intermedia* and *H. crassicosta* by Termier and Termier. He concluded that the Nevada and Moroccan specimens were similar, that they might be generically distinct from true *Halorella,* and that the Nevada occurrence should be considered to be of "Devonian? and perhaps Late Devonian" age. At that time Cloud was dubious of an assignment of these specimens to *Dzieduszyckia* because of the spiralia that were supposed to be found in this genus.

The age of *Dzieduszyckia* has been somewhat less of a problem. Originally assigned by Siemiradzki (with a query) to the *Hypothyridina cuboides* beds of Frasnian and upper Givetian age, the Polish specimens now are regarded as of Famennian age (Biernat, 1967, p. 140). A Famennian age also is established for the Moroccan and Russian specimens.

As a result of our restudy, and of the work of Biernat, we conclude that the Nevada specimens belong to the genus *Dzieduszyckia* and that a Famennian age is indicated by the ages of known occurrences of that genus in Morocco, Poland, and the Union of Soviet Socialist Republics.

Dzieduszyckia sp.

PLATE 1: FIGURES 6–17

The description below is based on thirty-four incomplete specimens from Nevada, of which only ten are good enough to illustrate. Unfortunately, the preservation even of these ten is too poor to warrant assignment or description at the species level.

EXTERIOR.—Both valves are strongly convex, the pedicle valve being the deeper, and both bear a broad, well-developed sulcus. The position of maximum width is near the midlength. The hinge-line is relatively short; it seems to be roughly about one-third of the maximum width. The beak of the pedicle valve is incurved. The posterolateral and lateral margins round evenly into the gently curved anterior margin. The surface of commissure is flat and medially incised in plan view. Ornamentation consists of numerous costae, crossed by a few concentric growth lines. The number of costae is quite variable among specimens studied, ranging from 12 to about 30. The number of costae in the sulci is also variable, with four to eight being observed. The prominent sulci present in both valves originate at a relatively early growth stage. The internal impressions of the costae and the interspaces separating them are U-shaped in cross section and increase in size anteriorly. The shell is asymmetrical about the median axis, one side appearing to be slightly more convex and having a larger number of costae than the opposite side—a feature that *Dzieduszyckia* and *Halorella* share in common.

INTERIOR OF BRACHIAL VALVE.—A well-developed median septum is present (Plate 1: figures 15–17). The septum extends anteriorly to about the midlength or beyond. The outline of the muscle field is not well displayed on the Nevada specimens. The impress of the external ornamentation is strong.

INTERIOR OF PEDICLE VALVE.—Short dental lamellae are present (Plate 1: figure 6). Secondary shell material was deposited in the area of the umbonal cavities, and the impression of the muscle field projects well beyond the impression of the umbonal chambers. Although the muscle field is poorly preserved, it appears to have consisted of paired, elongate, lateral elements separated by a median area that is raised off the floor of the valve relative to the lateral areas. It could not be determined whether the median area was occupied entirely by the adductor muscle attachments or not.

AFFINITIES.—Cloud (in Gilluly and Gates, 1965, p. 41) has already contrasted the external form of the Nevada material with that of Triassic *Halorella.* He noted particularly that the Nevada specimens seemed to lack the "sharply defined beak ridges and palintropes" of the Triassic forms, and also that the beak of Triassic *Halorella* is suberect, as opposed to the incurved condition observed in its Devonian homeomorph from Nevada and Morocco (and also Poland, Biernat, 1967, p. 146). Internally, the presence of a prominent median septum in the brachial valve distinguishes our specimens from Triassic *Halorella.*

Well-preserved specimens of *Dzieduszyckia baschkirica* (Plate 1: figures 1–5) are similar to the Nevada material in outline and general external form. However, the costae of the Russian specimens (*D. baschkirica*) are flatter across their crests and the interspaces are relatively narrow. The median septum is not conspicuous in the brachial valve of the Russian specimens that we examined, but Biernat (1967, p. 137) assures us that it is conspicuous in other specimens. The type-species, *D. kielcensis,* from Poland, described and illustrated in detail by Biernat (1967), closely resembles the Nevada material in its span of variation as regards costae and interspaces, and it displays a prominent septum in the brachial valve. Similarity is also observed between the Nevada specimens and the Moroccan species *D. intermedia* and *D. crassicosta,* which like other *Dzieduszyckia,* possess a median septum in the brachial valve (Termier and Termier, 1950, pl. 100, fig. 17).

In seeking to establsh suprageneric affinities, we sectioned one of the Russian specimens, *D. baschkirica,* and one of the Nevada specimens to see if we could find the spiralia reported by Siemiradzki (1909) to characterize the genus. Our results were negative, consistent wtih those of Biernat (1967), who also observes (Biernat, 1967, p. 19) that the spiralium-bearing specimen illustrated by Siemiradzki (1909, fig. 3b) did not belong to the type lot of *D. kielcensis* from the Devonian at Kielce but came instead from the Carboniferous of Maas, Belgium. Termier and Termier (1950) also found no spiralia in the Moroccan specimens. All evidence, therefore, is now consistent with the assignment of *Dzieduszyckia* to the Rhynchnelloidea. It probably belongs to the Dimerellidae, in the subfamily Halorellinae. It is evidently not a member of the Athyrisinidae, as assigned by Boucot (in Moore, 1965, p. H654).

Distribution.—The rarity of the genus *Dzieduszyckia* raises puzzling questions about how it became distributed so widely (Biernat, 1967, p. 146). Late Devonian brachiopods are among the most cosmopolitan marine invertebrates known in the northern hemisphere, and many of them are very abundant. With the open connections and free genetic exchange thus implied, it is hard to see why equally cosmopolitan forms like *Dzieduszyckia* should be so rare. One can only guess that they might have been ovoviviparous or limited to an extremely specialized environment.

Age of the Slaven Chert

Earlier reports on the Slaven Chert (Gilluly and Gates, 1965, pp. 40–41) enable a Middle Devonian and possibly Late Devonian age to be assigned to the unit. The presence of *Dzieduszyckia* is now interpreted to demonstrate that the Slaven Chert includes strata of Late Devonian age. In addition, however, Berdan (in letter dated 9 January 1967 to J. G. Johnson) concludes that some of the ostracodes from the Slaven Chert at Gilluly's locality F–106 are very similar to forms from the Siegennian *Quadrithyris* zone of the Windmill Limestone (Johnson, 1965). This suggests that part of the Slaven Chert also may be of Early Devonian age. Thus, it appears that the Slaven Chert spans much of the Devonian and that *Dzieduszyckia* comes from its upper part. On present evidence *Dzieduszyckia* appears to be distinctive of a Famennian age.

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J. Thomas Dutro, Jr.

The Brachiopod *Pentagonia* in the Devonian of Eastern United States

ABSTRACT

Pentagonia is a specialized meristellid brachiopod with a restricted stratigraphic and geographic distribution in the Devonian of eastern North America. The genus is characterized by its external pentagonal shape, both in plan view and in posterior outline. Internally, the pedicle valve has a large, flabellate muscle area bounded by relatively prominent dental plates. The brachial interior is dominated by a massive cardinal process and a low median septum, both of which are interpreted as evolving from meristellid structures. *Pentagonia* has no functional pedicle, and shell shape is apparently related to a free-living condition on the sea floor. An extraordinary feature of this brachiopod is a pair of pouchlike structures, near the postero-lateral margins, which may have been either brood pouches or the sites of the sexual organs.

Pentagonia was recognized as a separate genus more than a century ago. The genus was named by Isaachar Cozzens in 1846, with *P. peersii* as the type-species based on material obtained by the Rev. Benjamin O. Peers at the Falls of the Ohio River, Louisville, Kentucky. The oldest described species now assigned to the genus is *Atrypa unisulcata* Conrad, 1841. Conrad's fossils came from the Onondaga Limestone at Schoharie, New York. James Hall (1861), apparently unaware of Cozzens' paper, proposed the genus *Goniocoelia* based on Conrad's species. Later, Hall (1894) stated that *Goniocoelia* was an exact synonym of *Pentagonia* and therefore should be stricken from the list of brachiopod genera.

Other species ascribed to *Pentagonia* have been described and illustrated by Hall (1867), Butts (1941), and Cooper (1944). *Pentagonia peersii* was described and illustrated by Nettleroth (1889) from Kentucky as *Meristella unisulcata* Conrad. *Meristella lenta,* assigned herein to *Pentagonia,* was described by Hall in 1867. *Pentagonia*? *goldringae* (Howell), from the Esopus Formation, was inadequately described and illustrated by Howell (1942).

Occurrences of the genus in Ontario were listed by Stauffer (1915) and those in Kentucky were cited by Savage (1931). Stauffer (1909) did not report *Pentagonia* from Ohio, but the genus later was listed by Stumm (1942) as occurring in the fauna of the Prout Limestone. Devonian occurrences of the genus in Tennessee were discussed by Dunbar (1919), and those from rocks of Onondaga age in Virginia were listed and illustrated by Butts (1941).

A summary of the distribution of *Pentagonia* in rocks of Schoharie age was provided by Boucot and Johnson (1967, 1968). They reported the species *P. unisulcata* from the Kanouse Sandstone and Woodbury Creek Member of the Esopus Formation in southeastern New York, the Frog Mountain Sandstone of Alabama, the Camden Chert of western Tennessee and Devonian strata of the James Bay lowland in Canada. The specimens from the Schoharie itself are listed as *Pentagonia* cf. *P. unisulcata* (Conrad).

The only report of the genus outside eastern North America known to me is that by Caster (1939) from the Lower Devonian Floresta fauna of Colombia. Caster's species, *P. gemmisulcata,* appears to be very close to *P. unisulcata.*

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Pentagonia? sp., reported years ago by Williams and Breger (1916) from the Chapman Sandstone of Maine, was only doubtfully assigned to that genus. The assignment has been questioned by Boucot (in Boucot and others, 1964) and the illustrated specimens in the collections of the United States National Museum (USNM) were examined again in the course of this study. A positive generic identification is not possible on the basis of these poorly preserved internal molds. Because of the apparent absence of a septum in the brachial valve, these specimens are removed from *Pentagonia*.

Phylogenetic Relationships

With the exception of the highly doubtful Chapman Sandstone occurrence, the earliest true *Pentagonia* occurs in rocks of Schoharie age. During that time, in the late Early Devonian, the genus, although a rare element of the total brachiopod assemblage, apparently was rather widely distributed. *Pentagonia lenta* (Hall) from the "Oriskany" of Ontario is actually from the Springvale Sandstone, as pointed out by Stauffer (1915). This small species was apparently a local variant related to the much more widely distributed *P. unisulcata*. The genus is well represented by *P. unisulcata* in Onondaga age rocks from New York to Virginia, but that species has not yet been reported from the western equivalents of the Onondaga in Ohio, Kentucky, Indiana, and Illinois.

The Centerfield Limestone of New York and its correlatives in Ontario, Ohio, Pennsylvania, Kentucky, and Indiana have yielded many specimens of the youngest known species, *Pentagonia peersii* Cozzens. The species is especially abundant in the Beechwood Limestone of southern Indiana.

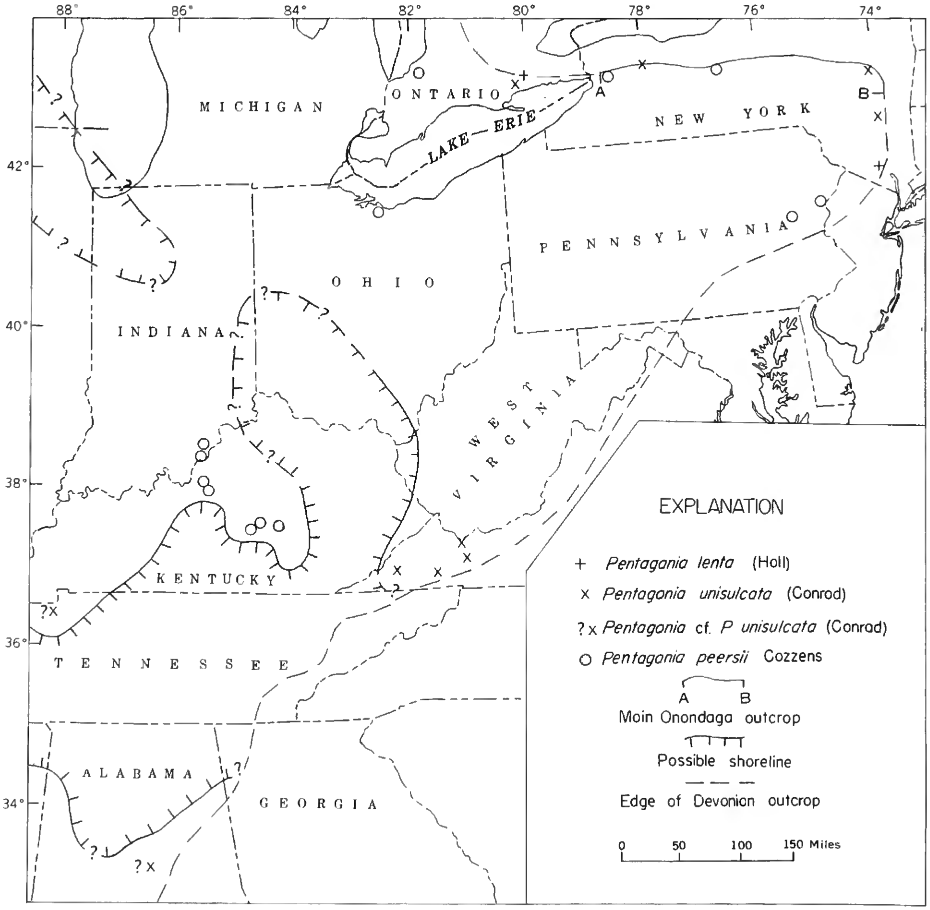

FIGURE 1.—Distribution of localities yielding *Pentagonia* in eastern North America.

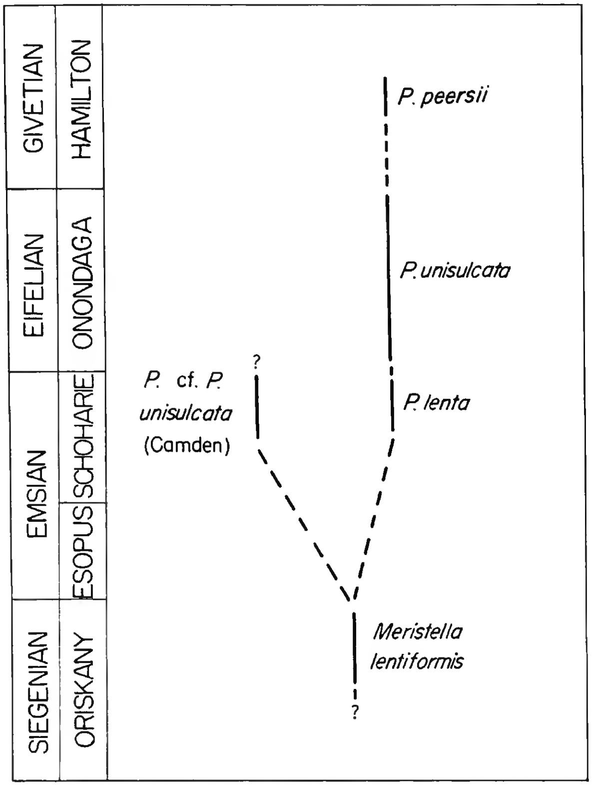

FIGURE 2.—Suggested phylogenetic relationships among the species of *Pentagonia* and *Meristella lentiformis* Clarke.

In searching for an ancestor of *Pentagonia*, species of *Meristella* in beds older than the Schoharie were examined. The most likely progenitor to the specialized *Pentagonia* appears to be *Meristella lentiformis* Clarke, 1900. This species was described from the Glenerie Limestone of southeastern New York.

Meristella lentiformis retained a foramen that suggests a functional pedicle throughout its lifespan. In *Pentagonia*, reduction of a functional pedicle resulted in, or was the response to, a free-living condition on the sea floor. The flattened pedicle valve probably reflects an adjustment to stabilize the shell on the bottom. *Pentagonia* lived with its pedicle valve down, and the development of a thick callosity in the posterior part of the pedicle valve undoubtedly aided in the stabilizing process (Rudwick, in Moore, 1965, p. H201; Grant, 1965, p. 27; Ager, 1967, p. 160).

The genus was widely dispersed during Schoharie time (see Figures 1, 2) but became more restricted and more specialized during the Middle Devonian. The large, robust species *Pentagonia peersii* had a more restricted range, and the genus became extinct before the end of the Middle Devonian.

The history of the genus, then, is one of increasing species size from Schoharie through Centerfield time (see Figures 3–5). Although other genera among the Meristellinae lasted until the end of the Middle Devonian (Tully time), no representative of *Pentagonia* has been reported from post-Centerfield rocks. The reason for the disappearance of the meristellids is not known, but their ecologic position in the brachiopod assemblage apparently was taken over by the closely related athyrids, which had external stabilizing mechanisms. Possibly, the unanchored condition of the *Pentagonia* shell made survival difficult in the relatively high-energy environments that resulted in well-sorted clastic carbonate rocks. No representative of the genus has been collected from mud or silt rocks; doubtless the free-living position of the shells would have resulted in rapid clogging and death of individuals in such an environment. There must have been a fine balance between current action and firm substrate for the genus to have survived at all.

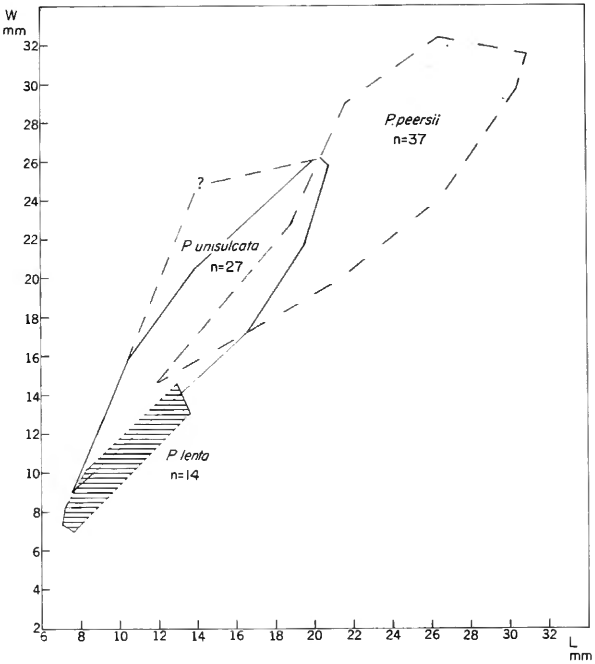

FIGURE 3.—Comparative-size polygons for *Pentagonia lenta* (Hall), *P. unisulcata* (Conrad), and *P. peersii* Cozzens, fitted visually.

Life Habit

In contrast to the other genera that are included in the subfamily Meristellinae, the adult *Pentagonia* had no foramen; hence, it apparently had no functional pedicle. Some very small specimens show what may be a tiny opening that could have accommodated a hair-like pedicle during early growth stages. With age, however, this opening was closed and the animal must have lived free on the sea floor. The flattened pedicle valve would have contributed to the stability in this position of life, as would the secondarily thickened posterior regions of the valves, especially the heavy umbonal region of the pedicle valve.

A number of specimens in the collections from the Beechwood Limestone of southern Indiana have organisms attached to the shell. Common epifaunal elements are the tabulate coral *Aulopora* and various kinds of bryozoans (Plate 2: figures 11, 12). These organisms are invariably found either on the brachial valves or on that part of the pedicle valve, lateral to the prominent carinae, where they would have been elevated above the water-sediment interface. Similar associations were reported by Ager (1961) in his paper on the epifauna of a Devonian spiriferid.

Many of the shells from the Beechwood locality near Charlestown, Indiana, have been drilled or bored by other organisms (Plate 2: figures 5, 8, 9). Three kinds of borings have been observed. One roughly circular cylindrical type of boring is by far the most common. A second type, commonly attributed to barnacles (Tomlinson, 1963), is elliptical to teardrop-shaped in plan. The third variety, an elongate tubular boring, perhaps of sponge origin, is quite rare.

Tabulated below are the kinds and number of borings observed in a single large collection consisting of 93 brachial valves, 410 pedicle valves, and 12 articulated shells.

Borings	*Brachial Valves (93)*	*Pedicle Valves (410)*	*Articulated Shells (12)*
Circular/cylindrical			
Single, per shell	5	35	1
Multiple, per shell	—	9	1
Elliptical/teardrop			
Single, per shell	1	1	—
Multiple, per shell	1	2	—
Elongate/tubular			
Single, per shell	—	—	—
Multiple, per shell	—	2	—

Clearly, because of the disproportionate number of disarticulated shells and the preponderance of the heavier pedicle valves, this collection represents an accumulation of shells as gravel on the sea floor. The petrography of the Beechwood Limestone supports its interpretation as a lag deposit at many localities. No doubt these particular shells were drilled after their disarticulation. However, such a large number of individuals of *Pentagonia* must reflect the existence of a considerable community of this species in the neighborhood of the Falls of the Ohio during Centerfield time. No other recorded locality of the genus has yielded more than a few specimens of what must have been a minor element of the total brachiopod assemblage.

Superfamily ATHYRIDACEA M'Coy, 1844

Family MERISTELLIDAE Waagen, 1883

Subfamily MERISTELLINAE Waagen, 1883

Genus *Pentagonia* Cozzens, 1846

1846. *Pentagonia* Cozzens, p. 158, pl. 10, figs. 3a,b.—Hall, 1867, pp. 309–311, pl. 50, figs. 18–35.—Hall and Clarke, 1894, p. 80, pl. 42, figs. 22–32.—Schuchert and LeVene, 1929, p. 95.— Caster, 1939, p. 171.—Cooper, 1944, p. 333.—Boucot, Johnson, and Staton (in Moore, 1965), p. H656.

1861. *Goniocoelia* Hall, p. 101.

ORIGINAL DIAGNOSIS.—"Shell bivalve, inequivalve, having five sides, somewhat gaping; lower valve with three sides, upper with two; *beaks* contiguous." (Cozzens, 1846, p. 158.)

EMENDED DIAGNOSIS.—Specialized, strongly biconvex meristellids with pentagonal shell form; pedicle valve with broad, flat sulcus bounded by angular carinae; brachial valve with high fold, generally having narrow median groove. Pedicle interior with striate, flabellate muscle area and flaring dental plates extending about halfway to anterior margin of muscle field. Brachial interior with enlarged brachial process that has rotated posteriorly to fill delthyrial cavity; process with concave anterior surface and a cardinal plate that extends posteriorly as a scoop-shaped concavity; low median septum extends downward across the anterior face of the cardinal process and anteriorly nearly to the anterior margin of the valve. No functional pedicle in the adult growth stages. Pouchlike developments in posterolateral regions.

TYPE-SPECIES.—*Pentagonia peersii* Cozzens, 1846.

Included species.—*Pentagonia peersii* Cozzens, *P. unisulcata* (Conrad), *P. lenta* (Hall), *P. gemmisulcata* Caster.

Rejected species.—*Pentagonia*? sp. Williams and Breger, *Pentagonia? goldringae* Howell.

Discussion.—In Cozzens' original diagnosis (1846), two significant points should be noted. The five-sided nature of the shell clearly refers to its appearance in posterior outline, as is shown by his figured specimen (Cozzens, 1846, pl. 10, fig. 3a). The second significant point is the emphasis on contiguous beaks. A significant feature of the genus, it would appear, is the absence of a functional pedicle in the adult animal.

In reverting to *Pentagonia peersii* as the type-species, I depart from Hall (1867) and all subsequent workers. *Pentagonia peersii* was based on material from the Falls of the Ohio, now recognized as coming from the Beechwood Limestone. Following Hall's suggestion, later usage referred to this Middle Devonian form as *P. biplicata*. Conrad's species *P. unisulcata* was described on material from the Onondaga Limestone. Nearly all workers have recognized the distinct specific differences between the Schoharie-Onondaga form and the one from the Centerfield and its equivalents. However, *P. biplicata* Hall is a synonym of *P peersii* Cozzens.

Pentagonia peersii Cozzens, 1846

Figures 3, 4; Plate 1: figures 9–12; Plate 2: figures 1–3, 5–12

1846. *Pentagonia peersii* Cozzens, p. 158, pl. 10, figs. 3a,b.
1862. *Meristella? unisulcata* (Conrad) var. *biplicata* Hall, pl. 2, p. 158, fig. 18.
1862. *Meristella? unisulcata* (Conrad) var. *uniplicata* Hall, pl. 2, p. 158, figs. 19, 24, 25.
1867. *Meristella (Pentagonia) biplicata* Hall, p. 311, pl. 50, figs. 30–35.
1889. *Meristella unisulcata* (Conrad).—Nettleroth, pp. 99, 100, pl. 15, figs. 9–16.
1894. *Pentagonia unisulcata* (Conrad).—Hall and Clarke, pl. 42, figs. 25–32.—Savage, 1930, pl. 4, figs. 24–26; 1931, pl. 30, figs. 17, 18.
1936. *Pentagonia* sp. Cooper, p. 9, fig. 8.8.
1942. *Pentagonia bicostata* Stumm, p. 556, pl. 84, fig. 46.
1944. *Pentagonia bisulcata* (Cooper), p. 333, pl. 127, figs. 32, 36.—Rickard, 1964, chart.—Oliver and others, 1969, chart.

Original description.—"Shell somewhat gaping, with five sides and three carinae; two of the carinae on the lower valve commence at the beak, and diverge toward the margin, and end at the opening, the valve being concave between them; the lateral margins small and nearly vertical, an elevated carina on the middle of the upper valve, rendering its sides somewhat concave. This carina has a shallow furrow in it, commencing at the beak and running more than halfway along the shell towards the opening. On each side of the upper valve and contiguous to the beaks, are two angular protuberances, giving the shell when viewed at the beaks, a pentagonal appearance, and at the same time a visage-form look; length 1.1 inch, breadth 0.9 inch." (Cozzens, 1846, p. 158.)

Emended description.—Shell large for the genus, unequally biconvex, pentagonal in plan view and posterior profile; wider than long with greatest width near anterior margin; shell structure fibrous, impunctate; external ornament consisting only of concentric growth lines.

Brachial valve strongly arched with high fold extending to anterior margin, fold with shallow furrow extending to midlength; sharp to rounded carinae variably developed on either side of beak, at acute angles to the plane of commissure, extending about one-third to one-half distance to anterolateral margins; generally one carina on either side of the beak, very rarely two carinae on either side; carinae are external reflections of internal pouches. Interior dominated by massive cardinal process with steep concave anterior face, cardinal plate depressed to form concavity that lies in the plane of the valve, process extending posteriorly to completely fill umbonal cavity, often with bilobed appearance in posterior view; narrow, low median septum extends across anterior face of process and about one-half distance to anterior margin; adductor muscle tracks, deeply impressed on either side of septum, reflect anterior movement of narrow, elliptical adductor marks; process bounded by deep sockets; crural bases project posteriorly from anterior face of cardinal process on either side of median septum; pouchlike depressions developed laterally from sockets, many with pitted inner surfaces.

Pedicle valve broadly sulcate with sharp carinae extending from beak to anterolateral margins, dividing sulcus from steep lateral slopes; thin costa in middle of sulcus, complimenting furrow in brachial fold. Interior with broad, flabellate, striate muscle area bounded by extensions of dental plates for about one-half

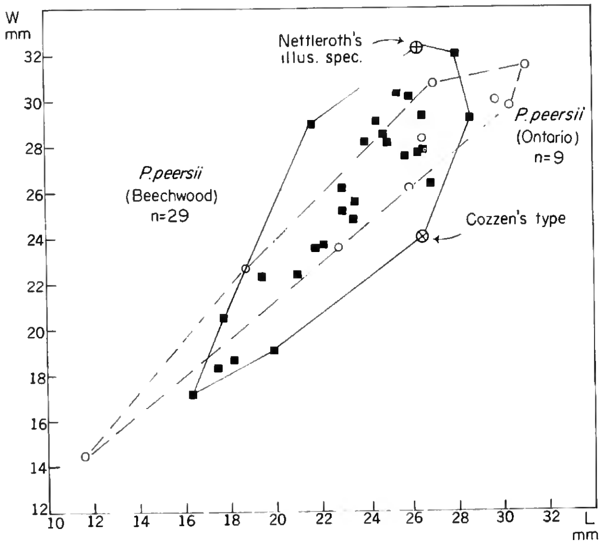

FIGURE 4.—Length-width relationships of collections of *Pentagonia peersii* Cozzens from the Hungry Hollow Formation of Ontario and the Beechwood Formation of southern Indiana.

its length; prominent teeth surmount the dental plates; pitted pouchlike areas lateral to the dental plates resemble those in the brachial valve.

DISCUSSION.—The character by which Hall originally suggested that this stratigraphically younger species be differentiated was the development of two carinae on either side of the brachial beak. This feature, however, appears to be only a very rare variant of the normal condition. Only three of 105 brachial valves in the collection from the Beechwood show these carinae. The main character which separates this species from *P. unisulcata* is average size. On the whole, the shells from the Beechwood and other Centerfield equivalents are much larger than those of *P. unisulcata* from the Onondaga (Figure 3). Immature shells, those up to about half the size of adults in *P. peersii,* are almost identical in form to adults of *P. unisulcata.*

It is a curious coincidence that two later species designations appear to fall into the category of unjustified emendations (Stumm, 1942; Cooper, 1944; Rickard, 1964; Oliver and others, 1969). These can be no more than inadvertent oversights because *"biplicata"* was clearly the trivial name advocated by Hall.

ILLUSTRATED SPECIMENS.—USNM 163807–13 from Beechwood Limestone, near Charlestown, Indiana, Greene Collection, USNM Acc. No. 232542.

Pentagonia lenta (Hall)

FIGURES 3, 5; PLATE 1: FIGURES 5–8; PLATE 2: FIGURE 4

1867. *Meristella lenta* Hall, p. 420, pl. 63, figs. 19–22.—Stauffer, 1915, pp. 79–82.

1959. *Pentagonia unisulcata* (Conrad)—Boucot, p. 748, pl. 94, figs. 9, 10.

ORIGINAL DESCRIPTION.—"Shell small, broadly ovate, or transversely oval, with a slightly projecting beak and very unequally convex valves. Ventral valve nearly flat in the upper part, with sharply angular cardinal margins becoming deeply and subangularly sinuate towards the front, where it is slightly bent upwards. Dorsal valve very ventricose in the umbonal portion, and subangular along the center, with the sides somewhat flattened. This species differs from any described form of the genus so far as it can be ascertained. In the form of the ventral valve it approaches somewhat the *M.* (*Pentagonia*) *unisulcata,* but the sinus is narrow instead of embracing the greater part of the valve, and it differs so materially in other respects that there is no danger of confounding the two." (Hall, 1867, p. 420.)

EMENDED DESCRIPTION.—Shell small, unequally biconvex, subovate, about as wide as long with the greatest width near midlength; triangular to flattened pentagonal shape in posterior outline; shell structure fibrous, impunctate; exterior smooth.

Brachial valve strongly arched with high fold extending to anterior margin; fold unmodified, without lateral carinae. Interior with massive cardinal process, as in *P. peersii,* and median septum extending about halfway to anterior margin; narrow adductor muscle tracks faintly impressed on either side of septum.

Pedicle valve flattened, sulcate, faintly carinate with two rounded ridges bounding sulcus, which occupies about one-third the width of the valve. Interior with broad, flabellate striate muscle field and dental plates like those of the type-species.

DISCUSSION.—Hall (1867) suggested the possible relationship of this species to *Pentagonia,* but he did not make the assignment because of differences in external shape. In most respects, however, this small species is an ideal progenitor of the two larger forms of *Pentagonia.* In addition, the interior, with its massive cardinal process, is identical to *Pentagonia. Meristella lenta* is herein assigned to that genus.

The stratigraphic position of this species needs clarification. According to Hall (1867), *M. lenta* was found "In rocks of the age of the Oriskany sandstone or

Upper Helderberg limestone, near Cayuga, C.W." Stauffer (1915) was able to pinpoint the occurrence of the species to the Springvale Sandstone. Oliver (1967, p. A3) suggests that the Springvale is of Bois Blanc age. Thus, the stratigraphic position of *Pentagonia lenta* is approximately the same as that of the earliest *P. unisulcata* reported from eastern New York. Although the two species probably represent geographically isolated communities in Schoharie time, it is possible that *P. lenta* represents a slightly older horizon. *Pentagonia unisulcata* appears in Onondaga rocks higher in the Ontario section and could be considered a descendant of *P. lenta.*

The *P. unisulcata* of eastern New York can be derived from *Meristella lentiformis* in the same geographic area through the small species of *Pentagonia* described by Boucot (1959) from the Woodbury Creek. Boucot's *P. unisulcata* is assigned to *P. lenta.*

ILLUSTRATED SPECIMEN.—USNM 28038 from "Upper Oriskany" (now the Springvale Sandstone), 6 miles west of Cayuga, Ontario, Canada. Collector: Charles Schuchert. USNM Acc. No. 30039.

Pentagonia unisulcata (Conrad)

FIGURES 3, 5

1841. *Atrypa unisulcata* Conrad, p. 56.
1861. *Atrypa uniangulata* Hall, p. 101.
1862. *Meristella? unisulcata* (Conrad), Hall, pl. 2, p. 158, figs. 17, 20–23 (not figs. 19, 24, 25).
1867. *Meristella (Pentagonia) unisulcata* (Conrad)—Hall, 1867, p. 309, pl. 50, figs. 18–29 (not figs. 30–35).
1889. Not *Meristella unisulcata* (Conrad), Nettleroth, p. 99, pl. 15, figs. 9–16.
1915. *Pentagonia unisulcata* (Conrad), Stauffer, p. 104, 245 (not pp. 160, 171, 175, 234).—Dunbar, 1919, pp. 87, 89.—Goldring, 1935, p. 148, figs. 53B–D.—Butts, 1940, pp. 300, 301, 304, 305; 1941, pl. 115, figs. 17–21, 35.—Cooper and others, 1942, chart.—Cooper, 1944, p. 333, pl. 127, fig. 37.—Oliver, 1954, pp. 633, 634, 638–640; 1956, pp. 1452, 1456, 1462, 1469.—Rickard, 1964, chart.—Boucot and others, in Moore, 1965, p. H656, pl. 533, figs. 2a–d (not figs. 2e–f).—Oliver and others, 1969, chart.
1930. Not *Pentagonia unisulcata* (Conrad), Savage, p. 47 50, 53, 62; 1931, p. 242, pl. 30, figs. 17, 18.

ORIGINAL DESCRIPTION.—"Trigonal, superior valve with a broad, prominent middle, sulcated longitudinally, the sulcus being obsolete towards the base; sides concave; the depression giving the margins a carinated appearance; inferior valve deeply concave, subangulated in the middle; umbonal slope carinated, and the area between it and the margin much depressed. Locality.—Schoharie, in Onondaga limestone." (Conrad, 1841, p. 56.)

EMENDED DESCRIPTION.—Shell medium-sized, unequally biconvex with triangular to pentagonal shape in plan view and in posterior outline, greatest width near anterior margin; shell impunctate with fibrous structure and ornamented only with concentric growth lines.

Brachial valve with prominent sulcated fold and two lateral carinae that extend at acute angles from the umbo across the posterolateral slopes; tendency towards deeply concave slopes between the fold and the lateral margins produces a corrugated appearance; sulcus in fold extends to or nearly to the anterior margin. Interior with prominent cardinal process, as in *Pentagonia peersii,* and median septum extending about two-thirds distance to anterior. Details of muscle scars and presence or absence of posterolateral pouches not determined.

Pedicle valve broadly sulcate with two prominent sharp carinae extending from umbo across lateral slopes to anterolateral margins. Interior with broad,

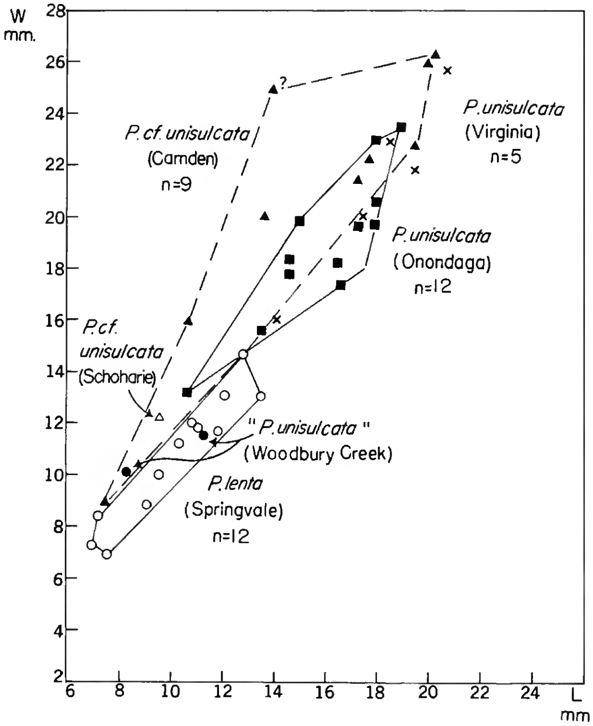

FIGURE 5.—Length-width relationships of several collections of *Pentagonia lenta* (Hall) and *Pentagonia unisulcata* (Conrad).

striate, flabellate muscle area bounded by dental plates that extend nearly half the distance to the anterior edge of the muscle field.

Discussion.—Much confusion has surrounded this species since its original description by Conrad. In the 1800s, and even as late as Savage's (1930, 1931) papers on the Devonian of Kentucky, there was a tendency to place all specimens of *Pentagonia* in *P. unisulcata* and to regard *P. peersii* as a synonym of Conrad's species. In 1862, Hall discussed the variations within this group of species and proposed two varietal names for the forms that differ from Conrad's *unisulcata* of the New York Onondaga. Hall suggested that the "Hamilton form" be called *Meristella*? *unisulcata* var. *biplicata* and that the "western form" be designated *M*? *unisulcata* var. *uniplicata*. By implication, the typical form would have been called *M*? *unisulcata* var. *unisulcata*.

I have been able to confirm the essential conspecifity of the Hamilton (i.e., Centerfield) and the western (i.e., Beechwood) forms. These are, in fact, included in Cozzen's *Pentagonia peersii*. The residue of forms left in Hall's original concept of the species thus becomes *P. unisulcata* (Conrad). This species has been well illustrated by Hall (1862, 1867).

Genus *Meristella* Hall, 1859

1859. *Meristella* Hall, p. 78; 1860, p. 74; 1867, p. 295.—S. A. Miller, 1889, p. 353.—Hall and Clarke, 1889, p. 73.—Schubert and LeVene, 1927, p. 82.—Cooper, 1944, p. 331.—Amsden, 1958, p. 128.—Boucot, Johnson, and Staton, 1964, p. 820.—Boucot and others, in Moore, 1965, p. H656.

Diagnosis.—"Unequally biconvex shells, commonly longer than wide; interarea obscure; ventral beak strongly incurved at maturity, commonly concealing foramen; deltidial plates may be exposed in early growth stages; dorsal fold and ventral sulcus may occur, or sulcation may affect only anterior commissure, or valves may be nonsulcate. Dental plates obsolescent; ventral muscle scar flaring strongly laterally, commonly deeply impressed into secondary shell material; cardinal plate strong, variable, triangular to subquadrate in outline; commonly concave on upper surface and depressed to form broad septalium; median septum originating beneath cardinal plate and extending part way to anterior margin; jugum produced backward as stem bifurcates and recurves dorsally, then anteriorly to reunite with stem." (Boucot and others, in Moore, 1965, p. H656).

Type-species.—*Atrypa laevis* Vanuxem, 1842, p. 120; by subsequent designation, S. A. Miller, 1889, p. 354.

Discussion.—I accept the diagnosis given in *Treatise on Invertebrate Paleontology* (Moore, 1965, p. H656) along with the discussion of the genus and its relationship to *Meristina* by Boucot, Johnson, and Staton (1964, pp. 820, 821). The synonymy listed above is abbreviated: Hall and Clarke (1894) give a full synonymy up to 1889, so only the pertinent, more recent references are included.

Meristella lentiformis Clarke, 1900

Plate 1: figures 1–4

1900. *Meristella lentiformis* Clarke, 1900, pp. 44, 45, pl. 6, figs. 5–11.—Van Ingen and Clark, 1903, pp. 1203, 1208.—Schuchert and others, 1913, pp. 126–129.—Stauffer, 1915, pp. 60–66.—Dunbar, 1919, pp. 99, 101.—Woodward, 1940, p. 147.—Boucot and Johnson, 1967, pp. 80, 81.

Original description.—"Shell unequally convex; outline transversely oval; pedicle valve with short incurved beak and narrow cardinal slopes bordered by obtuse cardinal ridges diverging from beak. Umbo slightly convex or flat, the surface sloping to the sides very gradually. A median sinus starts at the umbo and rapidly broadens, producing a general depression in the pallial region, which is rather sharply deflected. The sinus is produced into a linguate extension at the anterior margin. The general flatness of this valve is more marked in young shells, the anterior deflection becoming prominent with the increase of age. The brachial valve has a full beak curved into the delthyrium of the opposite valve, and is elevated medially into a broad ridge-like concavity terminating in a fold on the anterior margin. The lateral slopes are gently concave. The surface of both valves is smooth or bears only concentric growth lines.

"On the interior the apophyses and impressions are those characterizing the genus. Particularly well developed is the broad, flabellate muscular scar of the pedicle-valve and the median septum of the brachial valve, extending for more than half the length of the shell." (Clarke, 1900, pp. 44, 45.)

Emended description.—Shell unequally biconvex, generally wider than long, greatest width about at midlength, pedicle valve flattened with broad sulcus;

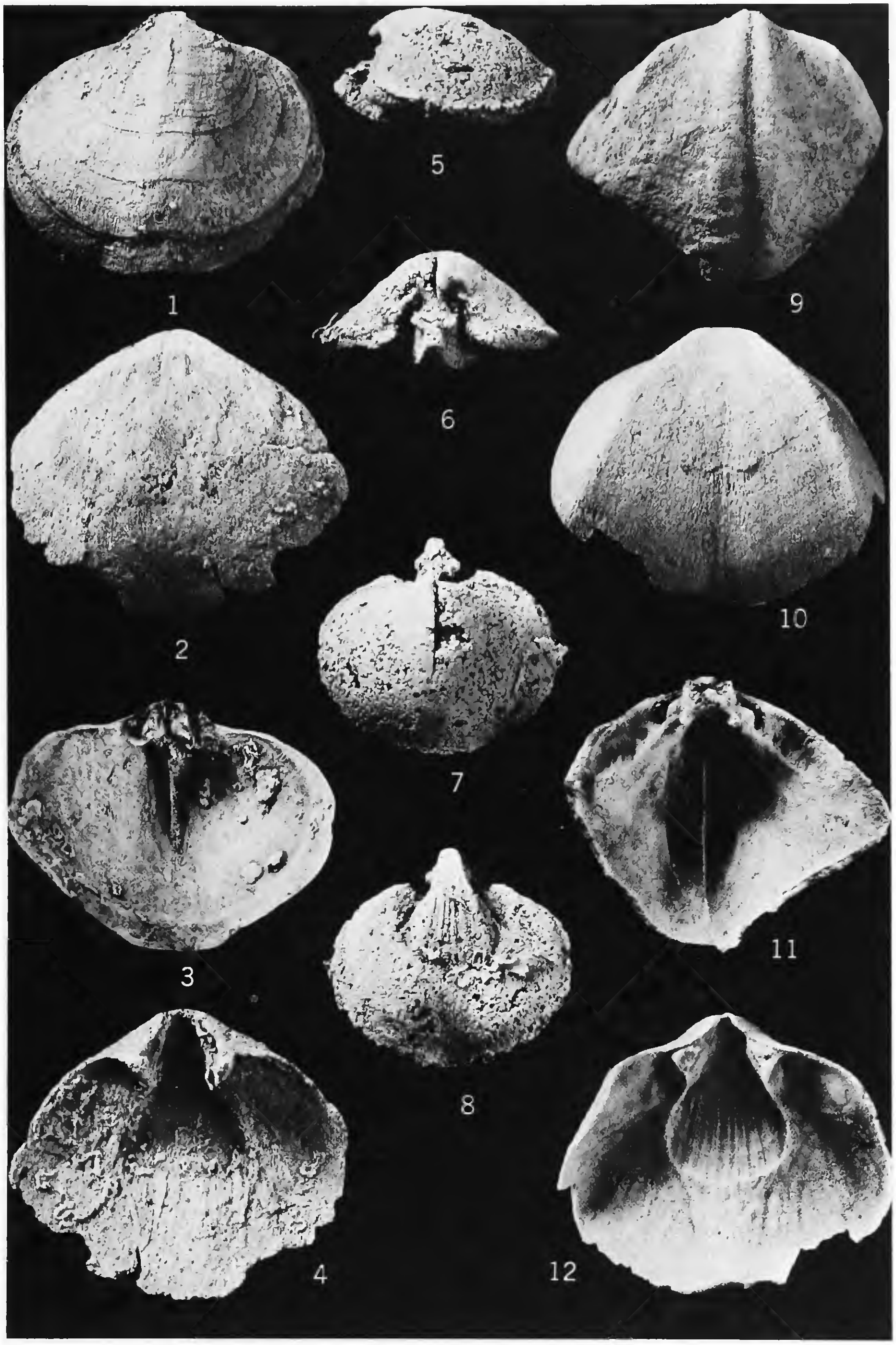

Plate 1: figures 1–4: *Meristella lentiformis* Clarke. 1, 3, External and internal views of a brachial valve, USNM 163805 (× 2); 2, 4, external and internal views of a pedicle valve, USNM 163806 (× 2). Figures 5–8: *Pentagonia lenta* (Hall). Lateral, posterior, brachial, and pedicle views of an internal mold, USNM 28038 (× 3). Figures 9–12: *Pentagonia peersii* Cozzens. 9, 11, External and internal views of a brachial valve, USNM 163807 (× 2); 10, 12, external and internal views of a pedicle valve, USNM 163808 (× 2).

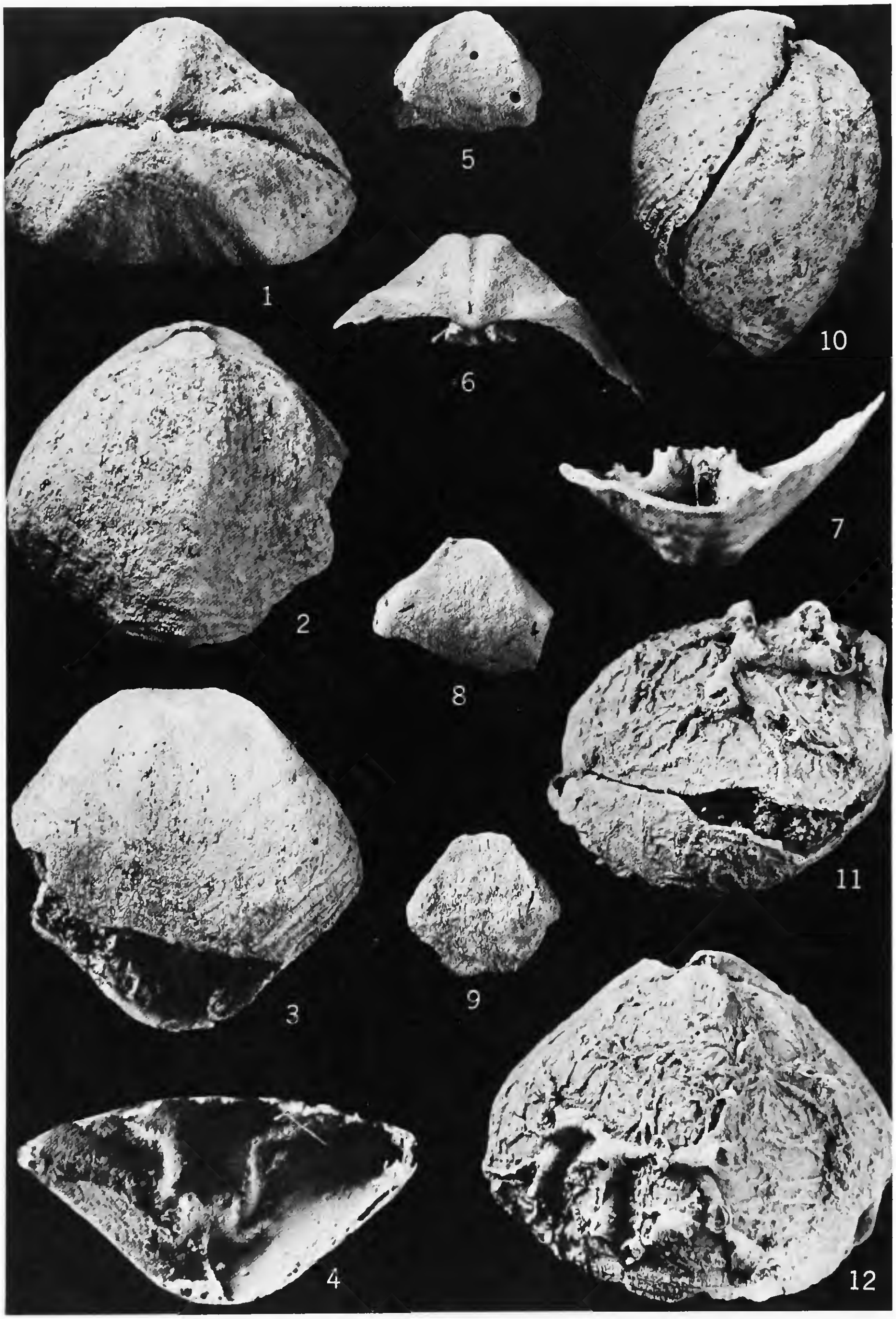

Plate 2: figures 1–3, 5–12.—*Pentagonia peersii* Cozzens. 1–3, 10, Posterior, brachial, pedicle, and lateral views of an average specimen, USNM 163809 (× 2). 5, 8, 9, Pedicle valves with two circular borings, USNM 163810; barnacle(?) borings, USNM 163811; and sponge(?) borings, USNM 163812 (all views same size). 6, 7, Posterior and anterior views (× 2) of brachial valve showing details of cardinal process and septum, USNM 163807. 11, 12, Lateral and brachial views (× 2) of shell with *Aulopora* in growth position, USNM 163813. Figure 4.—*Pentagonia lenta* (Hall). Latex cast of specimen USNM 28038 (× 5) showing dental plates, cardinal process, and median septum.

shell fibrous, impunctate; external ornament consisting only of concentric growth lines.

Pedicle valve with broad, indistinct sulcus; interior with flabellate striate muscle area, commonly deeply impressed; short dental plates with prominent teeth; open delthyrial area, pedicle opening as a notch at the posterior end of the delthyrium.

Brachial valve strongly arched with high fold extending full length of the valve; interior with prominent cardinal process having a flat hingeplate; lateral sockets accommodate the teeth of the pedicle valve; narrow, sharp medium septum extends about halfway to anterior margin.

DISCUSSION.—Internal characters of this species are transitional between *Meristella* and *Pentagonia*. The cardinal process is rather variable, in some specimens being very similar to the process in *Pentagonia*. Externally, the shell is a *Meristella,* although the broad, flattened pedicle valve gives a hint of the exaggerated form of the stratigraphically younger *Pentagonia*. Lateral carinae are not developed in *M. lentiformis,* nor is there any indication of the internal pouches of *Pentagonia*.

Clarke (1900, p. 44) discussed the similarity of this species to *Pentagonia lenta,* but indicated clearly the differences that set the two species apart. The species are certainly very close, suggesting that the slightly younger *P. lenta* probably evolved out of the *Meristella lentiformis* stock.

ILLUSTRATED SPECIMENS.—USNM 163805-6, from Glenerie Formation, on New York highway 9W, 1 mile south of Glenerie, New York, and 1 mile north of Cockburn, New York. Collector: B. Zimm. USNM Acc. No. 167820.

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William A. Oliver, Jr.

The Coral Fauna and Age of the Famine Limestone in Quebec

ABSTRACT

Rugose corals belonging to species of *Cylindrophyllum, Heliophyllum, Aulacophyllum, Heterophrentis, Siphonophrentis* and *Cystiphylloides* are present in the limestone part of the Famine Formation in southeastern Quebec. The corals indicate a Middle Devonian, probably late Onondaga or Hamilton, age for the limestone.

Cylindrophyllum stummi, new species, is formally described and specimens of eight other rugose coral species are illustrated and briefly described and discussed. Representatives of four tabulate coral species also were found in the Famine Formation.

The Famine Formation in southeastern Quebec is a small, isolated mass of Devonian sedimentary rocks surrounded by Ordovician clastic and volcanic rocks, the whole tightly folded and cleaved by post-Famine structural activity. A limestone unit in the middle part of the Famine is very fossiliferous and has been recognized as Devonian since it first was studied over 100 years ago. Kindle (in MacKay, 1921) and Clark (1923) considered the Famine Formation to be Onondaga in age, but this assignment has never been supported by published descriptions or illustrations of key fossils; also, an Onondaga age has seemed too young to some workers because of paleogeographic considerations. Recent restudy of the corals and other fossil groups has indicated, however, that the Famine is Middle Devonian, Onondaga or younger, in age and that paleogeographic prejudices must be set aside. The present paper reviews previous work, illustrates and describes the more important rugose corals, and discusses the evidence of these forms.

I am indebted to A. J. Boucot, Oregon State University, and to N. R. Gadd and L. M. Cumming, Geological Survey of Canada, for collecting and sending to me the corals on which this study is based.

All thin sections were prepared by W. C. Pinckney, Jr. Photographs are by D. H. Massie.

Previous Work

Logan (1863, p. 428) noted "dark fossiliferous limestones . . . which form a low short ridge, overlooking the Famine [River], in eastern Quebec." He listed several corals (Table 1, herein) and brachiopods from the limestones and noted that the fossils "have a Devonian aspect." Logan's list was based on identifications by Elkanah Billings, as noted by Ells (1888, p. 9).

Ells (1888, pp. 9–11) mentioned the same limestone and discussed its distribution in somewhat greater detail. In addition, he provided a slightly different list of corals (Table 1), brachiopods, pelecypods, and trilobites as identified by H. M. Ami.

The Famine "Series" was named and described by MacKay (1921, pp. 31–33) from the small area south of the Famine River near St. George, Quebec, that is referred to in the above reports. The formation includes a fossiliferous limestone "about 40 feet thick" (MacKay, 1921), an underlying basal conglomerate (50 feet thick), and overlying shales and limestones (greater than 120 feet thick) (L. M. Cumming, personal communication, 1968). MacKay considered all the

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beds as probably of Onondaga age on the basis of fossils from the middle unit determined by E. M. Kindle (MacKay, 1921, p. 32). Kindle's list includes two rugose and four tabulate corals (Table 1), several brachiopods, and trilobites.

TABLE 1.—*Previous identifications of corals from the limestone of the Famine Formation.* (A), *Billings,* in *Logan 1863;* (B), *Ami,* in *Ells, 1888;* (C), *Kindle,* in *MacKay, 1921;* (D), *Clark, 1923. Numbers in parentheses following species names indicate probable correspondence with the new identifications in Table 2.*

RUGOSE CORALS:	(A)	(B)	(C)	(D)
Diphyphyllum arundinaccum (1)	×	—	×	×
Diphyphyllum (1)	—	×	—	—
Cyathophyllum? (2)	—	×	×	—
Cyathophyllum sp. (2)	—	—	—	×
Heliophyllum oneidaense (2?)	×	—	—	—
Heliophyllum sp. (2)	—	×	—	—
Zaphrentis sp. (5 to 8)	×	—	—	×
Amplexus sp. cf. *A. hamiltoniae* (none)	—	—	—	×
Cystiphyllum vesiculosum (9)	—	—	—	×
TABULATE CORALS:				
Alveolites sp. (none)	—	—	×	—
Favosites gothlandica(us) (11)	×	×	—	—
F. basaltica (11?)	×	—	×	×
Favosites sp. (11)	—	×	—	—
Favosites sp. cf. *F. limitaris* (12)	—	—	×	—
Syringopora hisingeri (13)	—	×	×	—
S. tabulata (13)	—	—	—	×

Clark (1923) presented additional information on the limestone and an annotated list of fossils. "The limestone is dark gray, almost black; and is crowded with fossils wherever it outcrops . . . upon weathering breaks down into a rubbly mass. . . ." (Clark, 1923, p. 218). Clark annotated several species of corals (Table 1) and brachiopods and noted the presence of bryozoans and gastropods. He considered the corals to indicate an Onondaga age.

Boucot and Johnson (1967, p. 54) mentioned the Famine Limestone as of "Middle Devonian and probably Eifelian (Onondaga) age" on the basis of a species of *Brevispirifer*. An "*Athyris* of the *A. undata*-type and a pholidostrophiid of the *Teichostrophia*-type" are also present and suggest Old World faunal affinities (Boucot and Johnson, 1967, p. 54).

Cumming (1968, p. 1046) briefly mentioned the Famine Formation as "an isolated outlier of probably Onondaga age," stating that it "contains the corals *Siphonophrentis* and *Heliophyllum*."

Corals and Age

New identifications of corals from the limestone in the Famine Formation, based on collections made by A. J. Boucot (then with the United States Geological Survey) in 1955 and by N. R. Gadd (Geological Survey of Canada) in 1965 are listed in Table 2. The listed species are numbered, and these numbers are inserted parenthetically in Table 1 to indicate probable correspondence between these species and the earlier identifications. The remarkable similarity of the new and old lists suggests that the collections are representative, although relatively small and containing few species. The specimens listed in Table 2 are now in the collections of the United States National Museum (USNM) and the Geological Survey of Canada (GSC).

Cylindrophyllum stummi, new species, is probably the *Diphyphyllum* of the earlier lists, because it is common and is the only phaceloid rugose coral in the assemblage.

TABLE 2.—*Corals identified from the Famine Limestone, St. George, Quebec. Numbers of Specimens in collections made by A. J. Boucot in 1955 (USNM) and N. R. Gadd in 1965 (GSC) are listed. Asterisk indicates apparently common forms.*

RUGOSE CORALS:	USNM	GSC	Total
*1. *Cylindrophyllum stummi*, new species	10	7	17
*2. *Heliophyllum halli* E. and H.	6	2	8
*3. *Heliophyllum* sp. cf. *H. proliferum* Hall	5	2	7
4. *Aulacophyllum* sp.	1	—	1
5. *Heterophrentis* sp. 1	1	1?	2?
6. *Heterophrentis* sp. 2	—	1	1
7. *Siphonophrentis* sp. cf. *S. yandelli* (E. and H.)	—	3	3
8. *Siphonophrentis* sp. 2	1	—	1
9. *Cystiphylloides* sp.	1	1	2
TABULATE CORALS:			
10. *Cladopora* sp.	—	1	1
11. *Favosites* sp. 1	1	1	2
12. *Favosites* sp. 2	1	1	2
*13. *Syringopora* sp. 1	6	1	7

It is surprising that the earlier workers made so little of the excellently preserved and common *Heliophyllum halli,* though this is presumably the *Heliophyllum* sp. and *Cyathophyllum* sp. of their lists. Logan's list (by Elkanah Billings) does include *Heliophyllum oneidaense,* but this must have been intended to refer to the form now known as *Acrophyllum oneidaense* (Billings), which has quite different internal structure. However, *A. oneidaense* is limited to rocks of Schoharie-Bois Blanc age (Emsian; Oliver, 1967) and is unlikely to occur in association with the other Famine corals. Possibly the Billings identification is based on *Heliophyllum halli,* even though this would seem an unlikely error.

Zaphrentis on the earlier lists can refer to either *Heterophrentis* or *Siphonophrentis,* but Clark's description is certainly of a *Heterophrentis* as presently understood. Clark's *Cystiphyllum vesiculosum* is on my list as *Cystiphylloides* sp., but I have nothing that can be compared to his *Amplexus* sp. cf. *A. hamiltoniae.*

Similarly, the tabulate corals on the earlier lists correspond to my identifications. The only significant exceptions are Logan's two species of *Favosites,* which imply greater numbers and diversity of specimens than are present in the new collections, and Kindle's *Alveolites,* a genus that is not present in the new collections.

The corals listed in Table 2 indicate a Middle Devonian (Eifelian-Givetian) age for the fossiliferous part of the Famine Formation. In a following section, the significance of each species is discussed separately, but the results of this analysis can be summarized here.

The apparent abundance and variety of *Heliophyllum* and the presence of Onondaga and Hamilton-like species of *Heterophrentis, Siphonophrentis,* and *Cystiphylloides* indicate that the Famine faunule belongs to the eastern North American, Middle Devonian coral assemblage of Oliver (1968). These forms collectively preclude a pre-Onondaga assignment for the Famine Limestone.

An early Onondaga (Edgecliff and equivalents) coral assemblage is very widespread in eastern North America (Oliver, 1968, p. 741 and table 4, A,B,F,G). The lack of characteristic elements of this assemblage in the Famine Formation suggests that the Famine is post-Edgecliff in age. However, the corals that are present do not indicate a closer correlation of the Famine with the standard New York section than Onondaga to Hamilton.

Boucot and Johnson (1967, p. 54) suggest that the Famine brachiopods are a mixture of European and eastern North American types. The corals, on the contrary, are distinctly of eastern North American aspect and most of them probably belong to species already described from New York or Ontario. *Cylindrophyllum stummi,* new species, is an exception on the species level, but the genus is basically an eastern North American element and is rare or unknown in Europe.

Conodonts from the same collections as the corals have been studied by Gilbert Klapper (University of Iowa) and T. T. Uyeno (Geological Survey of Canada). They both found small, poorly preserved conodont faunas composed exclusively of members of the *Icriodus nodosus* group, indicative of Middle Devonian age. According to Klapper (personal communication, 1968) they "are comparable, in terms of evolution within *Icriodus* in the Middle Devonian, to specimens of *Icriodus corniger* from the Dundee Limestone of northwestern Ohio."

Locality

All collections recorded in the literature or discussed herein have come from a general area just north of St. George, Quebec, east of the Chaudiere River but south of the Famine River. St. George is approximately 60 miles southeast of Quebec City. MacKay (1921, geologic map no. 1835) shows his collecting locality as 0.6 mile (1 km) north of the east end of the bridge in St. George. Limestone outcrops extend eastward from this point (see MacKay map), and Clark's collections may have come from some of the other exposures as well as from MacKay's locality. The two collections that serve as a basis for this paper are from the MacKay locality.

Systematic Description and Annotations

Cylindrophyllum stummi, new species

PLATE 1: FIGURES 1–6; PLATE 2: FIGURES 4, 5.

DIAGNOSIS.—Phaceloid coralla with cylindrical corallites commonly in lateral contact with each other so as to form short "chains." Septa short, wedge-shaped, radially arranged; minor septa nearly equal to major septa in length; septal carinae present or very common. Dissepimentarium narrow with one to four rows of normal, globose dissepiments. Tabulae complete or incomplete, variable in form.

Material.—Seventeen incomplete coralla, including the holotype, two illustrated paratypes, and fourteen unillustrated paratypes. Preservation is mediocre; parts of all coralla are distorted and slightly crushed.

External Features.—Phaceloid (partly cateniform) colonies are as much as 17 cm or more in height and 30 cm or more in diameter; they are composed of cylindrical corallites 6 to 11 mm in diameter. Corallites are essentially parallel in astogenetically advanced parts of the corallum but are radiating in early stages. Corallite spacing was apparently less than one diameter, and many corallites grew in lateral contact with one or two neighboring corallites to form short "chains" (Plate 1: figure 3). Average or maximum distance between corallites is unknown, as all specimens are from a structurally disturbed area, and some crushing and distortion is evident in parts of most coralla. Offsetting is lateral.

Internal Features.—The major septa are radially arranged and very short, commonly extending from one-fifth to one-half the distance to the axis; minor septa are nearly as long. Major septa number 19 to 27 in cylindrical parts of studied corallites. Septa are wedge-shaped, somewhat thickened peripherally, and composed of trabeculae, the axes of which are confined to a single plane; trabecular fibers diverge at a high angle in the axial part of the septa, but the angle becomes less peripherally and the septa seem to merge imperceptably into the fibrous wall. Zig-zag carinae are inconspicuous in most transverse sections but are prominent in parts of most longitudinal sections. Locally, septa expand at their axial ends; in such places the trabecular structure of the septa is particularly clear (Plate 2: figure 5).

The dissepimentarium is narrow, commonly occupying less than three-tenths the corallite radius. Dissepiments are normal, commonly globose, and arranged in one to four rows. Inner dissepiments where present are as large or larger than peripheral ones. Size and shape variation is considerable, as can be seen from the illustrations.

The tabularium is wide and composed of complete tabulae supplemented by incomplete peripheral tabulae. Tabula shape varies from nearly flat to irregularly, but gently, convex or concave.

Types.—Holotype, USNM 163236; illustrated paratypes, GSC 24639 and USNM 163237; unillustrated paratypes, GSC 24640, 24797, 24798, and three others; USNM 13238, 163396–8, and four others.

Discussion.—*Cylindrophyllum stummi* is characterized by its very short, relatively thick septa. The type and other known species of the genus have longer, very attenuate septa and more prominent septal carinae. In transverse section *C. stummi* is similar to *Acinophyllum crassiseptatum* (Ehlers and Stumm 1949, pp. 28–29, pl. 6, figs. 1–6), but *A. crassiseptatum* differs in having a peripheral row of dissepiments that are larger than any inner dissepiments and in having very coarse septal trabeculae. *Acinophyllum rectiseptatum* Rominger (Stumm, 1955, card 269) is much smaller in diameter and has fewer rows of dissepiments.

Distribution.—*Cylindrophyllum stummi* is known only from the Famine Limestone, St. George, Quebec, at MacKay's (1921) locality (see locality section). Middle Devonian; Eifelian?

Heliophyllum halli Edwards and Haime, 1850

Plate 3: figures 1, 7, 9

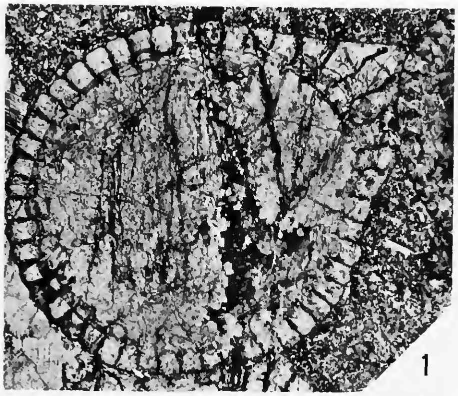
Heliophyllum halli E. and H. Wells, 1937, pp. 9–18, pl. 1, figs. 1–15.

Discussion.—Specimens of this species are in both the USNM and GSC collections (see Table 2). They are typical in showing wide variation in growth form, in having very attenuate septa and long cross-bar carinae in mature stages, and in having dilated septa in early stages.

In New York and Ontario the species is very common from the base of the Onondaga Limestone (Edgecliff Member) through the Tully Limestone. The genus, and possibly the species, occurs in the older Bois Blanc Formation (Emsian; Oliver, 1967) and the younger West Falls Formation (Frasnian) but is not common. I consider abundant *H. halli* to indicate a Middle Devonian age in eastern North America.

Material.—USNM 163239, the illustrated specimen, and seven unillustrated specimens.

Plate 1.—*Cylindrophyllum stummi*, new species. 1–3, Holotype corallum, USNM 163236: 1, 3, transverse thin sections (× 5 and × 1.5, respectively); 2, longitudinal section (× 5). 4–6, Paratype corallum, USNM 163237: 4, longitudinal section (× 5); 5, 6, transverse sections (× 2.5 and × 5, respectively).



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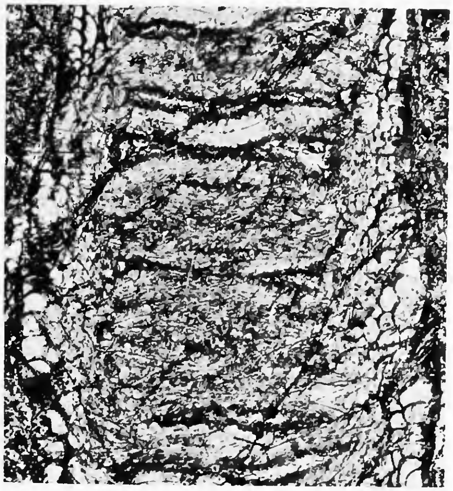

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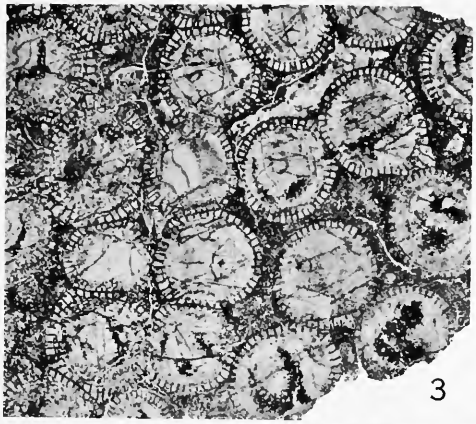

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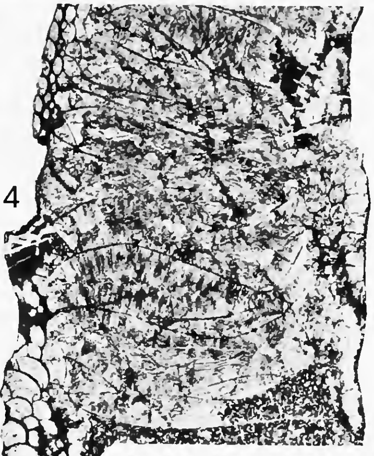

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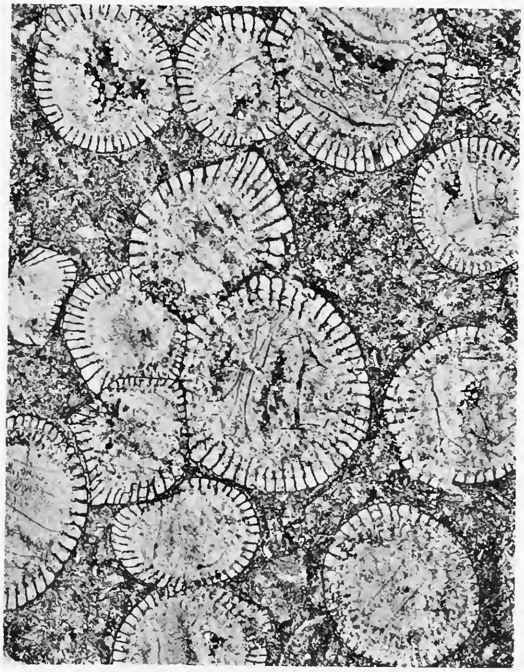

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PLATE 1

Heliophyllum sp. cf. *H. proliferum* Hall, 1877

PLATE 3: FIGURES 3, 4.

Cf. *Heliophyllum proliferum* Hall, 1877, pl. 26, figs. 1–2.
Not *Heliophyllum proliferum* Nicholson, 1874, p. 27–28.

DISCUSSION.—Seven fragments of *Heliophyllum* colonies show peripheral offsetting and are morphologically similar to *Heliophyllum proliferum* Hall (not Nicholson) from the Hamilton Group in New York. The largest fragment, 15 cm in diameter, includes 20 or more corallites.

Individual corallites differ from the associated *H. halli,* only in showing greater variability in septal carinae. In the colonial form the carinae are zig-zag or cross-bar and very long to almost absent.

Hall (1877) illustrated *H. proliferum* as a new species but the name had already been introduced for an Onondaga species by Nicholson (1874). Wells (1937, pp. 14, 15) considered Hall's species to be a form of *H. halli.* I agree that individuals of *H. halli* produced peripheral offsets, but consider it unlikely that the large, bushy colonies found in the higher parts of the Hamilton and represented here were no more than variants of the solitary species. Detailed study might show that the Onondaga-Hamilton sequence contains a record of the evolution of *H. proliferum*-like species from *H. halli* twice—an earlier Famine species and the later upper Hamilton species of Hall. Hall's name is a junior homonym but it would be inappropriate to rename the species until a detailed stratigraphic and morphologic study of the New York material has been completed.

MATERIAL.—GSC 24641 the illustrated specimen, and six unillustrated specimens.

Aulacophyllum sp.

PLATE 2: FIGURES 2, 3.

DISCUSSION.—One specimen has the characters of this genus, but it apparently differs from described species in having zig-zag carinae developed on the peripheral parts of many septa. Without more material and detailed comparison with named species, identification is impractical.

In North America, specimens of *Aulacophyllum* species are common in rocks of Onondaga and Hamilton age but extend downward into the Bois Blanc Formation and equivalents (Emsian).

MATERIAL.—USNM 163242.

Heterophrentis spp.

PLATE 2: FIGURES 1, 8; PLATE 3: FIGURES 6, 8

DISCUSSION.—A fragment of a horn coral, USNM 163243 (Plate 3: figures 6, 8), is similar to *Heterophrentis simplex* Hall, 1843 (Hall, 1877, pl. 21, figs. 5–11), in general morphology but shows much more septal dilation than is common in that species. *Heterophrentis ferronensis* and *H. curviseptata* (both Stumm, 1962b) show greater dilation than does *H. simplex* but they differ from the Famine form in tabula shape.

A second, more complete horn coral, GSC 24799 (Plate 2: figures 1, 8), also is referable to *Heterophrentis* but probably to a different species. This specimen has attenuate septa extending four-fifths the distance to the axis.

The degree of individual variation in these corals or in described species of *Heterophrentis* is not known, and identification of the Famine specimens is not practical. The genus, as presently understood, may range both above and below the Middle Devonian in eastern North America.

Siphonophrentis sp. cf. *S. yandelli* (Edwards and Haime)

PLATE 2: FIGURES 9, 10

DISCUSSION.—Three specimens represent a species of small *Siphonophrentis* 18–20 mm in diameter and with approximately 32 to 36 major septa. The Famine specimens are quite similar to *S. yandelli* (E. and H.) from the Jeffersonville Limestone at the Falls of the Ohio and the Onondaga Limestone in New York. In New York the species ranges from the Edgecliff through Moorehouse Members but is most common in the Edgecliff.

MATERIAL.—GSC 24642, the illustrated specimen, and two unillustrated specimens.

PLATE 2: figures 1, 8.—*Heterophrentis* sp. 2. Longitudinal and transverse thin sections (× 1.5); GSC 24799.

Figures 2, 3.—*Aulacophyllum* sp. Longitudinal and transverse thin sections (× 1.5); USNM 163242.

Figures 4, 5.—*Cylindrophyllum stummi,* new species. Paratype corallum, GSC 24639; transverse thin sections (× 5 and × 50, respectively).

Figures 6, 7.—*Cystiphylloides* sp. Longitudinal and transverse thin sections (× 1.5); USNM 163245.

Figures 9, 10.—*Siphonophrentis* sp. cf. *S. yandelli* (E. and H.). Transverse and longitudinal thin sections (× 1.5); GSC 24642.

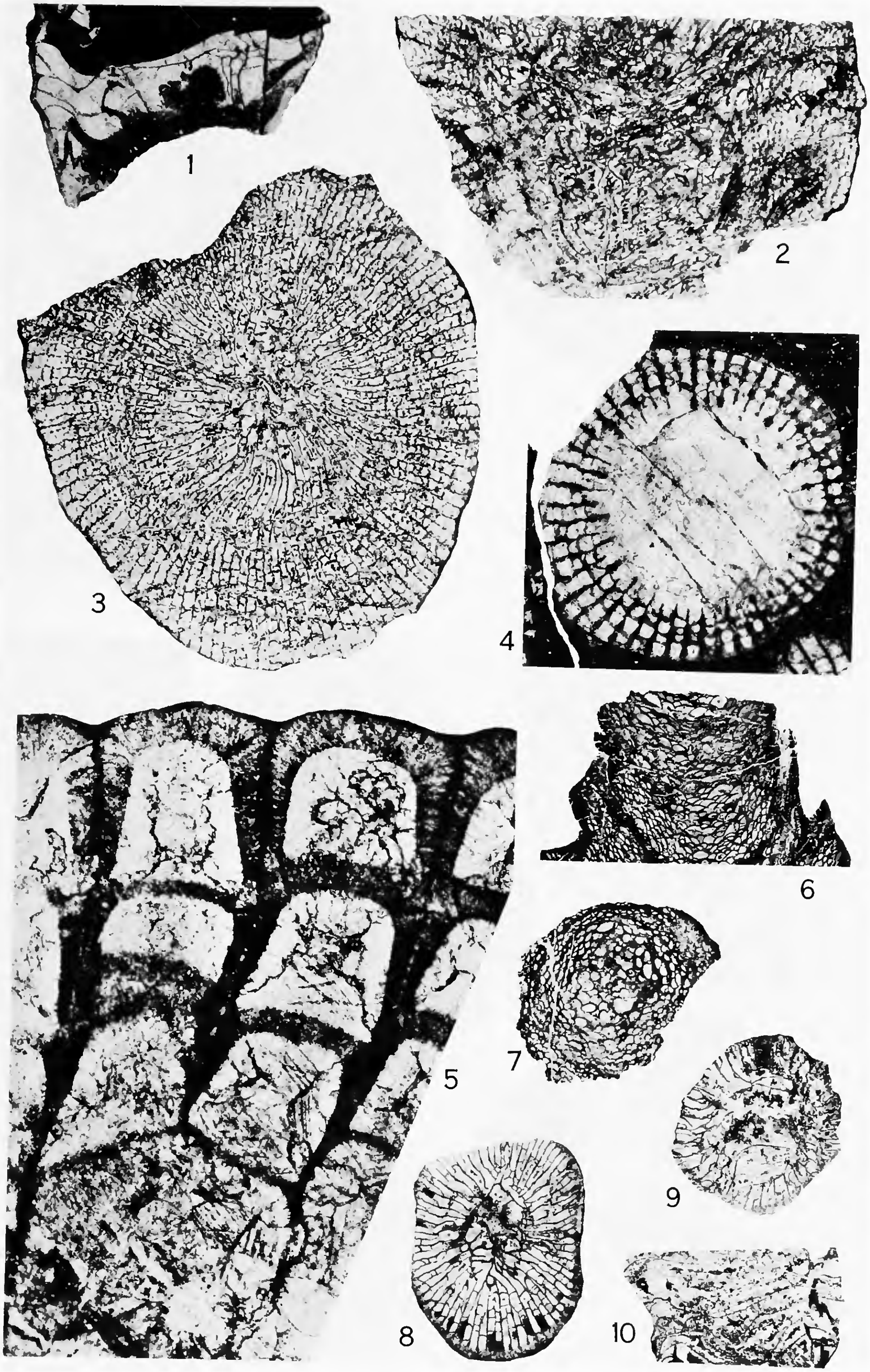
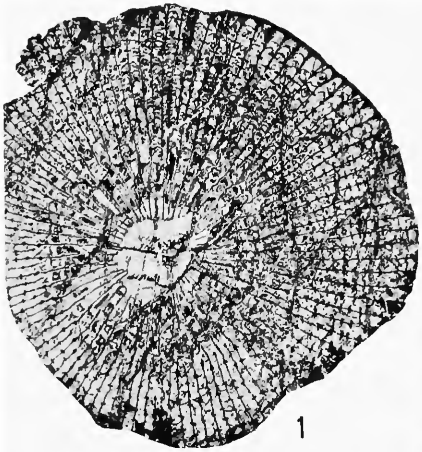


PLATE 2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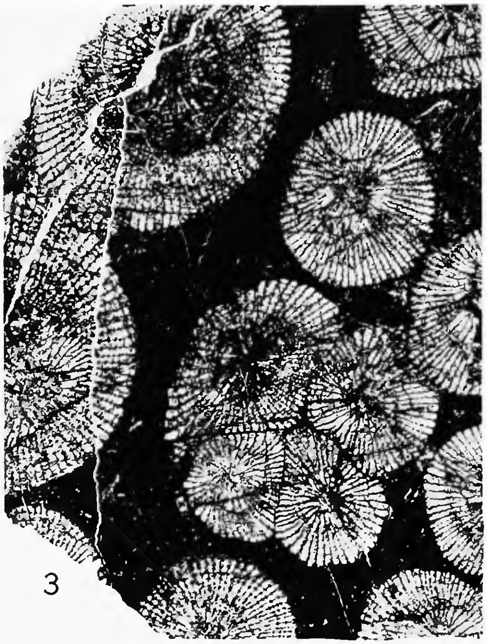
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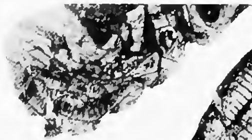
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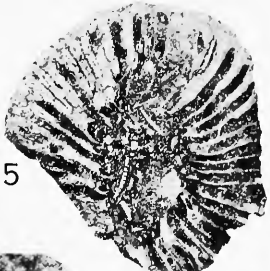
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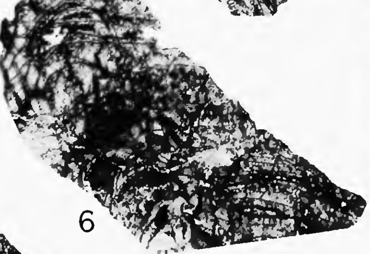
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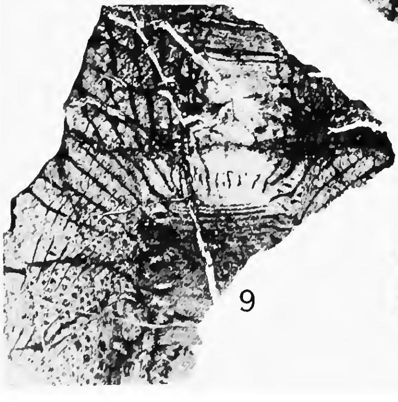
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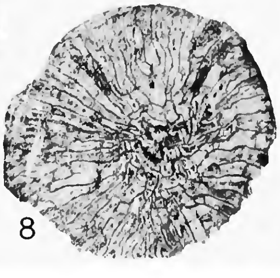
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PLATE 3

Siphonophrentis sp. 2

PLATE 3: FIGURES 2, 5

DISCUSSION.—A fragment of a specimen apparently referable to this genus is in the USNM collection. Septa are short, and a prominent fossula is marked by a short and attenuate cardinal septum. Tabulae are complete, concave axially, and strongly arched peripherally. The fragment is too incomplete for species-level identification, but similar forms occur in both the Onondaga Limestone (*S. gigantea*) and the Hamilton Group (*S. halli*).

MATERIAL.—USNM 163244, the illustrated specimen.

Cystiphylloides sp.

PLATE 2: FIGURES 6, 7

DISCUSSION.—Single specimens of this genus are in both the USNM and GSC collections. They resemble the described specimen of *C. alpenense* Stumm (1962a, pp. 220–221, pl. 2, figs. 3, 4), but may be simply a variant of the common Onondaga-Hamilton *C. americanum* (=*vesiculosum* of some authors). The Famine specimen has zones of thickened dissepiments that appear as concentric rings in the transverse section and as broad V-shaped zones in the longitudinal section.

The genus strongly suggests a Middle Devonian age.

MATERIAL.—USNM 163245, the illustrated specimen, and one unillustrated specimen.

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PLATE 3: figures 1, 7, 9.—*Heliophyllum halli* E. and H.; USNM 163239: 1, 9, transverse thin sections (× 1.5 and × 5, respectively); 7, longitudinal thin section (× 1.5).

Figures 2, 5.—*Siphonophrentis* sp. 2. Longitudinal and transverse thin sections (× 1.5); USNM 163244.

Figures 3, 4.—*Heliophyllum* sp. cf. *H. proliferum* Hall. Transverse and longitudinal thin sections (× 1 and × 1.5, respectively); GSC 24641.

Figures 6, 8.—*Heterophrentis* sp. 1. Longitudinal and transverse thin sections (× 1.5); USNM 163243.

Paul Sartenaer

Redescription of the Brachiopod Genus *Yunnanella* Grabau, 1923 (Rhynchonellida)

ABSTRACT

The genus *Yunnanella* Grabau, A. W., 1923, and its type-species *Y. hanburii* (Davidson, T., 1853), are redescribed. A considerable number of the forms that have been named *"Yunnanella"* actually belong to other genera. As a result, the stratigraphic position and the geographic distribution of the genera *Yunnanella* and *Nayunnella* Sartenaer, P., 1961, undergo drastic modifications, although information from China is not sufficient to permit definite conclusions.

RÉSUMÉ—Le genre *Yunnanella* Grabau, A. W., 1923 est redécrit ainsi que son espèce-type *Y. hanburii* (Davidson, T., 1853). Une grande partie des formes dénommées *"Yunnanella"* a un moment ou l'autre appartiennent en fait à d'autres genres. Il en résulte des modifications profondes dans la position stratigraphique et la distribution géographique des genres *Yunnanella* et *Nayunnella* Sartenaer, P., 1961, encore que l'insuffisance des informations en provenance de la Chine n'autorise pas des conclusions définitives.

"So little is known of Chinese fossils that every fresh discovery interests the palaeontologist." Is it not strange that 117 years after this sentence was written by T. Davidson (1853, p. 353) it has lost very little of its value?

Although widely mentioned in the literature over the past 40 years, the genus *Yunnanella* Grabau, A. W., 1923, is still unsatisfactorily known as regards its systematic definition, stratigraphic range, and geographic distribution. Some very interesting papers published in the last decade, while making important new information available, have indirectly emphasized the need for a better understanding of the genus.

I have been faced with the alternative of leaving the problems in which the genus *Yunnanella* is involved as they stand—an attitude suggested by the lack of precision of data—or of trying to solve them. The confusion has reached such a level, however, that the latter positions seems inescapable.

The negative elements rendering it difficult to deal with these problems are: (1) because most of the material is Chinese and Russian, its availability is either nil or limited; (2) stratigraphic information on Chinese collections is imprecise, vague, and sometimes conflicting; (3) I have had no field experience in the various regions considered.

On the other hand, there are several favorable circumstances. First, the primary types of *Y. hanburii* (Davidson, T., 1853), the type-species of the genus *Yunnanella,* are deposited in the British Museum of Natural History (BM) in London, where I studied them in 1961 and in 1968. During my first visit, all facilities, including photography, were put at my disposal by Dr. H. M. Muir-Wood; during the second visit similar courtesies were extended by Dr. H. Brunton. Secondly, specimens of the type-species as well as of the species *Y. triplicata* Grabau, A. W., 1931, and *Y. uniplicata* Grabau, A. W., 1931 (two species I do not consider valid), were examined in the United States National Museum (USNM) in Washington, D.C., in 1966. Moreover, Dr. G. A. Cooper generously

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sent this precious collection to Brussels for an extended period and allowed serial sections to be made of one specimen of the type-species. Thirdly, as a guest of the Russian Academy of Sciences, and under the auspices of the Belgo-Russian cultural agreement, I had the opportunity to visit some colleagues in Moscow and Leningrad in 1963–1964. Due to the kindness of Academician D. V. Nalivkin, Drs. E. A. Ivanova, M. V. Martynova, M. A. Rzhonsnitzkaia, Kh. S. Rozman, T. V. Sverbilova, S. V. Tcherkesova, and P. N. Varfolomeev, not only could most of the Russian species relevant to this paper be observed and form the subject of fruitful discussions but specimens were donated and permission was granted for making latex molds of any primary type or figured specimen in the collections, including some Chinese specimens received by Russian scientists. Fourthly, Dr. Herta Schmidt kindly showed to me, in 1968, all the material on which her study of the genus *Schnurella* Schmidt, H., 1964, was based.

Thus, in spite of many drawbacks, it is my opinion that I am in the best position for dealing with this intricate question with the hope of indicating the direction toward a solution and of stimulating controversy.

Genus *Yunnanella* Grabau, A. W., 1923

Nomenclatorial note.—In two papers dealing with nomenclatorial problems, Sartenaer (1961a, 1962) remarked that the nominal genus *Yunnanella* has been valid since 1923, when it was erected by monotypy by Grabau, and that the generic name *Yunnanellina* Grabau, A. W., 1931, is a junior objective synonym of *Yunnanella.* The second paper was written in answer to a publication by Ivanova (1961) opposing the views expressed in the first paper. I introduced the nominal genus *Nayunnella* Sartenaer, P., 1961, with *N. synplicata* (Grabau, A. W., 1931) as the type-species. Consequently, in the present paper, *Yunnanella*=A. W. Grabau's *Yunnanella* (before 1931) and Grabau's and some other authors' *Yunnanellina,* while *Nayunnella*=A. W. Gabau's (from 1931 on) and some other authors' *Yunnanella.* Some generic descriptions of the past have included characters of the genus *Nayunnella* considered as a subgenus, while others were not applicable to the genus *Yunnanella* because the species described did not belong to that genus. Most of the descriptions have concentrated chiefly on the ornament, however, and very little information has been given on internal characters. Therefore, it seems advisable to give a new complete description.

Diagnosis.—Small to medium size. Uniplicate. Anterolateral commissures low in the shell. Moderately deep to deep sulcus and high fold starting at some distance from the beaks. Sulcus wide at front. Tongue high, trapezoidal. Suberect beak. Ventral interarea clearly delimited. Top of shell usually at the frontal commissure. Few wide and simple costae, generally restricted to the anterior part of the shell, strongly indenting the commissure. Parietal costae have been observed in one specimen only. Surface covered by divided, and sometimes intercalated, costellae. Values of shoulder angle: 94° to 110°. Deltidial plates strong. Dental plates and teeth stout and long. Ventral umbonal cavities clearly separated. Septum stout and short. Septalium short, deep, wide, amphora-shaped, and uncovered. Dental sockets long and moderately deep. Crura long and slender.

Description.—Shell small to medium size, uniplicate, with a transversly subelliptical to subcircular and subpentagonal contour. Anterolateral commissures low in the shell, strongly indented by the costae, as is the frontal commissure, and seldom sharp on account of the verticality of the extreme margins of the flanks. Top of the shell usually at the frontal commissure, sometimes somewhat posterior to it. Width is the greatest dimension. Values of width and length sometimes approach each other. Height sometimes greater than length. Values of the shoulder and apical angles, respectively, between, 94° and 110°, and 105° and 120°. Few wide and simple costae, generally restricted to the anterior part of the shell. Median dorsal costae and internal ventral lateral costae are the only high costae. Parietal costae have been observed in one specimen only. Surface completely covered by costellae (3 to 8 per mm at midlength of the shell), which increase in number anteriorly by bifurcation or, exceptionally, by intercalation.

Pedicle valve generally slightly convex in the umbonal region with flat to slightly concave anterolateral parts; these two characters, together with the low position of the anterolateral commissures, explain why the umbonal region is the only part showing in lateral views. Flanks steep in their posterolateral parts, sometimes concave near the commissure. Sulcus starting imperceptibly between 30 and 55 percent of the length of the shell forward of the beak, or between 25 and 40 percent of the unrolled length of the valve. Sulcus moderately deep to deep, usually rapidly widening;

its width, where it starts, varies between 30 and 50 percent of its maximum width at the front, which varies between 60 and 75 percent of the width of the shell. Floor of the sulcus generally flat and sometimes slightly convex. High trapezoidal tongue with sharp borders. Upper part of the tongue tending to become vertical and even usually recurved posteriorly. Ventral median costae often protruding anteriorly beyond the sharp borders of the tongue. Greatest thickness located in the posterior quarter of the unrolled length of the valve. Very well-marked suberect beak. Interarea clearly delimited. Small half-circular foramen. Strong deltidial plates. Stout and long dental plates divergent posteriorly, becoming progressively parallel, then convergent anteriorly. Divergence and convergence are in relation to the median line of transverse serial sections. Clearly separated umbonal cavities. Teeth long and stout with undulated brachial side.

Brachial valve strongly convex, but never inflated. Flanks steep in their posterolateral parts, where they become concave near the commissure. Well-marked high fold starting imperceptibly at some distance forward of the beak. Top of the fold flat to slightly arched, exceptionally strongly arched. Stout and short septum supporting a short, deep, wide, and uncovered amphora-shaped septalium. Dental sockets long and moderately deep. Outer hinge plates concave. Moderately thick and wide crural bases passing to long, slender crura, crescent shaped in transverse serial sections.

TYPE-SPECIES.—*Rhynchonella hanburii* Davidson, 1853.

COMPARISONS.—The strikingly different pattern of ornamentation of the genera *Yunnanella* and *Nayunnella* makes it easy to separate them at first sight. In the genus *Nayunnella,* as emphasized by many scientists (Grabau, 1931a, p. 141, 1932, pp. 92, 94, 95; Likharev, 1934, p. 518; Tien, 1938, pp. 43, 44, 74; Roger, 1952, p. 90; *Basic Invertebrate Fossils of China,* 1957; Rozman, 1959, pp. 94, 95, 96, 98; 1962, pp. 130, 137; Rzhonsnitzkaia, in Rzhonsnitzkaia, Likharev, and Makridin, 1960, p. 243; McLaren, 1962, pp. 65, 66; in Moore, 1965, p. H586; Schmidt, 1965, p. 16), some costellae enlarge forward and become costae, others join in forming costae, and still others become obsolete before reaching the frontal and anterolateral commissures. Furthermore, the costellae undergo few divisions. In the material at my disposal, divisions have been observed only in the posterior third of the shell. In the genus *Yunnanella* the costellae not only are independent of the costae and cover the whole surface but they divide more often. I accept these differences, with the restriction that if costellae are present in the genus *Yunnanella* I am not ready to call costellae the narrow costae present in the genus *Nayunnella.* The term "costellae" is used here in a general way for designating fine costae. The term "capillae" would be more appropriate but it is rejected because it has been strictly defined in another order of brachiopods.

The unavailability of rich collections prevents the determining of the validity of many other differences. The material at hand, however, suggests that, commonly, in the genus *Yunnanella* height is more important, contour is transversely less elongated, costae are less restricted to the anterior part of the shell, sulcus and fold start nearer to the beaks, anterolateral margins of the flanks are abrupt, and the upper part of the tongue is recurved posteriorly. Insufficient material has prohibited the making of serial sections in species of the genus *Nayunnella* to investigate the internal characters. Although not precise enough, the serial sections found in the literature do not suggest major differences between the two genera. Finally, it must be noted that Grabau's (1931a, pp. 141, 142, 157) statement that *Yunnanella* was a subgenus of *Nayunnella* was later disregarded by Grabau (1932) himself.

The differences between the genus *Yunnanella* and the Givetian genus *Schnurella* are important and numerous. Some of them were recognized as far back as 1853 by Davidson, who compared the type-species of both. The genus *Schnurella* differs in the contour; the smaller size; the steep frontal and lateral sides with typical excavations in the flanks reminiscent of the lunules in the pelecypods; the commissure not sticking out; the greatest thickness somewhat posterior to the frontal commissure; the l./w., t./w., t./l ratios fluctuating around one, with width seldom being the greatest dimension; the greater thickness; the smaller apical angle; the very shallow sulcus excavating the pedicle valve and occupying almost the whole width of the shell at the front; the nontrapezoidal tongue without sharp borders and not recurved posteriorly in its upper part; no clear ventral interarea; the very low fold with its top always convex; more median costae; lower costae more restricted anteriorly and flattened on the frontal and lateral sides; the fine costae (different from costellae) not reaching the commissure; and in most of the internal characters.

Some of these differences have been indicated by Schmidt (1964, p. 506; 1965, p. 17; in Moore, 1965, p. H587).

The lower Famennian genus *Eoparaphorhynchus* Sartenaer, P., 1961, is very easily separable, as noted by Sartenaer (1961b, p. 2).

Yunnanella hanburii (Davidson, T., 1853)

PLATE 1: FIGURES 1–5; Plate 2

NOMENCLATORIAL NOTE.—Conditions of Article 32 (a) of the International Code of Zoological Nomenclature being fulfilled, *Yunnanella hanburii* is the only correct spelling, although it is quite clear, according to Davidson (1853, p. 353), that the person who presented four or five specimens of that species to the British Museum of Natural History was D. Hanbury. Nevertheless, since the problem is of little importance, I have no strong objection to the spelling *"Y. hanburyi"* if Recommendation 31A of the second edition of the Code (=Article 31 of the first edition) is followed and given retroactive power.

TYPES.—Lectotype, BM B42506; Province of Kwangsi, China; Devonian. The lectotype was purchased in a drug warehouse in Shanghai and was designated by Grabau (1931, pp. 157, 158) on the suggestion of F. A. Bather. It is illustrated herein as Plate 1: figures 1a–3 (=pl. 15, figs. 10, 10a–b in Davidson, 1853; fig. 137, p. 195, in Grabau, 1923; fig. 13, p. 158, in Grabau, 1931a; fig. 29, p. 92, in Grabau, 1932; fig. 462, 2a–c of McLaren in Moore, 1965).

Syntypes (=paralectotypes), same locality and same mode of acquisition as the lectotype: A, BM B42507 (Plate 1: figures 3a–b [=pl. 15, fig. 11, in Davidson, 1853]); B, BM B42508 (Plate 1: figure 2); C, BM B42509; D, BM B5290.

Only four specimens, designated as syntypes, are in the box containing the specimens presented to the British Museum of Natural History by D. Hanbury. During the last visit to London, in going through T. Davidson's collections, I managed to locate a fifth specimen with two labels, on one of which was written, in Davidson's own hand: "publ. in the Proc. of Geol. Soc. for June 1853." It is believed, therefore, that this specimen is one of the primary types (Syntype D), and that the expression "four or five" used by Davidson might be due to the fact that he had some doubt about the attribution of Syntype A to the species. This juvenile specimen is somewhat deformed and gives the false impression, at least on its right side, of having a long hinge line. A sixth specimen, from the D. Hanbury collection, was presented to the British Museum of Natural History in 1911 and now bears the registered number B82307.

Hypotypes, Province of Hunan(?), China; Yaoso Group, Devonian; USNM Cat. No. 60950; probably purchased in Canton: A, USNM 154996 (Plate 1: figures 4a–e); B, USNM 165708 (Plate 1: figures 5a–e); C, USNM 165709; D, USNM 165710; E, USNM 165711; F, USNM 165712; G, USNM 165713 (Plate 2).

LOCUS TYPICUS AND STRATUM TYPICUM.—According to Davidson (1853, pp. 353, 354, 356), the four or five specimens of the species described from the Province of Kwangsi were purchased in a drug warehouse in Shanghai and sent by W. Lockhart to D. Hanbury, who presented them to the British Museum of Natural History. A Devonian age has been assigned to them (Figure 1).

MATERIAL.—The following description is based on the 5 primary types; 16 specimens from the British Museum of Natural History (one in the D. Hanbury collection, B5290, and 15 in the R. Swinhoe collection, 46787); 36 specimens from the United States National Museum (29 identified as *Yunnanella hanburii,* 3 as *Y. triplicata,* and 4 as *Y. uniplicata*), 4 specimens from the Geological Institute of the Academy of Sciences, Union of Soviet Socialist Republics, presented to Kh. S. Rozman by Chi-pou Yang (2 identified as *Y. hanburii* and 2 as *Y. uniplicata*); 4 specimens figured by Kayser (1883); 14 specimens figured by Grabau (1931a–1933) (5 identified as *Y. hanburii,* 3 as *Y. hanburii lata,* 3 as *Y. triplicata,* and 3 as *Y. uniplicata*); 7 specimens figured by Tien (1938) (1 identified as *Y. hanburii,* 3 as *Y. hanburii sublata,* 1 as *Y.* cf. *triplicata,* 1 as *Y. uniplicata,* and 1 as *Y. triplicata latiformis*).

EXTERNAL CHARACTERS.—Pedicle valve is convex—generally slightly—in the umbonal region, which is the only part showing in lateral views. Flanks are steep in the posterolateral parts, and (sometimes) concave near the commissure. Anterolateral parts of the valve are flat to gently concave, but their extreme margins often are abrupt.

Sulcus starts usually imperceptibly between 41 and 55 percent of the length of the shell forward of the beak (but values as low as 30 percent have been measured) or between 28 and 38 percent of the unrolled length of the valve. Sulcus widens sometimes slowly, usually rapidly; its width, where it starts, varies between 30 and 50 percent of its maximum width at the front, which varies between 61 and 75 percent of the width of the shell. The sulcus is moderately deep to deep—3 to 5 times the height of the low costae at the front, where it is deepest. Floor of the sulcus is generally flat, and sometimes slightly convex. Sulcus passes progressively into a high trapezoidal tongue, the upper part of which tends to become vertical and commonly is even recurved posteriorly. The borders of the tongue are not indented by the costae. Median costae often protrude anteriorly beyond the sharp borders of the tongue. Greatest thickness of the shell is located posteriorly between 15 and 25 percent of the unrolled length of the valve forward of the beak. Suberect, well-marked beak ends with a small half-circular foramen. Interarea is clearly delimited; it may reach a height of 2 mm, and its length varies between 35 and 50 percent of the width of the shell. Large deltidial plates are best seen in transverse serial sections.

Brachial valve is strongly convex, although never inflated. Flanks slope gently to abruptly, but their extreme margins are always abrupt; they also are steep in the posterolateral parts, where they become concave near the commissure. Like the sulcus, the fold starts imperceptibly at some distance forward of the beak. It is strongly marked, and is higher than the sulcus is deep; its top is flat to exceptionally strongly arched. Greatest thickness of the valve commonly is at the frontal commissure but sometimes occurs somewhat posterior to it.

Ornament.—All costae are simple and round-flattish in their posterior part. Median costae start generally between 50 and 66 percent of the unrolled length of the valves forward of the beaks, but they may start at 25 percent of this length. Their average width at the front is 3 mm to 3.5 mm with a range from 2.5 mm to 4 mm. The dorsal costae are high and acute in their anterior part, and usually are irregular because of one or two costae being lower and narrower than the others. The ventral costae are low and obtuse. Parietal costae have been observed in a single specimen (Syntype c). Lateral costae are restricted to the anterior part of the shell, and the most external ones are mere identations of the commissure; these indentations are considered and counted as costae. Internal ventral lateral costae are high and acute in their anterior part. All other lateral costae are obtuse with rounded top, but, because of the angle under which they are cut by the commissure, they sometimes are acute or right at the commissure. Furrows have the same characteristics as the costae. Round-flattish costellae, starting at the umbones, cover the surface of the shell. They increase in number by successive bifurcation. Some costellae originate by intercalation. Four to six costellae per mm is an average number at mid-length. Costellae are superimposed on the costae. Fine growth lines are seldom seen.

Ratios of median and lateral costae are shown in Table 1. The general costal formula, which in rhynchonelloid brachiopods is a formula grouping at least 75 percent of the specimens in each category, is as follows in this species:

$$\frac{2\text{ to }4}{1\text{ to }3};\ 0;\ \frac{3\text{ to }5}{4\text{ to }6}.$$

General characters.—The species is of medium-size and uniplicate. The contour in ventral and dorsal views is variable. Most of the specimens are transversely subelliptical to subcircular. Some specimens have a subpentagonal contour. The commissure is strongly indented by the costae. The anterolateral commissures are low in the shell; they are not sharp, because the extreme margins of the flanks are often vertical, but still they are indented in high zigzags by the costae.

Table 1.—*Ratios of median and lateral costae.*

Number of costae	*Number of specimens*	*Percent*
	Median Costae	
2/1	12	14.1
3/2	63	74.1
4/3	10	11.8
	85	100.0
	Lateral Costae	
2/3	1	1.30
3/4	27	34.60
4/5	26	33.35
5/6	17	21.80
6/7	7	8.95
	78	100.00

The top of the tongue usually represents the greatest thickness of the shell.

The greatest width of the shell is generally between 60 and 66 percent of the length from the beak.

Dimensions.—Measurements (in millimeters) are given in Table 2 (l, length; w, width; t, thickness; p.v., pedicle valve; b.v., brachial valve). The figures

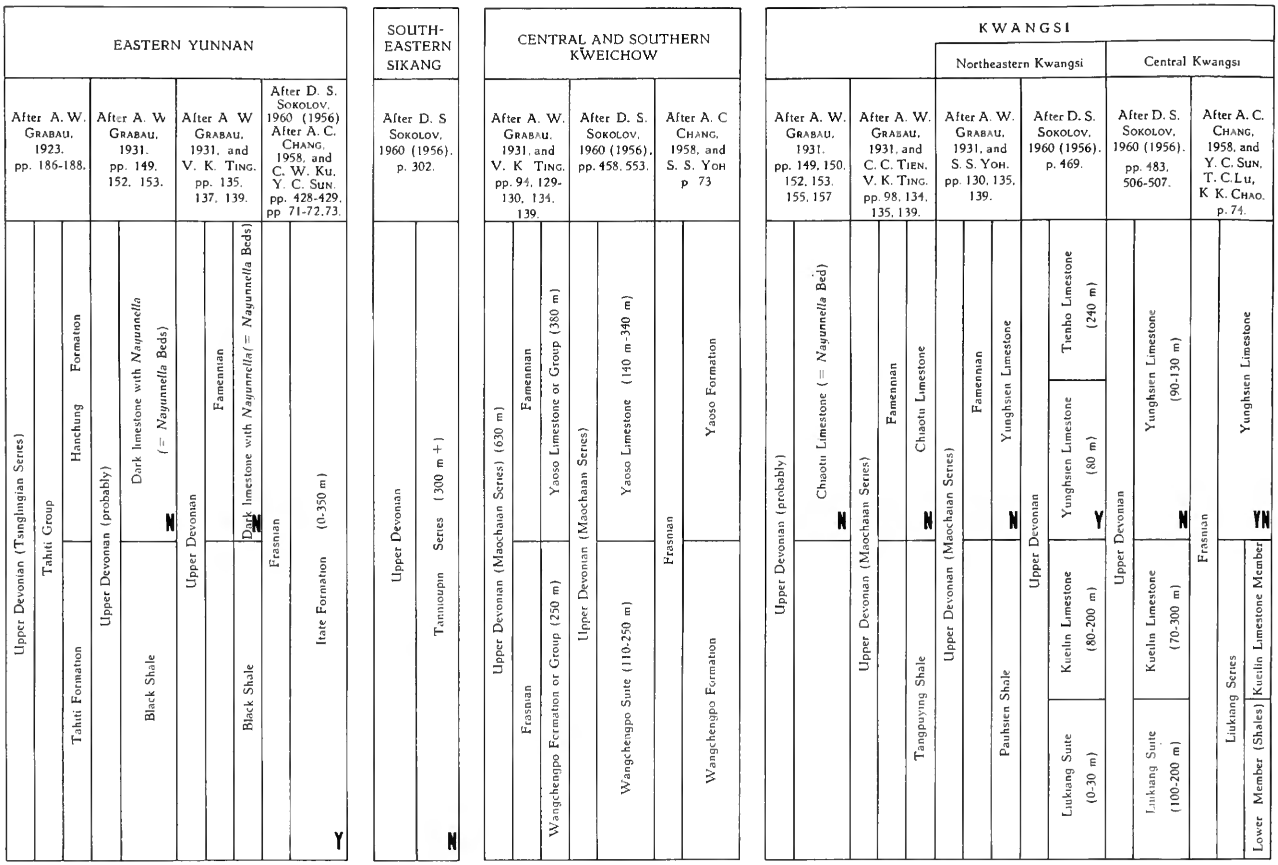


FIGURE 1.—Various interpretations on the age of the Upper Devonian formations in the area considered in this paper. When the genera *Yunnanella* and *Nayunnella* have been mentioned in the literature, they are indicated by "Y" and "N," respectively; the position of these letters on the figure has nothing to do with the genera's stratigraphic positions within the formation itself. This is not a correlation chart.

in parentheses in the table represent reasonable estimates only, because of damage to specimens. Length and thickness of the primary types are different from those given by Davidson (1853, p. 356) and Grabau (1931a, p. 158) because they are measured with the plane of commissure being horizontal. Width is the greatest dimension, but the l./w. ratios show that length and width sometimes have close values; t./l. ratios show that the height may be greater than length. The majority of specimens have shoulder angles between 94° and 110°.

INTERNAL CHARACTERS.—Internal characters are given under the description of the genus.

GROWTH.—Juvenile characters, observed on Syntype A: absence of costae, sulcus and fold not developed, height not developed.

REMARKS.—The original description by Davidson is brief and incomplete. In particular, almost no information is given on the internal characters, and the figures are somewhat stylized drawings. This indicates the necessity of a new study based on more material, including the primary types.

The species *Y. triplicata* and *Y. uniplicata* are considered as entering the range of variability of *Y. hanburii*. Therefore, they are included in the description, as are the "mutation *lata*" of A. W. Grabau (1931a–

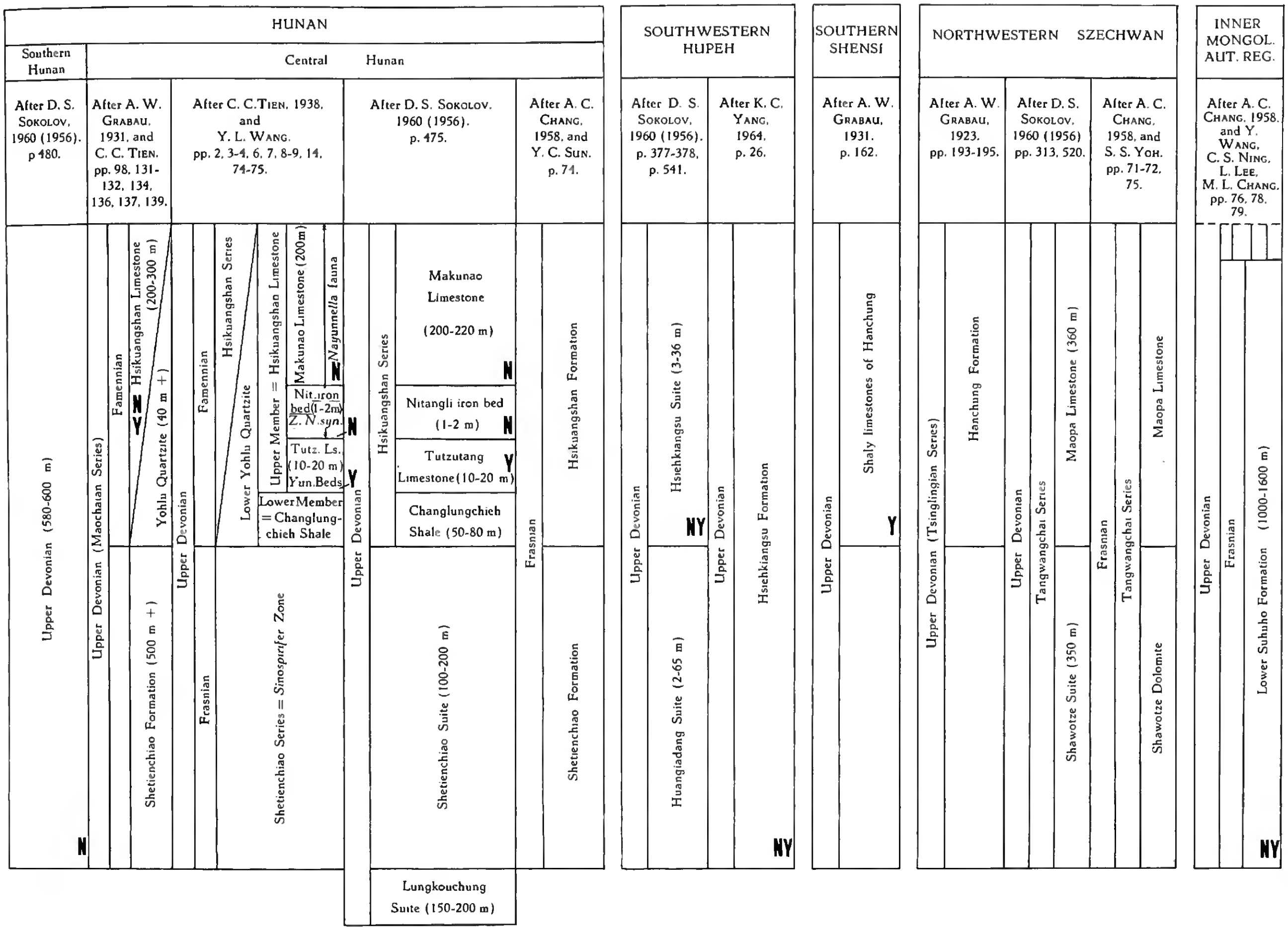


FIGURE 1.—Continued.

TABLE 2.—*Dimensions of type specimens (measurements in millimeters). Syntypes are paralectotypes.*

Specimen	*l.*	*w.*	*l.p.v.* (*unrolled*)	*t.*	*t.p.v.*	*t.b.v.*	*l./w.*	*t./w.*	*t./l.*	*Shoulder angle*	*Apical angle*
Hypotype B	17. 5	20. 7	26. 5	17. 1	3. 2	13. 9	0. 85	0. 83	0. 98	95°	120°
Syntype B	(17. 2)	18. 6	23. 5	(13. 8)	(2. 8)	11. 0	(0. 93)	(0. 74)	(0. 80)	105°	114°
Syntype C	17. 4	(17. 4)	26. 2	16. 5	3. 7	12. 8	(1. 00)	(0. 95)	(0. 95)	94°	?
Hypotype A	17. 1	18. 4	25. 0	13. 9	3. 4	10. 5	0. 93	0. 75	0. 81	100°	108°
Hypotype E	(16. 8)	20. 5	(29. 5)	15. 3	3. 8	11. 5	(0. 82)	0. 75	(0. 91)	110°	120°
Lectotype, BM B42506	(16. 6)	(20. 1)	(28. 5)	17. 6	3. 2	14. 4	(0. 83)	(0. 88)	(1. 06)	?	115°
Hypotype C	16. 4	21. 0	30. 7	16. 8	3. 5	13. 3	0. 78	0. 80	1. 02	103°	117°
Hypotype D [1]	14. 4	19. 6	25. 0	17. 1	3. 5	13. 6	0. 73	0. 87	1. 19	100°	116°
Hypotype F [2]	12. 2	14. 5	20. 5	12. 5	2. 5	10. 0	0. 84	0. 86	1. 02	105°	110°
Syntype A [3]	8. 3	9. 2	9. 2	3. 8	1. 7	2. 1	0. 90	0. 41	0. 46	?	102°

[1] A very high specimen.

[2] A young specimen having already developed adult features.

[3] A juvenile specimen.

1933), the "mutation *sublata*" and the *Y. triplicata* var. *latiformis* of C. C. Tien (1938); the first of these three forms, according to my analysis, includes adult specimens which did not develop the usual height of the species.

Discussion of the Forms Labelled *Yunnanella*

To my knowledge, 68 species and subspecies, some of which are introduced in the literature as mutations or varieties, have been labelled *Yunnanella* at one time or another; species mentioned merely as "*Y.* sp." are not included in this figure. The 68 forms include: (1) the species originally and correctly attributed to the nominal genus *Yunnanella*; (2) the species mentioned under the generic name *Yunnanellina* and which should, according to the Code (see above), have been assigned to the nominal genus *Yunnanella;* and (3) the species mentioned under the nominal genus *Yunnanella* that should be assigned, according to the Code, to the nominal genus *Nayunnella*. Except for *Yunnanella hanburii, Y. hanburii lata, Y. hanburii sublata, Y. triplicata, Y. triplicata latiformis,* and *Y. uniplicata,* which have been discussed under the description of *Y. hanburii,* the validity of these species and subspecies is not considered here.

(1) Seven species and subspecies (all Chinese) belong to the genus *Yunnanella: Y. hanburii* (Davidson, T., 1853); *Y. hanburii lata* Grabau, A. W., 1931; *Y. triplicata latiformis* (Tien, C. C., 1938); *Y. obesa* (Tien, C. C., 1938); *Y. hanburii sublata* (Tien, C. C., 1938); *Y. triplicata* Grabau, A. W., 1931; and *Y. uniplicata* Grabau, A. W., 1931. It is possible that the two species described in Novaya Zemlya under the following names by Tcherkesova (1961) could belong to the genus, but they are represented, respectively, only by three and two specimens, and more information is needed: *Junnanellina karina* Tcherkesova, S. V., 1961, and *J. triaequalis* (Nalivkin). The latter form has already been attributed to the genus *Yunnanella* by Rozman (1959, p. 97), and some specimens from the Tarbagatai Mountains of Kazakhstan that have been identified as *Paraphorhynchus triaequalis* by Sverbilova (in Litvinovitch and Sverbilova, 1963, pp. 277–278) also could belong to the genus *Yunnanella.*

(2) Eight Givetian species and subspecies belong to the genus *Schnurella* or to an undescribed genus: *Yunnanella custos* Schmidt, H., 1941; *Y. incisa* Schmidt, H., 1941; *Y. innae* Ivanova, E. A., 1962; *Y. olgae* Ivanova, E. A., 1962; *Terebratula schnurii* de Verneuil, E., 1840; *Rhynchonella schnurii transversa* Reed, F. R. C., 1908; *Yunnanella transversiformis* Tiajeva, A.P., 1962; and *Terebratula voltzii* d'Archiac, A., and de Verneuil, E., 1842. *Terebratula schnurii* and *T. voltzii* are correct spellings, as the conditions of Article 32(a) of the Code are met with. The names *T. schnuri* and *T. voltzi* also may be accepted (see the nomenclatorial note at the beginning of the description of *Y. hanburii*). Four species are known from Germany, two from the Kouznetzk Basin, one from the western flank of the South Ural Mountains, and one from Burma and Armenia. One species belonging to the group has been mentioned in the Givetian of the Kouznetzk Basin by Ivanova and Tchoudinova (1959, p. 612) under the name *Yunnanella* aff. *triloba.*

(3) Six names are nomina nuda, and the generic assignment may be fixed for five of them: *Schnurella schnurii kuzbassica* (Rzhonsnitzkaia, M. A., 1962); *Nayunnella multiplicata* Grabau, A. W., 1931); *N. tieni* (Grabau, A. W., 1931); *Yunnanella pentaplicata* (Grabau, A. W., 1931); and *Y. quadriplicata* (Grabau, A. W., 1931); these forms are found in China and in the Kouznetzk Basin. The sixth name is *Yunnanellina markovskii* Rozman, Kh. S., 1959, a Frasnian form from the Ural Mountains.

(4) The following six species do not belong to the genus *Yunnanella* and are not present in the area indicated by various scientists. The Yunnanese species *Leiorhynchus deprati* Mansuy, H., 1912 is present neither in Kazakhstan (contrary to Nalivkin, 1930, pp. 67, 68; Brongouleev, 1957, pp. 20, 22; and Sidiatchenko and Alekseeva, 1958, p. 159), nor in the Tian Chan Mountains (contrary to Poiarkov, 1960, p. 30, table 2), nor in Armenia (contrary to Abramian, 1957, p. 8, tables 2, 3, and Arakelian, 1964, pp. 61, 94), nor in the Altai Mountains (contrary to Komar, 1957, p. 36, 39). The Chinese species *Nayunnella ericksoni* (Grabau, A. W., 1931) is present neither in Kazakhstan (contrary to Rozman, 1959, pl. 6, figs. 1a,b,v; 1962, pp. 77, 80, table 11, pp. 90, 131, 132), and Alekseeva and Sidiatchenko, 1959, table 2), nor in Novaya Zemlya (contrary to Tcherkesova, 1961, p. 45). The Chinese species *N. grandis* (Grabau, A. W., 1931) is not present in Kazakhstan (contrary to Sidiatchenko and Alekseeva, 1958, p. 159). The Belgian species *Ptychomaletoechia gonthieri* (Gosselet, J., 1887) is not present in Kazakhstan (contrary to Nalivkin, 1937, pp. 78, 79; Simorin, 1956, pp. 241, 242; Martynova, 1956, p. 97; 1962, table 10; and Alekseeva and Sidiat-

chenko, 1959, table 3, p. 27). The Chinese species *Yunnanella hanburii* (Davidson, T., 1853) is present neither in Kazakhstan (contrary to Nalivkin, 1930, p. 66, and Brongouleev, 1957, pp. 19, 20), nor in the Tian Chan Mountains (contrary to Poiarkov, 1960, p. 30, table 2). The Belgo-French species *Eoparaphorhynchus triaequalis* (Gosselet, J., 1877) is present neither in Kazakhstan (contrary to Nalivkin, 1937, pp. 79, 80; Simorin, 1956, pp. 239–241; Martynova, 1956, p. 92; 1961, pp. 28, 30, 40, 42, 44, 68, 100–102; Sidiatchenko and Alekseeva, 1958, p. 159; Rozman, 1959, pp. 92, 97–99; 1962, p. 18, tables 7, 10, pp. 67, 69, 78, 80, table 11, pp. 90, 138–140; Alekseeva and Sidiatchenko, 1959, p. 19, table 2, pp. 20, 23, 25, table 3, p. 27; Sidiatchenko, 1961, p. 1159, table 1, p. 1161; and Sverbilova in Litvinovitch and Sverbilova, 1963, pp. 277, 278), nor in Novaya Zemlya (contrary to Tcherkesova, 1961, pp. 45, 49, 50).

(5) The two English species *Terebratula anisodonta* Phillips, J., 1841, and *Rhynchonella* (*Camarotoechia*) *partridgiae* Whidborne, G. F., 1897, do not belong to the genera *Yunnanella* and *Nayunnella* (contrary to Tien, 1938, p. 43, and Reed, 1943, p. 134), respectively.

(6) The following species constitute a very heterogenous group: *Paraphorhynchus badura* Nalivkin, D. V., 1937; *P. celak* Nalivkin, D. V., 1937; *P. fatima* Nalivkin, D. V., 1937; *Yunnanellina karatauensis* Rozman, Kh. S., 1960; *Y. kasakhstanica* Rozman, Kh. S., 1960; *Y. kurgandjarica* Rozman, Kh. S., 1960; *Y. mugodjarica* Rozman, Kh. S., 1960; *Paraphorhynchus zobeida* Nalivkin, D. V., 1937; and *P. zuleika* Nalivkin, D. V., 1937. The diacritical mark on the word "*celak*" is dropped in accordance with Article 27 and Article 32(c)(i) of the Code. It is not certain that these species include all forms that have been given their names. To this group may be added some forms identified as *P. gonthieri* (including a variety) and *P. triaequalis,* or *Yunnanellina gonthieri* and *Y. triaequalis,* by Russian scientists. None of these twelve species and forms belongs to the genus *Yunnanella,* from which they differ by shape, sulcus (shape, depth, delimitation, point where it begins), fold (point where it begins), longer costae, divided median costae, etc. Furthermore, these species and forms do not belong to a single genus; a small species like *Paraphorhynchus zuleika* has very little in common with a large species like *Yunnanellina kasakhstanica.* In fact, these species and forms belong to genera such as *Evanescirostrum* Sartenaer, P., 1965; *Porostictia* Cooper, G. A., 1955; possibly *Rugaltarostrum* Sartenaer, P., 1961; and, perhaps, one new genus if not two new genera. Each of the species and forms should be investigated thoroughly, but the lack of material does not permit me to proceed with such a study. It is of primary importance that a detailed investigation should solve these systematics problems and thus permit the inclusion of the regions concerned in the Famennian correlation scheme based on rhynchonellid zones proposed by Sartenaer (1967). Except for *Yunnanellina kurgandjarica* and *Y. mugodjarica,* which come from the Mugodjary Mountains, all these species and forms are found in Kazakhstan.

(7) The forms identified in Kazakhstan as *Camarotoechia hanburyi* by Nalivkin (1930, p. 66) and as *Yunnanella ericksoni* by Rozman (1959, pl. 6, figs. 1a,b,v; 1962, pp. 77, 80, table 11, pp. 90, 131, 132) and by Alekseeva and Sidiatchenko (1959, table 2) do show some similarity with the genus *Nayunnella* but, among various other differences, the median costae in those forms start nearer to the beaks. Although too little is known about these forms, the possibility cannot be dismissed that a new genus could include some Russian species that have been assigned to the genus *Nayunnella.*

(8) The following two species from Kazakhstan most probably belong to the genus *Eoparaphorhynchus* Sartenaer, P., 1961: *Yunnanella acutiplicata* Rozman, Kh. S., 1962; and *Y. nalivkini* Rozman, Kh. S., 1960. The latter species includes in its synonymy the forms attributed by Nalivkin (1930, pp. 67, 68) to *Leiorhynchus deprati* Mansuy, H., 1912. In addition, some specimens from Kazakhstan identified by Russian scientists as *Paraphorhynchus gonthieri* or *Yunnanellina gonthieri* may belong to the genus *Eoparaphorhynchus.* This attribution has been suggested by Sartenaer (1967, p. 1048; 1969, pp. 62, 63), who also had in mind some specimens from the Mugodjary Mountains included in species validly assigned to other genera.

(9) The following 26 Chinese species and subspecies, some of which have been introduced in the literature as mutations or varieties, belong to the genus *Nayunnella: N. abrupta* (Grabau, A. W., 1931); *N. ericksoni* (Grabau, A. W., 1931); *N. abrupta globosa* (Tien, C. C., 1938); *N. grandis* (Grabau, A. W., 1931); *N. hsikuangshanensis* (Tien, C. C., 1938) plus four varieties; *N. hunanensis* (Tien, C. C., 1938) plus one variety; *N. abrupta media* (Tien, C. C., 1938); *N. mesoplicata* (Grabau, A. W., 1931); *N. abrupta rostrata* (Tien, C. C., 1938); *N. abrupta schnurioides* (Tien, C. C., 1938); *N. simplex* (Tien, C. C., 1938); *N.*

abrupta subcuboides (Tien. C. C., 1938); *N. uncinuloides subpentaplicata* (Tien, C. C., 1938); *N. synplicata subtriplicata* (Tien, C. C., 1938); *N. supersynplicata* (Tien, C. C., 1938); *N. synplicata* (Grabau, A. W., 1931) plus one mutation; *N. triloba* (Tien, C. C., 1938); *N. tieni* (Grabau, A. W., 1931); *N. uncinuloides* (Tien, C. C., 1938); *N. wangi* (Tien, C. C., 1938). The only specimen described by Tcherkesova (1961, pp. 46, 47) in Novaya Zemlya as *Junnanella ericksoni polaris* Tcherkesova, S. V., 1961, could well belong to the genus *Nayunnella*, as could some specimens identified as *Paraphorhynchus triaequalis* in the Karaganda Basin of Kazakhstan.

(10) The genera *Yunnanella* and *Nayunnella* have been reported several times as present in North America, but this view is rejected.

Warren and Stelck (1950, p. 64) state that *Leiorhynchus walcotti* from the Mackenzie River Valley "appears to belong to the sub-genus *Yunnanellina* of the genus *Yunnanella*"; Sartenaer (1969, pp. 62, 63) includes this form in the lower Famennian species *Eoparaphorhynchus maclareni* Sartenaer, P., 1961. In the same publication Sartenaer (1969) attributes, with doubt, the *Nayunnella* cf. *N. mesoplicata,* cited by C. H. Crickmay (1952, p. 593) and collected at about 530 feet below the top of the Palliser Formation, to the species *Sinotectirostrum medicinale* Sartenaer, P., 1961.

Yunnanella? sp. has been mentioned recently by Dutro (in Jones, Hernon, and Moore, 1967, p. 22; 1967, personal communication) as occurring in the Percha Shale of southwestern New Mexico and the Upper Devonian rocks of northwestern Alaska. These two occurrences most probably can be referred to the genus *Rugaltarostrum* Sartenaer, P., 1961. Thanks to the kindness of Dr. Dutro, I had the opportunity to see the material in Washington in 1966, but a detailed study is needed before a more definite statement can be made.

Stratigraphic Position of *Yunnanella* and *Nayunnella*

One of the greatest handicaps in dealing with the genera *Yunnanella* and *Nayunnella* is the lack of precise stratigraphic information on Chinese outcrops. The Chinese literature is very vague on the subject, and contacts with colleagues in China are impossible for the time being; thus, stratigraphic problems can only be touched upon. Still, a few points, some of them already mentioned (Sartenaer, 1967, p. 1056; 1969, pp. 62, 63), may be discussed.

(1) There are two completely opposed lines of thought among Chinese scientists on the age of the beds containing the genera *Yunnanella* and *Nayunnella:* Famennian or Frasnian. In the latter case, the late Upper Devonian is generally considered absent in South China. One of the strongest arguments in favor of the Frasnian age of the beds containing these genera is used by Wang and Ning (1957) and by Chang (1958) in the Great Khingan (Inner Mongolian Autonomous Region), where the Upper Devonian is divided into an Upper Suhuho Formation and a Lower Suhuho Formation, separated by an hiatus. A *Sporadoceras-Prolobites* fauna, to which a lower to middle Famennian age is given, has been discovered in the Upper Suhuho Formation, in which the trilobite *Phacops granulatus* also has been found. The Lower Suhuho Formation contains the Hsikuangshan fauna (Frasnian, according to Chang). When the thickness (800 m to 1,200 m) of the Upper Suhuho Formation is considered, the fact that the *Sporadoceras-Prolobites* fauna has been collected in an unspecified limestone bed does not permit far-reaching conclusions. These views are strongly opposed, however, by Yao (1959), who accepts ideas expressed by Tien (1938). Hamada (1960, pp. 228, 229), who accepts the Frasnian age of the beds with *Yunnanella* and *Nayunnella,* does not agree with the absence of the Famennian in South China advocated by A. C. Chang (1958) and believes that the hiatus between the Lower and Upper Suhuho Formations is small. There is not much an outsider can do in this changeable situation, roughly illustrated on Figure 1, in which the various regions are separated in order to point out that the figure is *not* a correlation chart. Obviously, in some instances in China, either the genus *Yunnanella* or the genus *Nayunnella* is associated with a Frasnian fauna (e.g., in Grabau, 1923, pp. 194, 195), but not much importance can be put on this kind of information found in the literature, because the thickness of rocks involved may be great. In some instances (e.g., in Sokolov, 1960; 1956, p. 428) this thickness is as small as 5 meters.

(2) Although representatives of the genera *Yunnanella* and *Nayunnella* may occur together in China, the latter genus ranges higher in the sequence.

(3) The genus *Nayunnella* has been mentioned erroneously by Tien (1938, p. 49) in the Lower Carboniferous of China. The fact that Reed (1943, p.

134) has attributed to the genus *Nayunnella* the British species of the Pilton Beds, *Rhynchonella* (*Camarotoechia*) *partridgiae,* may also explain why the genus sometimes has been mentioned from the Lower Carboniferous.

(4) Neither genus is present in the Frasnian deposits of Kazakhstan. The mention of the genus *Yunnanella* in the South Ural Mountains is due to the attribution by Rozman (1959, pp. 92, 97) of the *Pugnoides triaequalis* mentioned by Markovskii (1948, p. 34) in the Barma Beds. I reject this attribution. Rozman (1959, p. 93, fig. 1, p. 98) also mentions the genus *Yunnanella* in the Upper Frasnian of the Mugodjary Mountains, but this is not substantiated by any information known to me. At any rate, these two references were later omitted by Rozman (1962).

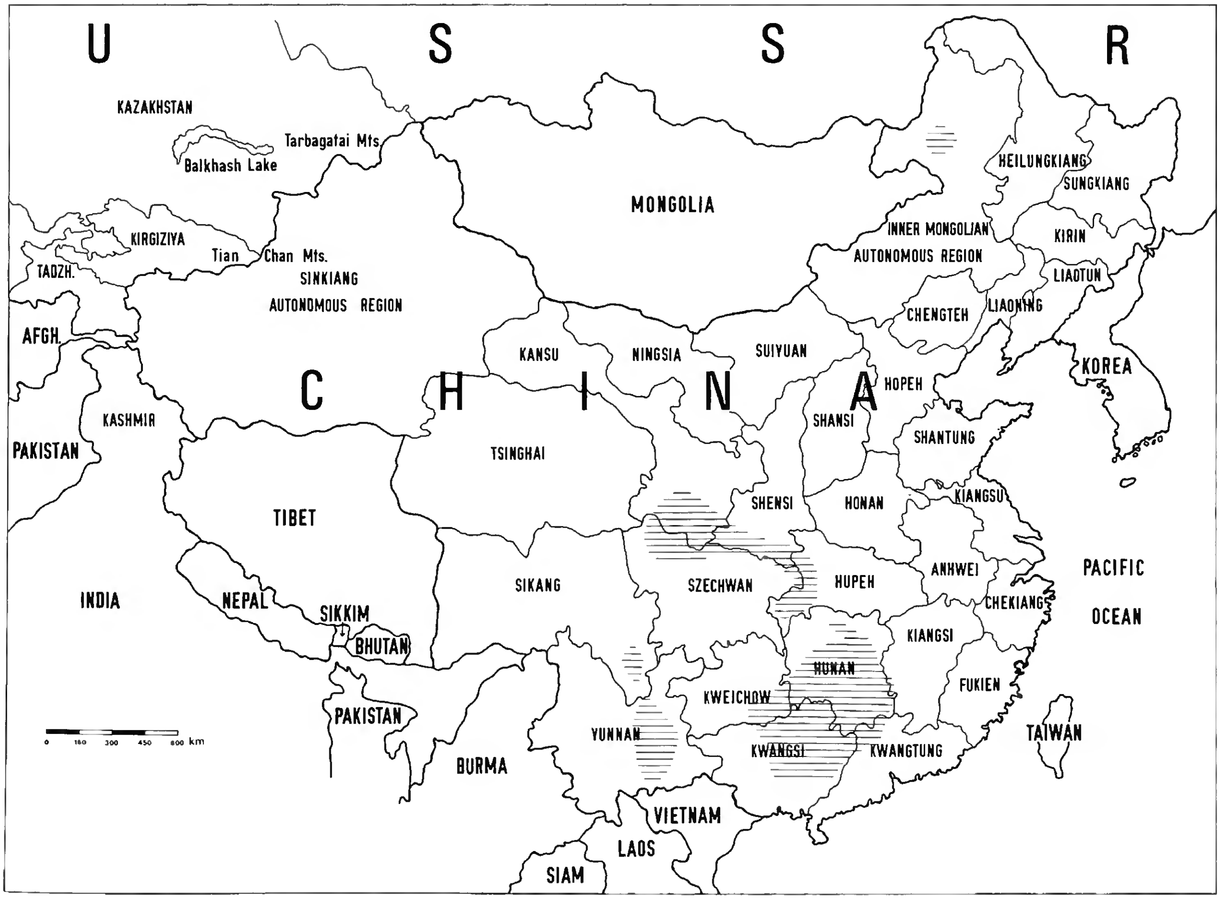
(5) Similarities between the fauna of the Famennian of western Europe and the fauna associated with the genera *Yunnanella* and *Nayunnella* are difficult to establish. Still, it must be born in mind that the Chinese fauna is still very poorly described.

(6) All Givetian species attributed in the past to the genus *Nayunnella* belong either to the genus *Schnurella* or to an undescribed genus.

(7) Although most of the species attributed in the Union of Soviet Socialist Republics to the genus *Yunnanella* do not belong to it, the presence of that genus in the Famennian cannot be dismissed.

(8) The stratigraphic range of both *Yunnanella* and *Nayunnella* is still unsettled in the type area.

FIGURE 2.—Known geographic distribution in China of the genera *Yunnanella* and *Nayunnella*.



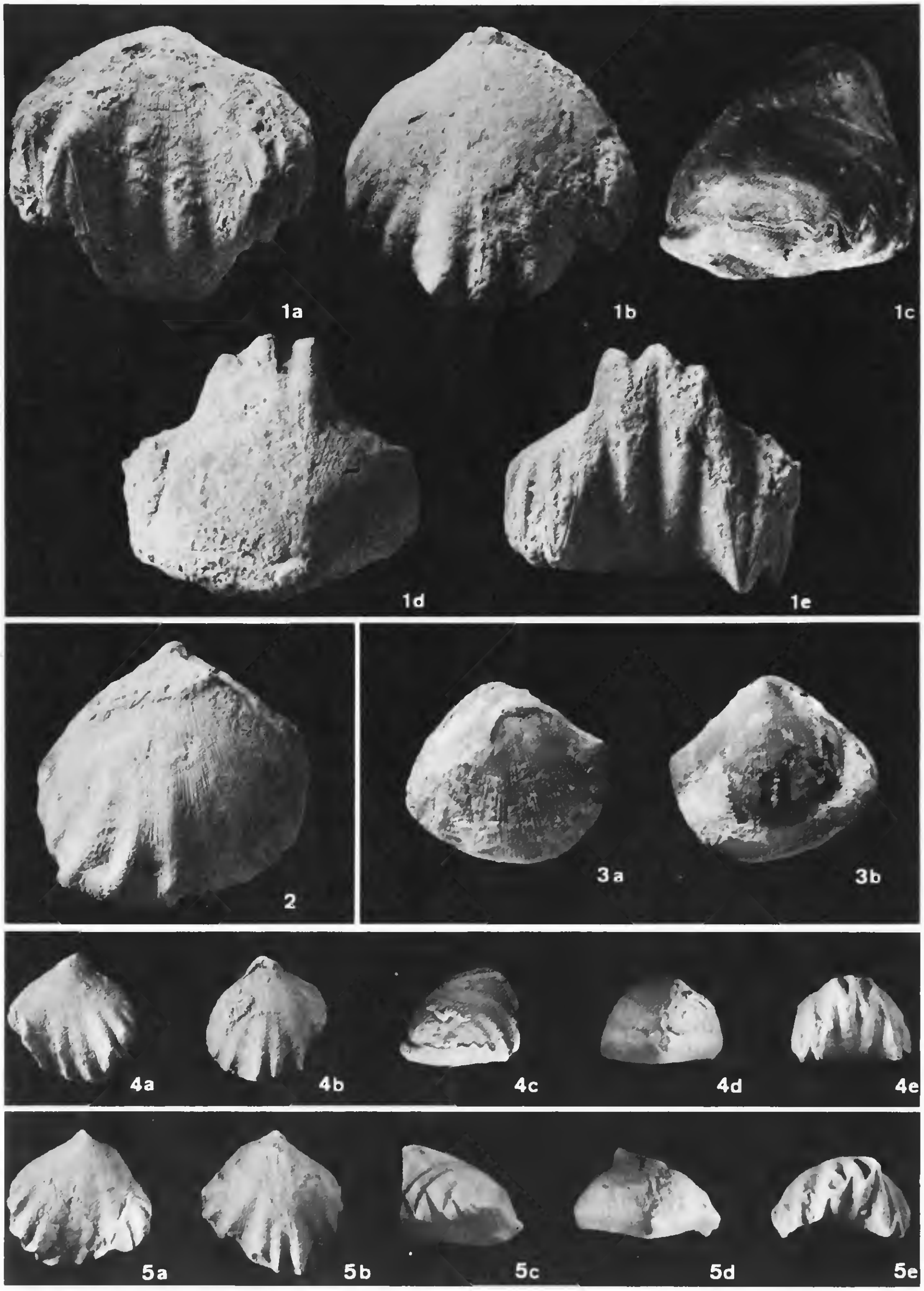


Plate 1.—*Yunnanella hanburii* (Davidson, T., 1853). Views are not necessarily oriented with the plane of commissure parallel or perpendicular to the plane of the plate. (Photos for figures 1–3 furnished by Museum of Natural History.) 1a–e, Lectotype, BM B42506; Province of Kwangsi, China; Devonian. Ventral, dorsal, lateral, apical, and frontal views (× 2). Costal formula: 3/2; 0; 4/5. 2, Syntype (= Paralectotype B), BM B42508; Province of Kwangsi, China; Devonian. Dorsal view (× 2). Costal formula: 3/2; 0; 5/6. 3a, b, Syntype (= Paralectotype A), BM B42507; Province of Kwangsi, China; Devonian. Dorsal and ventral views (× 3). 4a–e, Hypotype A, USNM 154996; Province of Hunan(?), China; Yaoso Group, Devonian. Ventral, dorsal, lateral, apical, and frontal views (× 1). Costal formula: 3/2; 0; 5/6. 5a–e, Hypotype B, USNM 165708; Province of Hunan (?), China; Yaoso Group, Devonian. Ventral, dorsal, lateral, apical, and frontal views (× 1). Costal formula: 3/2; 0; 5/6.

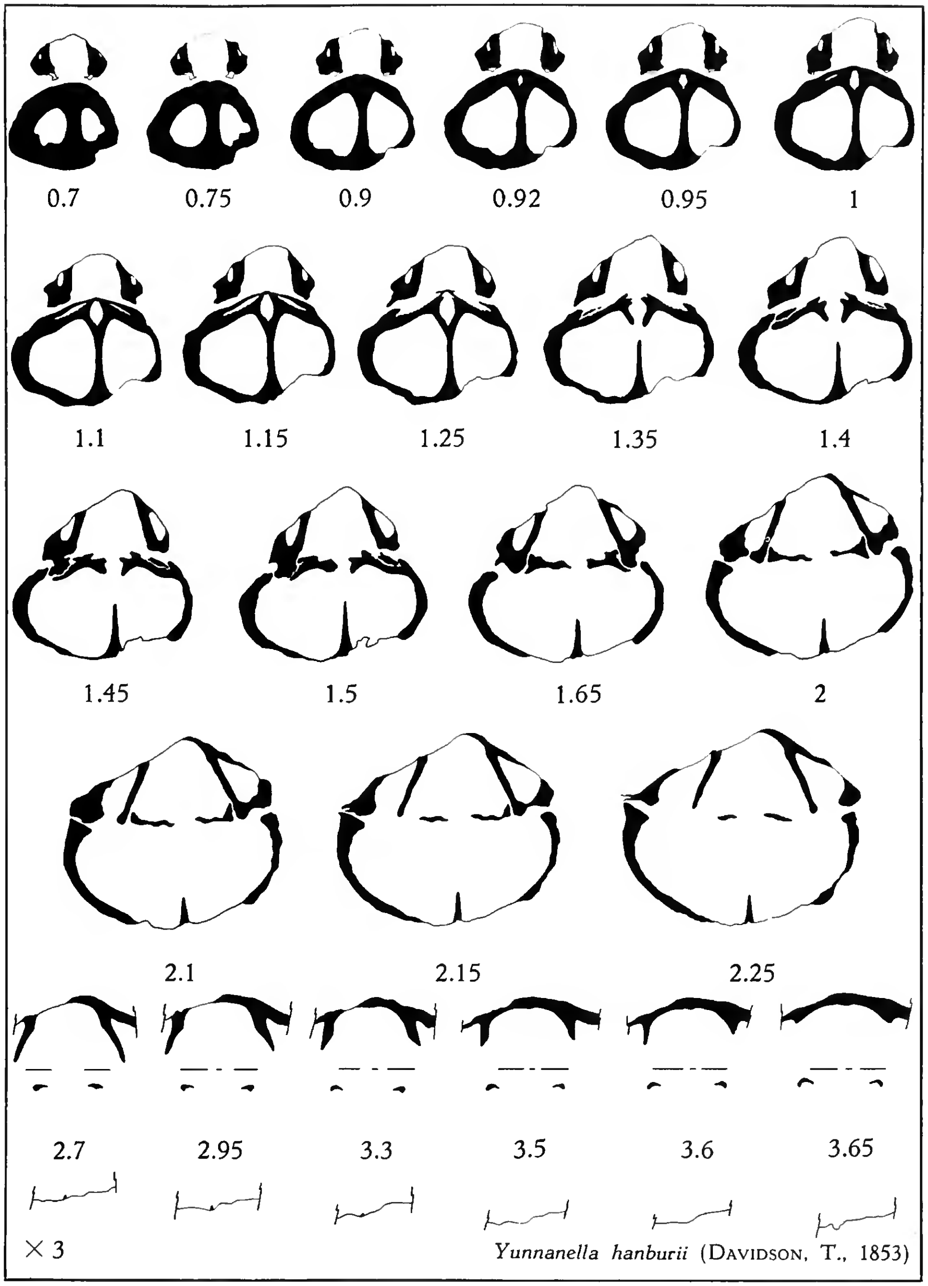


PLATE 2.—*Yunnanella hanburii* (Davidson, T. 1853). Hypotype G, USNM 165713; Province of Hunan(?), China; Yaoso Group, Devonian. Camera lucida drawings of serial transverse sections (× 3); distances are in mm forward from the crest of the umbo. Dimensions of specimen: length, 17.50 mm; width, 20.85 mm; thickness, 14.80 mm.

Geographic Distribution of *Yunnanella* and *Nayunnella*

The regions of China where species and subspecies of the genera *Yunnanella* and *Nayunnella* have been described or cited in the literature are indicated on Figure 2. Outside these areas, the genera could be present in Kazakhstan (Tarbagatai Mountains, Karaganda Basin) and in Novaya Zemlya, but additional studies are needed. The genera are not present in other parts of the Union of Soviet Socialist Republics, and certainly not in the Ural and Mugodjary Mountains. The attribution of various species and subspecies to the Givetian genus *Schnurella* and to an undescribed genus eliminates the genus *Nayunnella* from Armenia, Burma, Germany, the Kouznetsk Basin, and the western flank of the South Ural Mountains. As no English species belongs to either the genus *Yunnanella* or the genus *Nayunnella,* these genera are absent in Great Britain.

Conclusions

An effort to clarify and sort the problems involving the genus *Yunnanella* has been attempted. A clear definition of the genus has permitted the elimination of various species and subspecies attributed to it in the past and thus to clarify its systematic significance. The immediate result has been to restrict its geographic distribution to China, and perhaps Kazakhstan and Novaya Zemlya, and its stratigraphic range to the Upper Devonian. The lack of good information, and particularly of good stratigraphic sections from China, prevents a more precise statement about the stratigraphic range within the Upper Devonian, although it is quite obvious that the genus *Yunnanella* did not range through the entire late Devonian.

Once again, it is demonstrated that a considerable stratigraphic range (Givetian to Carboniferous) for a rhynchonellid genus immediately indicates that it is in need of revision and that it encompasses other genera. It will be possible to deal fruitfully with the problems of paleogeography, classification, and evolution only when the various genera are more precisely defined.

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J. Stewart Williams

The Beirdneau and Hyrum Formations of North-Central Utah

ABSTRACT

The Hyrum and Beirdneau Formations of north-central Utah have their best exposures in Blacksmith Fork Canyon, Cache County. Sections at this locality are described in detail. Three sections to the northwest and two to the southeast are compared with the Blacksmith Fork section.

The Hyrum Formation, about 1,000 feet thick, is composed of thin to medium beds of dark and medium gray dolomite with some calcitic dolomite, dolomitic limestone, and limestone. There are a few thin interbeds of sandstone and dolomitic sandstone. The fossiliferous Samaria Member at the base is of Middle Devonian (Givetian) age. The Hyrum Formation correlates with the Jefferson Formation to the north and east.

The Beirdneau Formation, 1,000 feet or less in thickness, is composed of thin-bedded dolomitic sandstone and argillaceous dolomite. It correlates closely with the Three Forks Formation to the east and north and is upper Upper Devonian (Famennian) in age.

In a paper on the geology of the Paleozoic rocks of the Logan quadrangle, the writer (Williams, 1948) described briefly three stratigraphic units in the local Devonian: the Water Canyon Formation of Lower Devonian age and the Hyrum Dolomite and Beirdneau Sandstone members of the Jefferson Formation. The "Contact Ledge" at the top of the section was assigned to the Mississippian. Shortly thereafter Holland (1952) defined the Leatham Formation beneath the Madison Limestone in Blacksmith Fork Canyon and reported that the "Contact Ledge" contained Devonian fossils. Later, Rigby (1959) related the high detrital content in the Beirdneau Sandstone Member to Late Devonian diatrophism in the Stansbury Range and adjacent areas, southwest of the Bear River Range outcrops.

In 1964 Mullens and Izett published a geologic map of the Paradise quadrangle, which includes the Devonian outcrops in Blacksmith Fork Canyon, and with the accompanying text is a figure of a measured section of the Hyrum and Beirdneau members. In the same year, the writer and Michael Taylor restudied the Water Canyon Formation and added considerable detail about the Bear River Range sections of that formation (Williams and Taylor, 1964).

In the past three years, Beus (1965, 1968) has reported his studies on the Paleozoic section in Samaria Mountain, northwest of the Bear River Range exposures, and has defined the Samaria Limestone Member of the Jefferson Formation.

Recent regional studies of the Devonian—namely, those of Benson (1966), Poole and others (1967), and Sandberg and Mapel (1967)—have shown that the Hyrum Dolomite and Beirdneau Sandstone are recognizable over a considerable area in southeastern Idaho and north-central Utah and that they probably are sufficiently different from time-equivalent sections to the northeast and north in Wyoming and Montana to warrant their elevation to formational rank.

Because of the growing interest in the Hyrum Dolomite and Beirdeau Sandstone (hereafter to be called the Hyrum Formation and the Beirdneau Formation), it seemed desirable to examine in detail the well-exposed sections of these strata in Blacksmith Fork Canyon, to describe them more accurately, to search them more diligently for fossils, and, on the basis of the information obtained, to attempt to describe the conditions under which they were deposited.

The section of the Hyrum Formation reported in this paper was measured in secs 1 and 12, T 10 N, R

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1 E, and that of the Beirdneau Formation in secs 7 and 8, T 10 N, R 2 E (SLB&M). Other sections that received the same examination are in Logan Canyon, sec 23, T 12 N, R 2 E (SLB&M); in old Laketown Canyon, Rich County, Utah, secs 17 and 18, T 12 N, R 6 E (SLB&M); in Mahogany Canyon north of Morgan in Morgan County, Utah, sec 24, T 4 N, R 2 E (SLB&M); along the north side of Portage Canyon, Box Elder County, Utah, secs 33 and 34, T 15 N, R 4 W (SLB&M); and north of Wide Hollow, west of Grace, Caribou County, Idaho, sec 35, T 9 S, R 39 E, and sec. 2, T 10 S, R 39 E (BB&M).

The beds in these sections were measured and then described in field notes, with chips taken for laboratory study and analysis. All samples taken from the Blacksmith Fork section were analyzed for calcium, magnesium, and acid-insoluble residue, with the residues retained for microscopic examination. Rock chips from the other sections that appeared to offer differences in kind also were analyzed.

The color terminology is that of the "Rock-Color Chart" distributed by the Geological Society of America. The nomenclature used in describing the rocks, which are mostly carbonate with a varying admixture of detrital material, is that of Guerrero and Kenner (1955) and Mather (1955).

The certain presence of Devonian rocks in northern Utah has been known since E. M. Kindle (1908) published his study of the Jefferson Limestone from its type section in Montana to the outcrops in the Bear River Range. Geologists at Utah State University long have been aware that the local section contains thick and well-exposed representatives of the Devonian, and one of the earliest master's theses completed in the department was devoted to these rocks (Cooley, 1928).

The writer is indebted to Mr. James Eliason for his excellent work as a field assistant; to the University Research Council, Utah State University, for funds to support the field and laboratory work; to Dr. G. Arthur Cooper of the United States National Museum for assistance in identifying brachiopods; to Dr. Gilbert Klapper of the University of Iowa for processing samples and identifying the conodonts; and to Mr. Robert H. Denison of the Field Museum of Natural History for identifying the fishes.

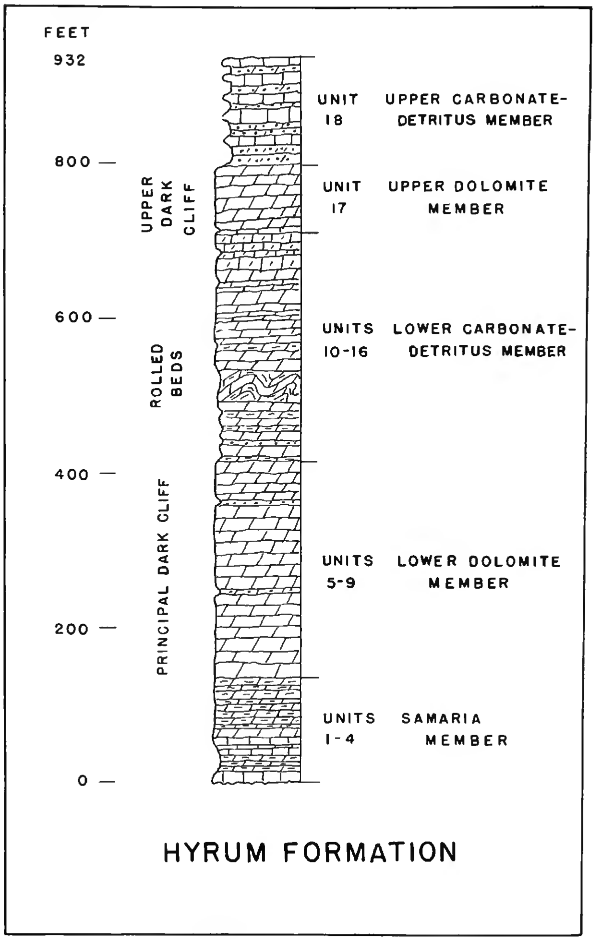

FIGURE 1.—Stratigraphic diagram of the Hyrum Formation in Blacksmith Fork Canyon showing lithology and members.

Hyrum Formation

GENERAL LITHOLOGY.—The Hyrum Formation is generally a cliff-former, in contrast to the weaker Beirdneau Formation, which, in most localities, forms smooth slopes. However, there are few massive beds in the formation, and thin to medium bedding is common. Dark and medium gray are the common colors, with the argillaceous and sandy beds showing such colors as light gray, yellowish gray, and light olive gray.

Dolomite is the common rock in the formation but there are beds of limestone, dolomitic limestone, and calcitic dolomite. The detrital component is fine-grained, being generally clay, silt, or fine sand. Only two relatively thin beds of sandstone occur in the formation, and one of these is dolomitic. The Blacksmith Fork section is readily divisible into five members (Figure 1), which may be traced northwestward into the Portage Canyon section.

The Hyrum Formation, exposed in Blacksmith Fork Canyon, Cache County, Utah, Secs 1, 12, T 10 N, R 1 E (SLB&M)—by far the best section exposed in the region—is as follows:

	Thickness	
Unit and Member	*Feet*	*Meters*
UPPER CARBONATE-DETRITUS MEMBER		
18. Limestone: massive, forming ledges up to 10 feet thick, medium gray to medium light gray, very finely crystalline to compact, some with oolitic texture; grading above and below into interbeds of dolomitic limy sandstone; thin-bedded, wavy-bedded, yellowish gray, very fine-grained; halite casts, ripple marks, dessication cracks. Deformation and brecciation common, with limestone-sandstone breccias.	134.0	40.8
UPPER DOLOMITE MEMBER		
17. Dolomite: thin- to medium-bedded, medium dark gray to medium gray, very finely crystalline.	84.0	25.6
LOWER CARBONATE-DETRITUS MEMBER		
16. Dolomitic limestone: thin- to medium-bedded, medium gray to medium light gray, very finely crystalline to aphanitic; near base of unit several beds of dolomite, medium dark gray, very finely crystalline; some thin beds of limestone; considerable intraformational breccia; ledges weather with rounded profiles.	95.0	29.0
15. Calcitic dolomite: thin- to medium-bedded, dark gray to medium gray, finely crystalline; some thin, more sandy beds of arenaceous calcitic dolomite.	55.0	16.8
14. Same as 13. Some of the carbonate beds are limestone. Some interbeds are silty limestone.	91.5	27.9
13. Dolomite, in massive ledges, which in detail are laminated with contorted bedding and intraformational breccia; medium dark gray to medium gray, very finely crystalline; interbeds (silty dolomite) which separate ledges thin-bedded to laminated, medium gray. Interstratal contortions including "fists" and "roll-ups" developed here.	30.5	9.3
12. Sandstone: laminated to medium-bedded, light gray to yellowish gray, generally fine-grained; subparallel cross-lamination, sharp contacts to beds above and below.	11.5	3.5
11. Dolomite: thick-bedded, medium gray weathering light gray, medium crystalline.	10.5	3.2
10. Silty or argillaceous dolomite: laminated, wavy bedding, light gray weathering dusky olive; thin interbeds of sandstone; sharp wavy contacts to dolomites above and below.	3.0	0.9
LOWER DOLOMITE MEMBER		
9. Dolomite: medium- to thick-bedded, medium gray, finely crystalline; laminations not visible in thick beds.	50.0	15.2
8. Calcitic dolomitic sandstone: thin-bedded to laminated, light olive gray, very fine-grained; grades into dolomite below through medium light gray silty dolomite and into dolomite above through laminated, shaly, light olive gray silty dolomite; edgewise conglomerate and intraformational breccia common.	7.7	2.3
7. Dolomite: cliffs massive, but in detail the beds appear thin-bedded or laminated; medium dark gray weathering medium gray, finely crystalline.	110.0	33.5
6. Arenaceous calcitic dolomite: thin-bedded, yellowish gray, fine-grained; grades above and below into adjacent dolomites through beds of laminated, light gray, silty or argillaceous dolomite. Ripple marks; microcontortions in some laminated beds.	4.0	1.2
5. Dolomite: medium- to thick-bedded, medium dark gray, finely crystalline.	111.0	33.8
SAMARIA MEMBER		
4. Silty calcitic dolomite: thin- to medium-bedded, medium dark gray weathering medium gray.	53.0	16.2
3. Dolomite: medium-bedded, medium gray weathering light gray, finely crystalline: thin partings of silty or argillaceous dolomite, laminated, light gray; with microdeformation.	26.3	8.0
2. Dolomitic limestone: thin- to medium-bedded, dark gray to medium dark gray, weathering light olive gray, compact to coquinoidal. In lower part silty or argillaceous dolomite: thin- to medium-bedded, medium gray weathering light olive gray. *Rennselandia* midway up unit.	45.0	13.7
1. Limestone: medium- to thick-bedded, medium gray, brecciated in part.	10.4	3.2
TOTAL	932.4	284.1

LOWER BOUNDARY.—The basal unit of the Hyrum Formation, a rounded ledge of gray limestone, rests upon the lighter-colored sandy sediments of the Grassy Flat Member of the Water Canyon Formation. The contact, generally fairly sharp, is to be seen in the al-cove beneath the basal limestone, where the weaker Water Canyon sediments have weathered back. At some localities, however, where the basal limestone is brecciated and where there is also intraformational breccia in the uppermost beds of the Water Canyon, it is more difficult to select the boundary, and additional study of the breccias above and below the contact is needed. One such locality is at Grassy Flat in Logan Canyon (Williams and Taylor, 1964, p. 47). Another is the Portage Canyon section where Williams and Taylor (1964, p. 50) and Beus (1968, p. 789) selected different positions for the boundary that are 134 feet apart in the section. The difficulty of selecting the formational boundary at Portage is heightened by the fact that the upper part of the Grassy Flat Member contains well-bedded dark gray dolomites, with traces of marine fossils, that resemble the beds of the Hyrum Formation.

SAMARIA MEMBER.—The basal member of the Hyrum Formation can be distinguished by its generally lighter color and thinner beds, which contrast with the darker dolomite beds above that form the principal cliffs on any outcrop of the formation. The lower part of the member is limestone or calcitic limestone, and here fossils are common. Beus (1965) has described part of the fauna from this member, which he named the Samaria Limestone Member of the Jefferson Formation (Beus, 1968). The writer proposes to extend the use of this name to the sections in the Bear River Range.

In Blacksmith Fork Canyon the lower half of the member is limestone and dolomitic limestone, which grades upward into silty calcitic dolomite. In Logan Canyon the member has essentially the same development as in Blacksmith Fork Canyon except that the exposures are somewhat better and fossils are more abundant. In Portage Canyon the member reaches its maximum thickness (338 feet) in the study area, being about twice as thick as in Logan and Blacksmith Fork Canyons. Here the member appears as a succession of three limestone ledges (Plate 1: figure 6) separated by two weaker units of thin-bedded silty calcitic dolomite or silty dolomitic limestone, dusky yellow or yellowish gray in color. These erode back, and bring the limestone beds into relief. The ledges of limestone grade from limestone into silty dolomitic limestone.

As stated above, the writer has not drawn the boundary between the Water Canyon Formation and the Hyrum Formation in the Portage Canyon section at the same position as has Beus (1968, p. 789, fig. 5). According to the writer's interpretation, the Samaria Limestone Member of Beus would be 508 feet thick in the State Line section. In Portage Canyon the writer's measurement of the Samaria Member is 338 feet. The Samaria Member is not recognizable in the Laketown Canyon section.

AGE OF THE SAMARIA MEMBER.—The Samaria Limestone Member at the base of the Hyrum Formation is by far the most fossiliferous part of the formation. Fossils are rare in the sandstone-carbonate and in the dolomite members above it. Some fossils have been recovered from the Samaria Limestone Member in each of the sections studied except the Laketown Canyon section and the Morgan section, where the Hyrum is represented by the Lower Dolomite Member only.

The Portage Canyon section, some two miles south of Beus's (1965) State Line section, produced the most abundant fossils. These came, of course, from the southward continuation of the type Samaria Limestone.

Beus (1965, pp. 23, 24), who discussed at some length the probable age of the fauna of the Samaria Limestone, concluded that the Middle Devonian-Upper Devonian boundary might well occur in the fossiliferous limestone unit, making the lower 300 feet of the Hyrum Formation Middle Devonian in age. In summary reports, Sandberg and Mapel (1967, p. 857) and Poole and his co-authors (1967, p. 902) agreed.

The writer's faunal list for the Samaria Limestone Member is not long, despite assiduous collecting:

Thamnopora sp.
Zaphrentid coral
Lingula sp.
Rennselandia cf. *R. missouriensis* (Swallow)
Schuchertella sp.
Atrypa oneidensis Beus
Tenticospirifer utahensis (Meek)
Allanaria engelmanni (Meek)
Ambothyris utahensis Beus
Cyrtina sp.
Reticularia sp.
Raphistomina (?) sp.
Hormotomina (?) sp.
Bembexia (?) sp.
Naticopsis sp.
Aviculopecten cf. *A. cancellatus* (Hall)
Proetus sp.
Icriodus sp.
Icriodus nodosus, sensu lato
Polygnathus decorosus, sensu lato
Atopacanthus dentatus Hussakof and Bryant
Ptyctodus sp.
Dipterus sp.

The item in the above list that appears to be important is *Rennselandia* cf. *R. missouriensis* (Swallow). According to Cloud (1942, p. 96), *Rennselandia* and *Stringocephalus* are coexistent in Europe and parts of North America, and *Rennselandia* is essentially as good a marker of the *Stringocephalus* zone as *Stringocephalus* itself. This is confirmed by Dr. G. Arthur Cooper (personal communication), who states that *Rennselandia* is unknown above the Middle Devonian. With *Rennselandia* occurring in the same beds as *Allanaria allani* in both Logan Canyon and Portage Canyon, it appears that a strong argument can now be made for the Middle Devonian age of the Samaria Limestone Member.

LOWER DOLOMITE MEMBER.—The Lower Dolomite Member of the Hyrum Formation is nearly 300 feet thick and forms the conspicuous dark gray cliffs that characterize the formation (Plate 1; figure 1). Three-fourths of the way up this member is an eight-foot bed of calcitic dolomitic sandstone, probably representing one of the detrital units recognized by Benson (1966, p. 2572) to the north and east. A four-foot bed of arenaceous calcitic dolomite, a third of the way up the member, also interrupts the expanse of dark gray dolomite, and it may be correlatable in other sections as a detrital unit.

In Logan Canyon the Lower Dolomite Member has approximately the same expression and thickness as in Blacksmith Fork Canyon, and the same is true in Portage Canyon. The member is well-developed in Laketown Canyon. In Mahogany Hollow, north of Morgan, there is 135 feet of mostly dark gray dolomite between the unconformity with the Cambrian and the base of the Beirdneau Formation. These dolomite beds appear to represent the Lower Dolomite Member.

LOWER CARBONATE-DETRITUS MEMBER.—The Lower Carbonate-Detritus Member of the Hyrum Formation is notable in the Blacksmith Fork section (Plate 1: figure 2) for the presence of an eleven-foot sandstone bed, the most conspicuous detritus unit in the Hyrum Formation; for the presence of rounded, lighter-gray cliffs separated by less-resistant units of silty or argillaceous light gray, yellowish gray, or dusky olive, dolomite or limestone, that are involved in intrastratal deformation on a large scale; and for the presence of a considerable amount of limestone. This same member is readily recognized in Logan Canyon (Plate 1: figure 3), between the upper and lower dolomite members, but there the "fists" and "roll-ups" are not so well developed. In Portage Canyon the same beds appear to be present, but the amount of work the writer has been able to devote to exposures in that section has not resulted in their positive identification.

The Laketown Canyon section is partly covered, and the boundaries between the Lower Dolomite Member and the Upper Dolomite Member and the intervening detritus-rich beds are not clearly seen, but the presence of the Lower Carbonate-Detritus Member is evidenced by the presence of a 10-foot sandstone bed, evidently the same as Unit 12 of the Blacksmith Fork section. No beds that can be equated to this member appear in the thin Mahogany Canyon section.

INTRASTRATAL DEFORMATION.—Intrastratal deformation is present to some degree throughout the Hyrum and Beirdneau Formations, from beds in the Samaria Member to those just below the "Contact Ledge." The structures vary in size from a few inches to tens of feet. Perhaps the most common form is that of a broken-through, slightly overturned fold, a "fist," but there are also Z-folds, and "roll-ups," where the beds have been turned into a vertical position, and then truncated, perhaps produced when a fist-like structure moved forward and away, leaving only the lower part of the truncated fold (Plate 1: figures 2, 3).

The largest of these structures in the Blacksmith Fork section are present in the Lower Carbonate-Detritus Member, and where the section was measured (Plate 1: figure 2), particularly in Unit 13, but there are similar structures in the Upper Carbonate-Clastic Member—well seen in Logan Canyon, and, on a smaller scale, in the Samaria Member at Portage and in the Beirdneau Formation in Blacksmith Fork and Logan Canyons.

These structures are marked in gray, medium-thick beds of carbonate rock that are separated by thin-bedded units of silty limestone or dolomite weathering light gray or yellowish gray. The transfer of material necessary to produce the deformation appears to have taken place in these thinner beds, while the thicker-bedded, more richly carbonate rocks above accommodated themselves to the flowage underneath. When the contorted beds are exposed to erosion, the thin beds with greater detrital content are recessed, and the thicker carbonate ledges are brought into relief. The greater mobility of the thin beds probably is due both to a greater number of bedding planes and the greater detrital content.

UPPER DOLOMITE MEMBER.—The Upper Dolomite Member repeats the dark gray cliffs of the Lower Dolomite Member, but not so high and with a sharp rectangular profile at the top, in contrast to the rounded profiles of the cliffs in the Carbonate-Detritus members above and below it (Plate 1: figure 3).

The Upper Dolomite Member appears to be the equivalent of the Birdbear Member of the Jefferson as defined by Sandberg and Hammond (1958) and traced into the Blacksmith Fork section by Benson (1966, p. 2588). The thickness of 84 feet measured for this member in the Blacksmith Fork section agrees in general magnitude with the average thickness of 60 to 115 feet reported for the Birdbear Member.

UPPER CARBONATE-DETRITUS MEMBER.—The lighter gray, rounded ledges of the Upper Carbonate-Detritus Member which top the Hyrum Formation in the Blacksmith Fork section (Plate 1: figure 4) are well represented in Logan Canyon and have been recognized in both the Laketown and Portage Canyon sections. In this member the ledge-forming rock is limestone, and the weaker interbeds are dolomitic limy sandstone. Although in lithology this member repeats essentially the Lower Carbonate-Detritus Member, intrastratal deformation is not developed to the same extent as in the lower member.

Since the Birdbear Member marks the top of the Jefferson Formation over a wide area, and since the angular profile of the top of the Upper Dolomite Member in the study area is a readily recognized horizon that could be mapped without difficulty, there are reasons for drawing the upper boundary of the Hyrum Formation at the top of the Upper Dolomite Member. But considering the make-up of the two formations, the Upper Carbonate-Detritus Member essentially repeats the lithology of the Lower Carbonate-Detritus Member. At the same time it is unlike any part of the Beirdneau Formation and, further, it was included in the Hyrum Formation in the original description of the Hyrum and Beirdneau members (Williams, 1948, p. 1140) where Units 7, 8, and 9 are the Upper Carbonate-Detritus Member and Unit 6 is the Upper Dolomite Member. Also, the uppermost limestone bed at the top of the member is as mappable as the top of the Upper Dolomite Member. For these reasons the writer prefers to stay with the original definition of the members, now called formations.

REGIONAL RELATIONSHIPS.—The Samaria Member, the Lower Dolomite Member, and the Upper Dolomite Member appear to have, in a general way, the same lithology as the type Jefferson Formation (Sandberg, 1965, p. 6), and in total they have about the same thickness. The difference between the type Jefferson Formation and the Hyrum Formation might be considered to consist of the introduction of the Lower and Upper Carbonate Detritus members, members that are transitional to the overlying Beirdneau Formation. Mullens and Izett (1964, p. 28) and I seem to have drawn the boundary between the Beirdneau and Hyrum formations at the same position; Benson (1966) appears to have drawn it at the top of the upper dark dolomite cliff and to have thrown the writer's Unit 18 into the Beirdneau Formation. The carbonate-detritus members may represent surges of detrital material from the Stansbury and Uinta Uplifts to the southwest and southeast.

Examination of the section in the Fish Creek Range north of Wide Hollow, Caribou County, Idaho, was disappointing in that the section is so badly faulted and so poorly exposed as to be of little use in stratigraphic studies. The light-colored dolomite in the section (Benson, 1966, fig. 12) which appears to be repeated three times is the Card Member of the Water Canyon Formation. No fossiliferous limestones representing the Samaria Member were seen.

CONDITIONS OF DEPOSITION.—The Hyrum Formation accumulated in a basin at the edge of the miogeosyncline north of the Uinta Uplift (Poole and others, 1967, fig. 9). Other basins in the miogeosyncline farther west accumulated greater thicknesses of sediment during Frasnian time, perhaps with more influence from the Antler Peak orogenic belt. The sea that deposited the formation spread southward and eastward from the miogeosyncline, as reflected in the greater thickness of the Samaria Member in the Portage section. However, the two carbonate-detritus members in the Bear River Range sections appear to represent a more rapid accumulation of detrital material than occurred farther north in the vicinity of the type section of the Jefferson Formation.

In the advancing sea, calcium carbonate mud was the principal sediment, accumulating below wave base, with frequent small impulses of fine detrital material that marked thin beds in the depositing sediment. In these waters lived an epineritic fauna of corals, brachipods, pelecypods, and snails; their remains were buried after transportation by bottom currents for short distances, with the resulting rocks constituting the Samaria Member.

A decrease in the arrival of detrital sediments appears to have coincided with an increase in salinity of the sea water, resulting in the dolomitization of the detritus-free carbonate muds and the production of the Lower Dolomite Member. Dolomitization largely destroyed the fossils, which may have been fairly abundant in these beds, as they are in the undolomitized beds of the Samaria Member. Even under this new regime, there were short periods of large detrital import, producing two thin but notable detrital interbeds. A relatively long period of more rapid detritus arrival interrupted the deposition of the Lower Dolomite Member and originated the Lower Carbonate-Detritus Member.

Near-shore depositional conditions are recorded in the 11-foot sandstone bed, Unit 12, near the base of this member. The sea had become much shallower. Detrital sediment arrived in much larger quantity, and units of carbonate mud were deposited alternately with detritus-rich interbeds. The presence of a slight gradient on the shallow sea floor toward the east set the stage for the intrastratal deformation that marks this member. Before the deposition of the Hyrum Formation had been completed deeper-water conditions returned to create the upper Dolomite Member, and shallow-water conditions were repeated to deposit the Upper Carbonate-Detritus Member. The latter indicates conditions transitional to those that produced the shallow-water Beirdneau Formation.

Beirdneau Formation

General lithology.—The Beirdneau Formation was first conceived and described by the writer as consisting of thin-bedded sandstone (Williams, 1948, p. 1140). The type locality was the Beirdneau Peak trail in secs 16 and 21, T 12 N, R 2 E (SLB&M), north of Logan Canyon. In describing the section in Blacksmith Fork, Mullens and Izett (1964, p. 27) and Benson (1966, p. 2596) pointed out that dolomite is an important part of the formation. The Leatham Formation disconformably overlies the Beirdneau Formation in Blacksmith Fork Canyon.

The Beirdneau Formation (Figure 2), exposed in Blacksmith Fork Canyon, Cache County, Utah, Secs 7, 8, T 10 N, R 2 E (SLB&M), is as follows:

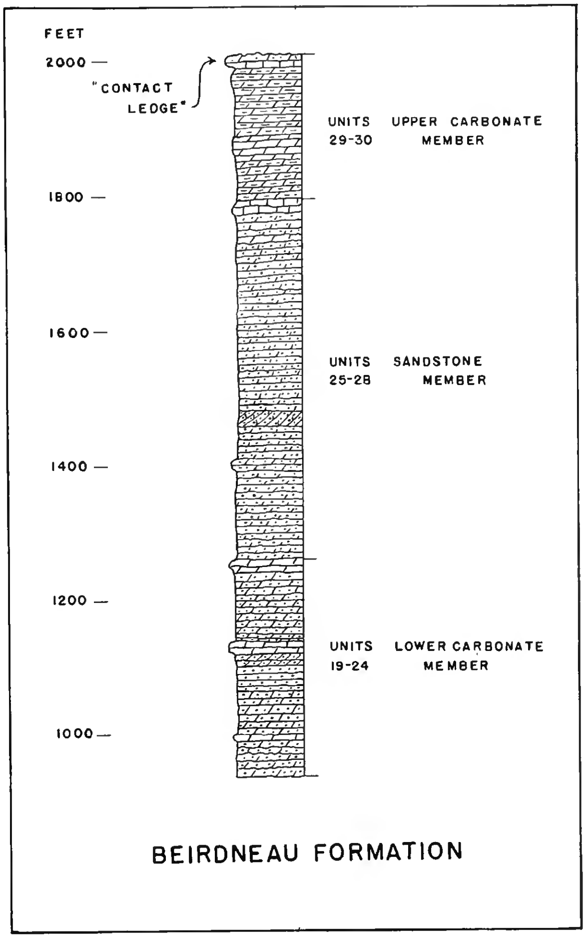

Figure 2.—Stratigraphic diagram of the Beirdneau Formation in Blacksmith Fork Canyon showing lithology and members.

	Thickness	
Unit and Member	*Feet*	*Meters*
Upper Carbonate Member		
30. "Contact Ledge" of limestone, interbedded with some arenaceous calcitic dolomite.	25	7.6
29. Silty or argillaceous calcitic dolomite: thin-bedded, medium light gray and light olive gray, very fine-grained; ripple marks, desiccation cracks; about midway in unit, calcitic dolomite, medium gray to medium dark gray.	200	61.0
Sandstone Member		
28. Dolomitic sandstone and arenaceous dolomite as below, but with some beds of limestone, medium gray, compact with stringers of white chert; also, some beds of dolomite, medium gray, finely crystalline.	135	41.1

Unit and Member	Thickness	
	Feet	Meters
27. Dolomitic sandstone and arenaceous dolomite as in Units 25 and 26, with ripple marks and desiccation cracks common. In parts dolomite, laminated, medium gray, very fine-grained.	160	48. 8
26. Dolomitic limy sandstone in beds of varying thickness, yellowish gray, medium grained, with strongly cross-bedded strata up to one foot thick; ripple marks common; some arenaceous calcitic dolomite as in Unit 25.	93	28. 4
25. Dolomitic sandstone: thin-bedded, light olive gray weathering yellowish gray, ripple marks common. Upper 15 feet arenaceous dolomite, medium light gray weathering yellowish gray.	155	47. 2
LOWER CARBONATE MEMBER		
24. Calcitic dolomite: thin-bedded with bedding planes wavy in part, straight in part; medium gray weathering light olive gray, very fine-grained to compact.	10	3. 0
23. Arenaceous dolomite: uniformly thin-bedded, light gray weathering yellowish gray, very fine-grained with scattered larger grains. Makes blocky cliffs; upper portion medium-bedded.	105	32. 0
22. Calcitic dolomite: thin to medium-bedded, medium light gray, fine-grained. Parts show flowage and contortion.	18	5. 5
21. Calcitic dolomitic sandstone: medium to thick-bedded, light gray weathering yellowish gray, grains a mixture of coarse and medium with fine. Marked cross-bedding, some on a scale of a few inches and some on a scale of several feet. Forms prominent cliff.	56	17. 1
20. Arenaceous calcitic dolomite: thin-bedded, wavy-bedded, light olive gray weathering yellowish gray, very fine-grained to silty; halite casts, ripple marks, desiccation cracks common.	65	19. 8
19. Arenaceous calcitic dolomite: thin-bedded, wavy-bedded, light olive gray weathering yellowish gray, very fine-grained to silty; halite casts, ripple marks, desiccation cracks common. Unit is topped by 2-foot bed of dolomite: medium gray; finely crystalline.	65	19. 8
TOTAL	1087	331. 3

The thickness of the Beirdneau Formation is of immediate interest because it varies substantially in the course of a few miles along the north side of Blacksmith Fork Canyon. Mullens and Izett, measuring in sec 1, T 10 N, R 1 E, obtained 699 feet; Benson, at the same locality, recorded 777 feet. The writer, seeking excellent exposures lower in the canyon, measured the lower part of the section in NE¼ sec 7 and the remainder in NW¼ sec 8, T 10 N, R 2 E. Here the total thickness is 1,087 feet. Because of these differences, the writer's measurements were carefully checked. Eastward at the forks of Blacksmith Fork Canyon, in sec 3, T 10 N, R 2 E the thickness is 937 feet. Since at all three localities along the north side of Blacksmith Fork Canyon the formation is capped by the "Contact Ledge" beneath which are other parts of the Upper Carbonate Member, it must be concluded that the formation actually was deposited to a greater thickness in the middle section—opposite the reservoir in the canyon—than to the west or the east.

Other thicknesses (by the writer's measurement) of the Beirdneau Formation in the study area are Logan Canyon, 651 feet; Laketown Canyon, 524 feet; and Gardner Canyon, Idaho (Beus, 1968, p. 791), 808 feet. At the latter two localities the "Contact Ledge" limestone was not recognized, but there was an increase in carbonates in the upper part of the section, indicating the presence of at least part of the Upper Carbonate Member.

LOWER AND UPPER CARBONATE MEMBERS.—The lower 319 feet of the formation is distinguishable from the thicker middle member (Figure 2) by the presence of several units of medium gray or medium light gray dolomite or calcitic dolomite that are thicker-bedded and more resistant to erosion than the thin-bedded arenaceous calcitic dolomite or calcitic dolomitic sandstone that makes up most of the formation. These differences justify the designation of the member as the Lower Carbonate Member (Plate 1: figure 4).

Again in the upper 225 feet of the formation the rocks become generally grayer and the ledges steeper and more resistant as the carbonate content of the formation increases (Plate 1: figure 5). Hence, the upper member has been designated the Upper Carbonate Member. Here the characteristic rock type is silty or argillaceous calcitic dolomite, medium light gray or light olive gray.

SANDSTONE MEMBER.—The middle portion of the formation, where the clastic content is highest, has been designated the Sandstone Member (Plate 1: figure 5). Here thin-bedded dolomitic sandstone and dolomitic limy sandstone predominate over arenaceous dolomite and over the few thin beds of dolomite and

Plate 1.—Members of Hyrum and Beirdneau Formations. Figure 1.—Blacksmith Fork Canyon. Between markers, from bottom to top, are Lower Dolomite Member, Lower Carbonate-Detritus Member, Upper Dolomite Member, Upper Carbonate-Detritus Member of Hyrum Formation. 2. Blacksmith Fork Canyon. Between markers is Lower Carbonate-Detritus Member of Hyrum Formation with intrastratal deformation. 3. Logan Canyon, Hyrum Formation. Between markers is Upper Dolomite Member; beneath it is Lower Carbonate-Detritus Member with intrastratal deformation. 4. Blacksmith Fork Canyon. Between markers is Upper Carbonate-Detritus Member of Hyrum Formation; above it is Lower Carbonate Member of Beirdneau Formation. 5. Blacksmith Fork Canyon. Between markers is Upper Carbonate Member of Beirdneau Formation (with "Contact Ledge" at top); below it is Sandstone Member. 6. Portage Canyon. The three ledges of the Samaria Member.

limestone that are present. Unit 26, with its medium-grained sandstone, strongly cross-bedded in part, marks the maximum deposition of clastic material in the formation. This unit probably correlates with the 60-foot orthoquartzite unit that Beus (1968, p. 790) recognized from Gardner Canyon, Idaho to Little Mountain, Utah.

REGIONAL RELATIONSHIPS.—Despite variations in thickness, the Beirdneau Formation appears to maintain its tripartite character from the Bear River Range localities northward and westward into Idaho. All three members are recognizable in the Portage and Gardner Canyon sections.

In the Laketown Canyon section to the east, the midpart of the section representing the Sandstone Member of the Beirdneau Formation is occupied by massive beds of limestone intraformational breccia. The limestone is silty and light brown to pale yellowish brown, and it may well be a solution breccia representing the Logan Gulch Member of the Three Forks Formation. At the upper and lower parts of the section, the lithology is more like that in the Blacksmith Fork section. The Laketown Canyon section then is transitional between the facies of western Wyoming and those of the Beirdneau Formation. From this point northeastward, the term Three Forks is appropriate, but westward the term Beirdneau can replace it.

In Mahogany Canyon north of Morgan, the Beirdneau Formation is only about 200 feet thick, but it consists largely of sandstone and probably represents the shore zone of the late Upper Devonian sea at its maximum transgression onto the Uinta Uplift.

It appears that the Lower Carbonate Member followed by the Sandstone Member of the Beirdneau Formation may reflect the filling of the intracratonic basin, as it happened in Montana (Sandberg and Mapel, 1967, p. 873), and the spread of evaporite precipitation from the type area of the Logan Gulch Member of the Three Forks Formation. Evaporite precipitation reached as far south as Laketown Canyon. The climax of the recession may be represented in the strongly cross-bedded sandstone of Unit 26. The upper Carbonate Member may reflect the widespread transgression that produced the Trident Member of the Three Forks Formation (Sandberg and Mapel, 1967, p. 874). More particularly, the two lower members of the Beirdneau Formation would represent the argillaceous dolomite facies of the Logan Gulch Member (Benson, 1966, p. 2595) modified by the addition of more and coarser clastic material. The Upper Carbonate Member would represent the carbonate facies of the Trident Member (Benson, 1966, p. 2597).

CONDITIONS OF DEPOSITION.—The thin-bedded argillaceous and silty dolomites and dolomitic sandstones that make up the Beirdneau Formation appear to represent generally fine-grained, probably partly autocthonous and partly allocthonous sediments deposited in a very shallow, epineritic area which sank steadily but slowly. The bottom of this very shallow sea was occasionally exposed by neap tides and off-shore winds, causing the formation of dessication cracks, and the growth of skeletal halite crystals in the fine muds. Most of the time, moderate to weak currents in the shallow water, probably largely of tidal origin, formed ripple marks and from time to time received greater amounts of noncarbonate clastic material, resulting in more silty and sandy beds. Disturbance of the bottom produced intraformational breccias and microdeformation during storms or particularly strong tides. Continuous arrival of sedimentary material and frequent disturbance of the bottom by tidal currents probably account for the lack of fossils. The bottom of the Beirdneau sea was generally a marine desert (Bowsher, 1967, p. 341). During the deposition of Unit 26 the currents were much stronger, the supply of sand was much greater, and marked cross-bedding was produced. In this unit thin beds of light-colored, structureless, medium-grained sand may represent discontinuous deposits of aeolian origin and mark the presence of the littoral zone.

The fine clastic material probably came to this shallow coastal area from the south and southwest, where and areas existed in Beirdneau time (Rigby, 1959, p. 213) and where the shoreline was never more than a few tens of miles away.

AGE OF THE BEIRDNEAU FORMATION.—The Beirdneau and Hyrum Formations are comformable throughout the study area, with the possible exception of the Morgan section. At all other localities deposition appears to have been continuous from Hyrum into Beirdneau time and the lithology of the Upper Carbonate-Detritus Member is transitional to that of the Beirdneau Formation.

The Middle Devonian (Givetian) age of the Samaria Member of the Hyrum Formation has been discussed. Above this basal member the writer has not collected any fossils except at the very top of the Beirdneau Formation, where *Cyrtospirifer* and a rhynchonellid brachiopod are common. These represent a fauna which, according to Sandberg and Mapel (1967, p. 869), is equivalent to that of the *Cyrtospirifer monticola* Zone. Thus, the top of the Beirdneau is lower Famennian; Frasnian and earliest Famennian times are represented in the Hyrum Formation above the Samaria Member and in the Beirdneau Formation.

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Ellis L. Yochelson

A New Late Devonian Gastropod and Its Bearing on Problems of Open Coiling and Septation

ABSTRACT

Nevadaspira cooperi is described from beds of late Frasnian age in the upper Devils Gate Limestone exposed in the southern part of the Spotted Range, Nye County, Nevada. The genus, so far, is known from a single species, confined to the type locality. Specimens of *N. cooperi* have characteristics atypical of gastropods in that the whorls are not in contact and they contain numerous septa.

Open coiling may come about through one or more different geometries of growth. There may be a minimum limit to the logarithmic spiral in open coiling, because shell forms that expand rapidly are unknown. The septa in *N. cooperi* are more closely spaced than in any other known genus. The whole question of why septa are produced is debatable. It may be that septa strengthen the shell, but there are so many septa in Devonian specimens that they may have served to keep the body relatively small as the shell grew. The open-coiled gastropods could have been sedentary in habit.

In 1965, during stratigraphic investigations at the Nevada Test Site, F. G. Poole, United States Geological Survey (USGS), discovered a most interesting fossil mollusk. The specimens superficially resemble cephalopods, but are actually atypical gastropods which are open coiled and multiseptate. These characters are unusual enough to warrant the naming of a new genus.

Appreciation is expressed to Prof.-Dr. H. K. Erben, Institut für Paläontology, Bonn, Germany; to Prof.-Dr. Ulrich Jux, Geologisches Institut, Cologne, Germany; and to Dr. William Ball, Keeper of Palaeontology, British Museum (Natural History), for lending specimens of *Straparollus* (*Serpulospira*) under their charge for comparison. Drs. Robert M. Linsley, Colgate University, and David M. Raup and Steven Stanley, both of the University of Rochester, discussed the problems associated with this unusual genus. It is particularly appropriate that a Devonian form be named for G. Arthur Cooper, of the United States National Museum (USNM).

Occurrence and Age

A few specimens of this genus were first collected in the Spotted Range, within the Mercury 7½-minute quadrangle, in Nye County, Nevada, during 1965. Because the area contains virtually no human habitations or artificial landmarks, a locality description is difficult. Geographic coordinates of the locality, USGS 7601–SD, are 36°39′05″ N and 115°54′44 W. Specimens are in a dense, dark-gray, coarse-grained limestone in the Devils Gate Limestone, 110 to 115 feet below the top of the formation. They are exposed on a dip slope and practically none weathers free. The shell adheres tightly to the matrix and exfoliates from the steinkern during weathering or preparation.

In spite of the difficulty in obtaining specimens from this massive limestone, Poole in 1966 was able to obtain sufficient material on which to base a meaningful concept of the species. Without his efforts, this study would

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not have been possible. Specimens of this taxon have not yet been collected outside the type locality. This fossil is so distinctive that the genus may be easily identified in the field, and Poole (personal communication, 1968) reports its probable occurrence in the Pahranagat Range, Lincoln County, Nevada; eventually it may be a useful fossil for local correlation.

Stratigraphically higher beds at this locality contain numerous brachiopods. J. Thomas Dutro (personal communication, 1968) identifies *Cyrtospirifer* cf. *C. portae* Merriam as the principal species in these beds. Rare athyrids, *"Cleiothyridina"* cf. *"C." angelicoides* (Merriam), also are present. Dutro further states: "This assemblage represents the *Cyrtospirifer* zone of Merriam in a broad sense. It is most likely of late Frasnian age." According to Poole (personal communication, 1968), *Cyrtospirifer* occurs throughout a "clayey limestone unit" at the top of the Devils Gate Limestone. He notes that the multiseptate gastropods occur near the boundary between the *Cyrtospirifer*-bearing unit and an underlying unit of cliff-forming limestone (see Poole and others, 1967, p. 885, fig. 26, column 12.)

Superfamily EUOMPHALACEA de Konnick, 1881

Family EUOMPHALIDAE de Konnick, 1881

Nevadaspira, new genus

DIAGNOSIS.—Large, very slightly hyperstrophic, open-coiled euomphalid gastropods; whorl section suboval with a greatly thickened upper angulation; early part of whorls containing numerous concave septa.

TYPE-SPECIES.—*Nevadaspira cooperi* new species.

DISCUSSION.—The hyperstrophic open coiling immediately differentiates this new genus from all other described Devonian gastropods. It shows a slight resemblance to *Straparollus* (*Serpulospira*), but that taxon is orthostrophic in coiling; for comparison, see Plate 1: figures 1, 2.

Nevadaspira bears more similarity to Ordovician open-coiled forms but can be distinguished readily from two of the three genera that show this feature. *Calaurops* has a flattened whorl profile and a more rapidly expanding coil. *Lytospira* is more strongly trochoid in coiling. Differentiation from *Ecculiomphalus* is exceedingly difficult, except for the difference in age between Early Ordovician and Late Devonian. *Ecculiomphalus* may be conveniently distinguished as having a smaller number of septa—though this may be a spurious character—and in having a generally smaller average size for specimens; the inclination of the lower part of the outer whorl face also may be greater in that genus. Rate of logarithmic expansion may be different in the two genera, but little is known of the taxonomic significance or variability of such a feature. Most *Ecculiomphalus* specimens are steinkerns, thus making comparison of whorl profiles impossible.

This new genus is known only from the type-species.

Nevadaspira cooperi, new species

PLATE 1: FIGURES 3–8; PLATE 2: FIGURES 1–3

DESCRIPTION.—Hyperstrophic open-coiled gastropods with a prominent acute angulation in the upper whorl profile and numerous partitions within the early part of the whorl.

Earliest growth stages unknown. Juvenile through mature stages open-coiled, the angle of tangency of the logarithmic spiral greater than 80°. Upper surface of shell distinctly concave; lower surface very slightly convex, expanding in essentially one plane for most of the growth and being only very slightly hyperstrophic.

Upper whorl surface profile straight, inclined upward and outward (at an angle of nearly 30° from horizontal) to the wide bluntly rounded outer angulation; lower edge of angulation probably forming the periphery, outer whorl face profile below nearly verti-

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PLATE 1: figures 1,2.—*Straparollus* (*Serpulospira*) *centrifuga* (F. A. Roemer). Two specimens (× 1.5) showing variation in coiling; from Upper Givetian, Bücheler beds, at Büchel, Herrenstrunden (Bergisch Gladbach), Germany; in collection of the "Naturfreunde," Cologne, Germany.

Figures 3–8.—*Nevadaspira cooperi* Yochelson, new species. 3a,b, Two sides of a rock (× 1) broken at essentially right angles to the plane of coiling (the white dot near the center is the calcite filling of an inner whorl): holotype, USNM 164181. 4, Fragment of a steinkern (× 1.5) showing the whorl profile (specimen has been tilted slightly with reference to figure 3); paratype, USNM 164182. 5, A natural section (× 1) in which some septa may be observed at lower right; paratype, USNM 164183. 6, A large natural section (× 1) in which the earlier whorls are filled with recrystallized calcite; paratype, USNM (164184. 7, Polished section (× 1.5) of a whorl fragment; paratype, USNM 164185. 8, Thin section (× 2) of a juvenile specimen; paratype, USNM 164186.


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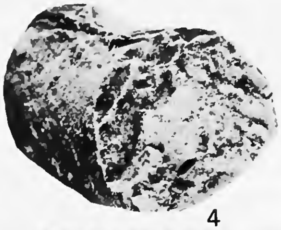
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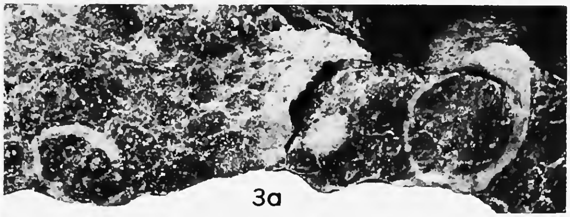
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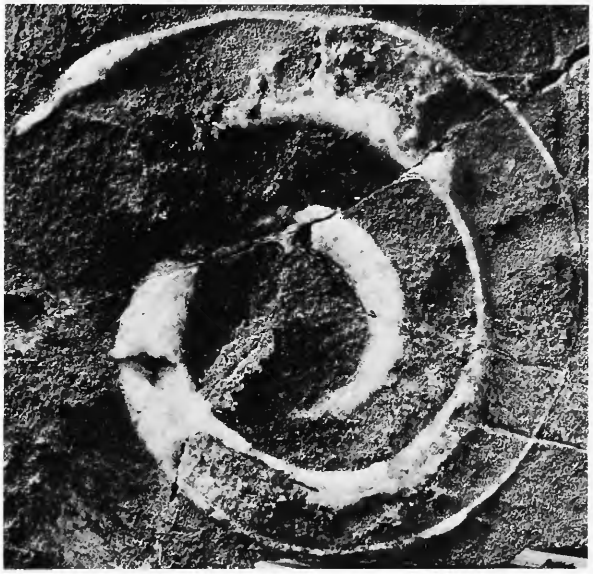
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PLATE 1

cal for approximately half of total length, curving downward and inward below midwhorl; outer basal angulation obtuse, near 140°, basal surface essentially straight; inner basal angulation also obtuse, near 120°; profile in inner whorl face a gentle curve deviating little from a straight line inclined inward and upward to its abrupt juncture with the upper whorl face, the total length of this inner face about half of the outer face.

Profile of steinkern deviating only slightly from circularity, but reflecting the inner basal angulation. Shell probably of two layers: inner layer thin and relatively constant in thickness; outer layer varying markedly, being thin on the inner whorl face and the basal face, except at the basal angulation, thick along the outer face, especially along the upper one-third of its length, and very greatly thickened below the upper angulation.

Penultimate and earlier whorls filled with calcium carbonate, interrupted by dark-colored septa; individual septum exceedingly thin in section, concave forward following the arc of a circle for about one-third of its circumference, presumably a truncated hemisphere when viewed in three dimensions; septa closely, but irregularly, spaced.

Growth lines and apertural details unknown; ornament unknown, but presumed absent.

Discussion.—Although this species originally was known from half a dozen specimens, F. G. Poole subsequently collected more than two dozen additional specimens at the original locality. Because both collections were made by the same person from essentially one bed through a five-foot interval, all material has been combined under a single locality number. Most specimens apparently occur base downward on the bedding surface, in a matrix of dense light-gray limestone. Many individuals have the upper part of the whorls worn away, exposing the prominent septation seen in some weathered specimens.

A few fragmentary steinkerns weather free on the outcrop (Plate 1: figure 4), but these are not particularly useful for study. The specimens are best studied by polished and thin sections, which give a good idea of internal details but do not indicate the cross section. Fortunately, two specimens do show the cross section (Plate 1: figure 3a,b), and much of the description of this important feature is based upon them.

The specimens vary widely in preservation. For the most part, those that have the upper surface weathered away show only coarse calcite filling the inner part of the whorl (Plate 1: figure 6; Plate 2: figure 2). However, exceptional specimens do show septa standing in relief (Plate 1: figure 5). Even in the sectioned material there is considerable variation in preservation. Although almost every specimen of the early whorls shows some partitioning, the number and distribution of septa vary. One is led to the conclusion—expressed earlier when a study was made of a limited number of specimens of *Omphalocirrus goldfussi* (Yochelson, 1966, p. 44)—that diagenetic changes may alter the number of septa that may be observed, or may even destroy all trace of such features (Plate 2: figure 3).

Even though no operculum is known, the species is considered to be hyperstrophic rather than sinistrally coiled. In general shape and whorl profile it is similar to most euomphalaceans, and these are conventionally oriented as normally coiled, nonsinistral gastropods.

Types.—Holotype, USNM 164181. Paratypes: USNM 164182–8 (figured); USNM 164189a–z (not figured). As 17 additional specimens are too poorly preserved to have played a part in this study, they are not designated as paratypes. All of the specimens of this new species illustrated in Plates 1 and 2 are from USGS loc. 7601–SD, described above.

Review of Literature

No described species referable to the new genus *Nevadaspira* were found in the American and European literature examined. References to early and mid-Paleozoic open-coiled gastropods are scattered. With the exception of this Nevada material, all described Devonian species might be placed within *Straparollus* (*Serpulospira*), although they presently are under a variety of generic names. All the species appear to have in common early whorls in contact, orthostrophic coiling, and a generally oval to circular cross section. The one apparent exception is the recently named *Strapa-*

Plate 2.—*Nevadaspira cooperi* Yochelson, new species. 1a–c, Paratype, USNM 164187: 1a, thin section (× 2) showing numerous septa; 1b, enlargement showing some details of the walls and septa (× 5); 1c, the septum at the body chamber and five earlier septa (× 10). 2, A broken specimen (× 1) that has been partly smoothed to show the calcite in the early whorls; paratype, USNM 164188. 3, Enlargement (× 15) of figure 8 on Plate 1; near the center on the left wall is a septum that has been destroyed in the recrystallized calcite between more prominent septa.

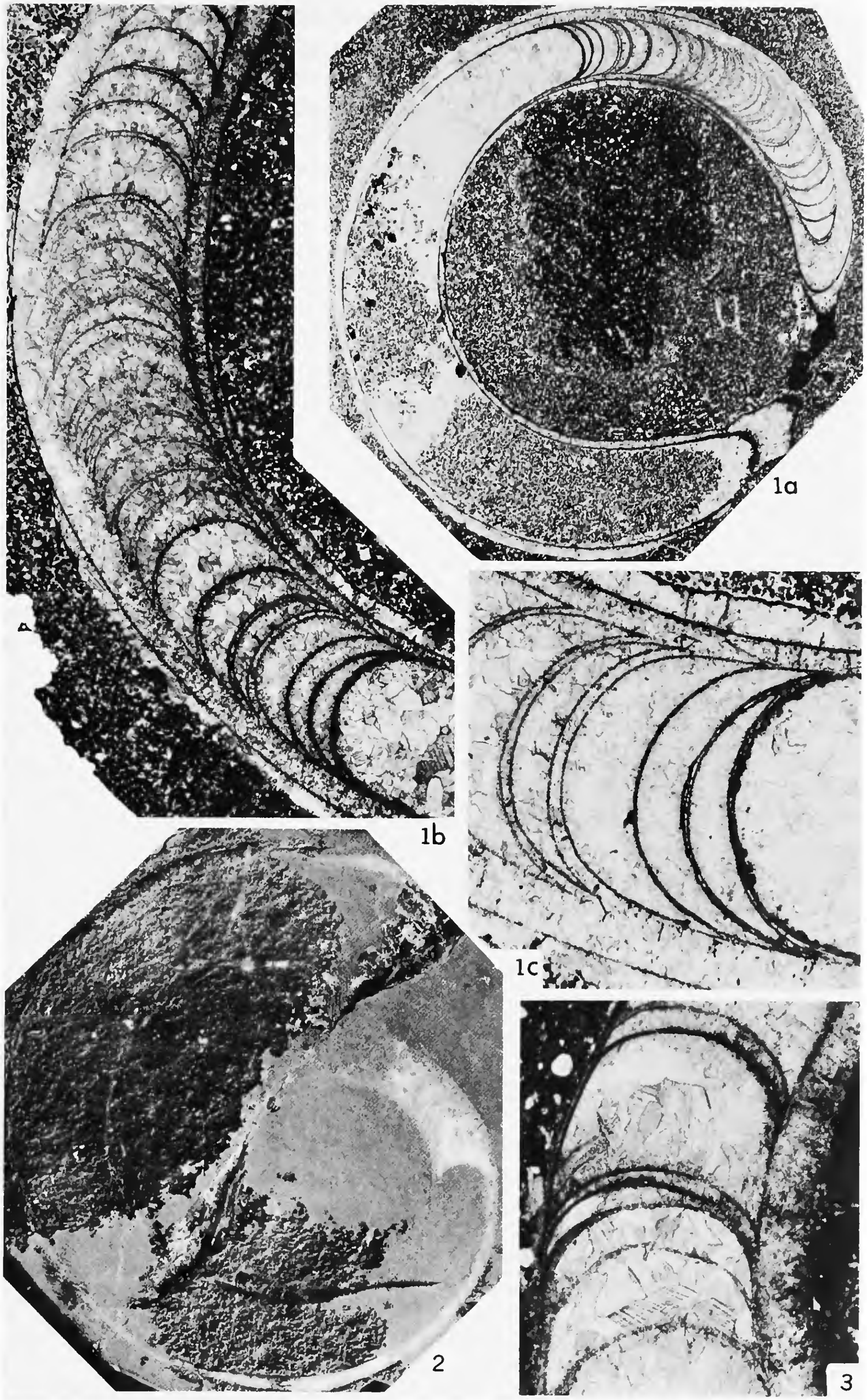

PLATE 2

rollus (*Sinistrispira*) (Jhaveri, 1969, p. 163), from the Early Devonian of the Carnic Alps; it is described as having an oblique oval cross section, but this feature is not illustrated and no close comparison to *Nevadaspira* can be drawn. Any projected revision of open-coiled species, however, should include examination of specimens as well as literature.

A problem may result when coiling is close to a plane of bilateral symmetry. So far as known, open-coiled nautiloid cephalopods invariably show bilateral symmetry, and open-coiled euomphalaceans invariably show asymmetry. The differences between these two modes of coiling may be slight, and both shell forms may become deformed after death. Some authors illustrate only a top view of specimens, so the degree of coiling in the third dimension, if any, cannot be determined. It is quite possible that a few Paleozoic open-coiled "gastropods" actually are bilaterally symmetrical cephalopods and are not correctly assigned on the class level.

A second problem is loss of one or both shell layers from a fossil; this is particularly common among the euomphalaceans. In at least one species the outer shell layer is calcite and the inner layer aragonite (Yochelson, White, and Gordon, 1967); if this is a superfamilial characterisitc, it might explain some of the peculiarities of preservation encountered within the group. In a classic case, Philip and Talent (1959, pp. 50–52) were able to duplicate a shell referable to the Early Devonian open-coiled *Liomphalus* Chapman by breaking off the outer shell layer of a specimen of *Straparollus* (*Euomphalus*) *northi* (Etheridge), thus demonstrating the spurious nature of Chapman's generic concept. The effect of loss of a potentially great thickness of outer shell should always be considered before assuming that a specimen is open coiled. In addition to open coiling, an inner shell may show a profile different from that of the outer shell (Yochelson, 1956, p. 216).

Open Coiling of Gastropods

In many introductory courses in invertebrate paleontology, the hard parts of gastropods are treated as shells characteristically trochoid in shape, that is, coiled in a third dimension without bilateral symmetry. In partial contrast, cephalopods are considered as bilaterally symmetrical shells which may change from straight orthocones, through curved shells to those tightly coiled. The exceptions to both generalizations seldom are emphasized. For example, shells of most bellerophontacean gastropods are bilaterally symmetrical; as a consequence, they occasionally are confused with cephalopods. Also, shells that deviate only slightly from this plane of symmetry may be misinterpreted as symmetrical.

Raup (1966) has discussed and clarified geometry of coiling in detail. For this paper, it is appropriate merely to mention some simple generalizations concerning gastropod coiling. The gastropod shell may be considered as a cone expanding at a uniform rate. The cone (shell) is curved, and the curvature follows a logarithmic function in almost every case. The cone may be bilaterally symmetrical (isostrophic). More typically, however, the cone is also inclined into a third dimension with this deviation from a plane of symmetry also varying at a logarithmic rate. Following conventional English and American orientation, almost all shells curve downward (orthostrophic) to the right (dextral) or, less commonly, to the left (sinistral). Far less commonly they may curve upward (hyperstrophic) and to the right or to the left. All the possibilities are illustrated by Knight (1952, p. 8), but it should be emphasized that hyperstrophic coiling is atypical.

Gastropod shells generally have the individual whorls in contact, and it is the exceptional shell in which the latest (body) whorl does not impinge upon, or at least touch, the preceding (penultimate) whorl. It is also the exceptional shell that does not following a logarithmic function throughout most of its growth. Once the postjuenvile stage is past, allometric change is rare, especially among the more primitive Paleozoic gastropods.

Some gastropods, for example the Holocene *Vermetus*, grow irregularly once the very early stages are passed. This is a consequence of their habits of cementing the apex of the shell and, in part, of growing in dense colonies. In addition, occasional extremely large individuals in many diverse groups may have part or all of the body whorl free; and irregularity in growth lines, thickened shells, and other features indicate that the free body whorl may be aerontic condition. In descriptions of either the exceptionally old shells or the profound deviations caused by changes in life habit, terms such as "disjunct" or "uncoiled" should be used as adjectives to describe such changes in shape.

On the other hand, I propose to use the term "open-coiled" to designate those gastropod shell forms that fail to have some or all of the whorls in contact but that do not obviously deviate from logarithmic factors in rate of coiling. Unfortunately, only a few well-preserved specimens exist, and, so far as I know, no detailed mathematical studies have been made of such forms. As a consequence, the opinions given here are unsupported by any except the most qualitative of data.

Raup (1966) distinguishes four variables in coiling. The shape of the whorl (S) is basic to gastropod morphology, but this feature may be ignored here because it has little significance in interpreting the phenomenon of open coiling. The other three geometric components are: expansion rate of the whorl (W), distance of each whorl from the axis (D), and translation into the third dimension around the axis of coiling (T). In bilaterally or nearly bilaterally symmetrical shells, the angle of tangency of the logarithmic spiral varies inversely to (W).

Open coiling may occur if any of these components is large enough to prevent contact of the whorls. For convenience, the most obvious case is discussed first. Many Paleozoic Platyceratacea show relatively simple open coiling. This is especially evident in species of *Platyceras* (*Orthonychia*). The shells are all high-spired and are coiled through more than one whorl. The whorls are not in contact because the factor (T) is so large. In effect, the form has simply been elongated so that whorls do not touch. Were the specimens lower spired, the whorls would be in contact. In this factor of coiling, the Paleozoic *Orthonychia* show geometric similarity to the unrelated *Vermicularia* through part of its growth, except that representatives of the Holocene genus have a far greater number of whorls.

In isostrophic shells, such as the bilaterally symmetrical Bellerophontacea, translation (T) is not a factor, and open coiling could come about through either an increase of each whorl in distance from the axis (D) or in expansion rate of the whorl (W), or by a combination of both factors. However, no open-coiled Bellerophontacea are known.

Within the Macluritacea, the members of which are not characteristically open-coiled, the genus *Macluritella* has whorls that are not in contact. The whorl profile of *Macluritella* is very low, and for practical purposes the shell may be considered as nearly isostrophic. The rate of coiling of *Macluritella* is normal for a gastropod, and the only unusual feature is that the whorls do not quite touch. If the whorls were only slightly larger in cross section—that is, if (W) were decreased slightly—they would be in contact, and *Macluritella* would be an otherwise undistinguished member of the Macluritacea.

Among the Paleozoic gastropods, the greatest variety of open-coiled forms occur within the Euomphalacea. In particular, the orthostrophic coiled *Straparollus* (*Serpulospira*) contains species which appear to have variations of both (D) and (T) components. An excellent example has been described by Linsley (1968, pp. 375, 376) from the Middle Devonian Anderdon Limestone Member of the Lucas Formation in Michigan. Judging from other gastropods, his specimens of *Serpulospira* show enough variation in shape to be placed in a minimum of four species, but because they all were obtained from a small outcrop area and there is a suggestion of intergradation one may alternatively conclude that they all belonged to a single biologic population. The large variation in height of spire and openness of coil may be the result of relatively trivial changes in geometric components which are not, in themselves, significant. The few European specimens of *Serpulospira* that I have examined also show a remarkably high degree of variability and reinforce Linsley's observation. Clearly, variation within gastropod species tends to become stretched beyond normal limits when open coiling becomes a factor in gastropod morphology.

Hyperstrophic coiling seldom leads to the same amount of variation in shape as does orthostrophic coiling. Hyperstrophic gastropods with a higher spire than *Serpulospira* are very rare in the fossil record. Open-coiled hyperstrophic genera have a base that is essentially flattened, or very nearly so. The factor (T) cannot be completely ignored, but it is so small in *Nevadaspira* that it cannot possibly account for much of the openness of coil. In fact, so far as one can tell in *Nevadaspira* and its allies, (T) is so small and constant that it is not responsible for any of the whorl disjunctness.

Although most hyperstrophic open-coiled specimens are incomplete, enough is known of *Nevadaspira* to permit some measurements. By ignoring (T) and assuming that all coiling is in a single plane, Raup (personal communication, 1968) was able to measure the angle of tangency of the logarithmic spiral as near 83° In his terminology, assuming (T) as zero, (D) is 0.64 and (W) is 2.1. However, if (D) were decreased to 0.48, the whorls would be in contact; if (W) were decreased to 1.56, the whorls again would be in contact. In more general terms, assuming isostrophic coiling and a circular cross section, if (D) is greater than (1/W) or if (W) is greater than (1/D), the shell will be open-coiled.

By way of comparison with *Nevadaspira,* several species of typical tight-coiled Permian Euomphalidae have a logarithmic spiral angle that varies between 79° and 84° (Yochelson, 1956); these earlier measurements are not as accurate as those of Raup. Other Ordovician open-coiled gastropods such as *Lytospira* and *Ecculiomphalus*—which were particularly well illustrated by Knight (1941, pl. 71) to show hyperstrophic coiling—also have logarithmic spirals close to 80°. The early Carboniferous *Phanerotinus* also has a similar angle of tangency.

It is evident, therefore, that in some factors of coiling *Nevadaspira* and similar forms are not distinguished from other Euomphalidae. *Nevadaspira* is open-coiled not because it curves in an atypical manner but because the whorls are so narrow in cross section that they do not touch. If the whorls were just a bit wider, the external morphology of this gastropod would hardly be worthy of a second glance. In essence, *Nevadaspira* is too narrow a cone to expand at the rate at which it does and still have the whorls in contact. The "error," if that word is proper, lies with the inner edge of the whorl, not the outer and certainly not with a dramatic change in the logarithmic spiral.

In his review of the curvature of nautiloid shells, Flower (1955) suggested that some sort of "saltation" was involved. All known nautiloid shell forms are straight or slightly curved on one hand, or fairly strongly curved with the whorls varying from no contact to tightly coiled, on the other. Flower attributed the absence in the fossil record of any nautiloid shell with intermediate curvature to possible difficulty the animal might encounter in contact with the bottom. Although this important idea has been virtually ignored, Raup (1967) has provided strong support for the concept by noting that of the many theoretically possible geometric shapes available for coiled ammonoids, there is a distinct preference for a limited number of general shapes and an apparent absence in the fossil record of some of the theoretically possible shapes.

Another remarkable Devonian open-coiled genus is *Mastigospira* (La Rocque, 1949). Specimens are large and show such a slight degree of curvature that for many years they were assumed to be straight and were assigned to *Hyolithes,* a mollusk unrelated to the Gastropoda. This slight logarithmic curvature stands in marked contrast to all the open-coiled but strongly curved shells discussed above. The German Devonian *Odontomaria* also might be a slightly curved euomphaloid, or a calcareous worm tube.

I have found no gastropods that show logarithmic curvatures bridging the pronounced morphologic gap between very slightly curved and strongly curved shells. Except for the strikingly atypical *Mastigospira* and the less well known *Odontomaria,* open-coiled Paleozoic gastropods are like other gastropods in being strongly curved.

There has been a tendency in classification (Knight, Batten, and Yochelson, in Moore, 1960) to differentiate between tightly coiled and open-coiled gastropods so that such diverse forms as *Nevadaspira* and *Mastigospira* are lumped together. The range of curvature theoretically available between that of a few degrees, as in *Mastigospira,* and that of 75° or greater may not be represented in the shell-bearing gastropods. The concept of a "saltation" in logarithmic curvature has not hitherto been applied to interpretation of gastropod shapes, but I suspect that this idea may provide a fruitful field for future investigation.

Whorl Blockage in Paleozoic Gastropods

Another myth perpetuated in beginning paleontology courses is that cephalopods are readily distinguished from gastropods by the presence of septa. Actually, it has long been known that some gastropods contain septa. Only one feature distinguishes a cephalopod shell from a gastropod shell—the "key" characteristic of having the septa pierced by a siphuncle. Because the prime significance of this feature was not properly emphasized, d'Orbigny and other early workers confused bilaterally symmetrical bellerophontaceans with cephalopods. *Nevadaspira* is nearly bilaterally symmetrical and has septa, but it definitely is not a cephalopod because it lacks a siphuncle.

Septa occur in a variety of gastropod shell shapes in specimens from rocks at least as old as Early Ordovician. So far, they are known from members of the Euomphalacea, Pleurotomariacea, and Loxonematacea. There is an increasing suspicion that simple presence or absence of septa may be a particularly poor taxonomic criterion at all levels of classification. In septate specimens assigned to the last two superfamilies, the septa appear to be confined to the early whorls. So few good examples are known that one cannot be certain whether a single septum occurs, whether a few septa are present, or whether the early whorl is filled entirely with calcite, ending at a rounded partition. No particular advantage appears to have been gained by sealing off the soft parts from the early whorls.

So far as known, extensive septation in the Paleozoic gastropods is confined to the Euomphalacea, although some typical tight-coiled *Straparollus* (*Euomphalus*) appear to show only juvenile whorl septation. This stands somewhat in contrast to the hyperstrophic open-coiled specimens which, when well preserved, show more than half-a-dozen septa. Any generalization must be approached with caution, for it has been demonstrated that septa originally present in a tight-coiled euomphalid may be destroyed during diagenesis and not appear in an average specimen (Yochelson, 1966).

Virtually nothing is known about ontogenetic changes in the number and spacing of septa, let alone about individual variation in these features. Several specimens of the Early Ordovician *Ecculiomphalus* give an impression of uniform or logarithmic spacing of septa. The numerous specimens of *Nevadaspira* do not give such an impression of regularity, even if one makes allowance for possible erratic destruction of septa after the death of the individuals. Although the evidence is not sufficient to build a firm interpretation of septal distribution, I suggest that the data from the *Nevadaspira* specimens point to randomness in distribution of septa in all known open-coiled gastropods.

An open-coiled form appears to be more fragile than a tightly coiled one. Accordingly, one might conclude that the multiseptate condition is a device for strengthening the shell, an opinion that has been advanced by some authors as the explanation for cephalopod septation. The sediment in which *Nevadaspira* occurs, and that of many of the occurrences of the Early Ordovician *Ecculiomphalus,* gives no indication, however, of a high-energy environment that would require strengthened shells.

At least one example of a large number of septa in a tightly coiled shell is known. The paratype of *Arctomphalus grandis* Tolmachoff, a Middle Devonian species, shows at least ten septa irregularly spaced at intervals averaging about 2.5 millimeters (Yochelson, 1966). These septa occur in a part of a whorl intermediate in size; dozens may be present in the earlier whorls. If strengthening an open-coiled shell is the primary reason for multiple septa, there should be no need for the closely spaced septa in a tightly coiled form. This does not, in itself, disprove the need for strengthening, but it does cast some doubt on the suggestion. Finally, gastropod shells commonly are thicker than cephalopod shells and probably do not need internal strengthening. I suggest that strengthening of the shell is at best a secondary result and that a more basic reason for septation lies elsewhere.

It is placing the cart before the horse to think of growth of body mass as keeping up with the rate of tube growth, for it is the soft parts that build shell, not vice versa. However, this change in outlook may illustrate a point. When septation occurs, the body no longer occupies the early part of the shell. Septation allows a smaller than average body mass to function within the shell. For septation confined to the early part of the shell, this is a trivial effect, but it is not a minor feature at more advanced growth stages. Repeated septation obviously is not detrimental to life, for the existence of the multiseptate fossils proves this.

It is well known from the most elementary growth studies that volume increases more rapidly than surface area. One result of the body mass moving forward in the tube is that expansion of its mass need not follow anything approaching a circumference to area ratio. Rather, the volume addition would be smaller than this ratio and would tend to approach the rate of shell addition. Eliminating the need for a greatly elongated body mass actually may allow for greater efficiency in construction of the shell.

Septation or partitioning carries with it the concept of an open space between partitions. In cephalopods, camerae automatically develop each time a partition is inserted. It is reasonable to question whether septation in gastropods is really the same as septation in cephalopods or simply appears to be the same. If septation is taken to include both the partition and a chamber behind, there is no doubt that a few living gastropods are truly septate in the apical part of the whorl. There is also no doubt that some others deposit solid calcium carbonate in this shell area without any development of chambers. In fossils diagenetic changes may complicate the shell material and mask evidence for either interpretation.

There has always been a general assumption that Paleozoic gastropods are septate as the term is generally understood, the evidence for septation commonly being a steinkern ending abruptly at a rounded surface, though the latter could be equally as well the result of a solid apical filling. Partitions are especially evident in a few eroded Early Ordovician specimens. The same phenomenon of partitioning may be seen in a few weathered specimens of *Nevadaspira* (Plate 1: figure 5); others show a solid calcite mass in the early part of the whorl (Part 1: figure 6).

Polished specimens of *Nevadaspira* show many more septa than do weathered surfaces. Weathering differentially affects the partitions, some of which, but not all, stand in relief. The partitions are clear in section and begin with a dark line, following the arc of a circle in thin section (Plate 1: figure 8). Anterior to this is an area of calcite. The sequence is closed by another dark line. As might be expected, no clastic impurities occur between the dark lines; calcium carbonate seems to be the only material present in the interspaces (Plate 2: figure 1).

The large size of the calcite crystals suggests recrystallization between partitions. Recrystallization is emphasized, for in some regions a dark line may extend from one wall part way into the mass of calcite and then be lost (Plate 2: figure 3).

The alternatives are that either the early whorls were filled solidly by calcium carbonate, interrupted irregularly by deposition of dark material, which has now recrystallized, or that camerae were open and were subsequently filled after death. The available evidence supports the interpretation of later filling, for some areas between partitions show small crystals near the partition faces and larger ones in the intervening area. (Steven Stanley, personal communication, 1968.) See Plate 2: figure 1c.

Interpretations of septation, as contrasted with solid filling of whorls, have been made in the past on insufficient evidence. Fortunately, information from *Nevadaspira* supports septation, and it now rests on a much firmer basis. There seems little doubt that the open-coiled euomphaloid genera formed partitions as a life process. The partitions were formed by secretion of calcium carbonate by the apical part of the body mass, though the precise mechanism is as much a mystery as it is in the cephalopods.

Interpreted Functional Morphology

The open coil of *Nevadaspira* and similar gastropods appears poorly adapted for locomotion when compared with the more common tightly-coiled gastropod shells. The numerous partitions that shorten the body mass suggest that these gastropods would have even greater difficulty than normal gastropods in balancing the shell on the foot. It seems quite reasonable to rule out an active benthonic existence for all Paleozoic open-coiled gastropods.

It seems almost as reasonable to assume a sedentary life habit. This may have been sessile, but morphologic evidence of any attachment or cementation is lacking. However, if the animal spent most of its adult life resting in one area with the flattened profile of the shell on the substrate, an increase in area of contact with the bottom, as would come through open coiling, should have an advantage in maintaining this position. Increasing weight with increasing size may have caused a slight sinking of the shell into even a fairly firm substrate. Hyperstrophic coiling would keep the aperture out of the sediment and thus would appear to be a natural response in shape change for a coiled animal living a sedentary life on a mud bottom.

Many kinds of fossils deposited partitions of some sort within their exterior hard parts. Groups which come immediately to mind are rugose corals, richtofenid brachiopods, and rudistid pelecypods. These all have in common a sessile mode of life. Septation may be a consequence of a sessile habit, for there may have been a physiological requirement to remove calcium carbonate from the soft parts; however, septation in cephalopods shows the danger of overgeneralization. *Nevadaspira* may not have had a concomitant reason to extend the shell at a maximum rate. Internal deposition gets rid of much calcium carbonate but does not materially enlarge the shell.

If the concept of a sedentary life habit is valid, it may give some suggestion as to feeding habits. Heretofore, it has been tacitly assumed that the Euomphalacea, as primitive archaeogastropods, were probably herbivorous. It may be that members of this group were, in part, deposit feeders. The atypical open-coiled representatives may have further specialized toward ciliary feeding and evolved toward simply moving in and out of a tube to gather food, rather than foraging. *Nevadaspira* may have been a "sedentary worm," in a functional sense, rather than a typical gastropod.

The hyperstrophic, low-spired, open-coiled euomphalid gastropods are extinct. None of the living gastropods is similar either in presumed phylogenetic position or shell form. Some sort of analogy can be drawn with the unrelated Vermetidae. In a summary of the family, Morton (1965, p. 616) notes that septation is most frequent in the genus *Dendropoma*. As a consequence, the body is "plump and finger-shaped, no longer occupying the earlier convolutions of the tube." The animal has an operculum as wide as the aperture and "its quickness of response in darting back and closing the tube with the operculum is very striking." (Morton, 1965, p. 620.) Because the body is relatively short, the columellar muscle is short and straplike rather than elongate. Many of Vermicularidae have developed a most remarkable method of feeding by secreting strings and sheets of mucus into the water to entrap other organisms. This habit apparently is an outgrowth of ciliary feeding. In *Dendropoma*, ciliary feeding is more common than in genera having the body more elongate and wormlike. I have not had the opportunity to observe a living member of the Vermetidae, and my conclusions regarding a sedentary life for *Nevadaspira* were formed prior to reading Morton's paper.

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CARBONIFEROUS

John L. Carter

New Early Mississippian Silicified Brachiopods from Central Iowa

ABSTRACT

Two new Mississippian brachiopod genera, based on new species, and a new species of the conservative rhipidomellid genus *Perditocardinia* Schuchert and Cooper, 1931, are described from a small silicified faunule found in the Eagle City Limestone Member of the Hampton Formation of central Iowa. This faunule appears to be latest Kinderhookian in age but precise means of correlation or age determination are not presently available.

The brachiopod fauna of the upper Hampton Formation of central and north-central Iowa has not been described. Undoubtedly this has been due to the difficulty in collecting well-preserved specimens in quantities adequate for accurate identification. The more fossiliferous beds in north-central Iowa frequently contain only molds and casts and the available shell material commonly fares unusually poorly in "crack-out" collecting from these beds, especially in central Iowa. The sum total of several weeks collecting can compare very poorly indeed with the materials of similar age readily obtainable in southeastern Iowa and northeastern and central Missouri.

It was my good fortune to discover, after some days of arduous rock-breaking in the Eagle City Limestone Member sequence near LeGrand Iowa, several small blocks of clean limestone that appeared to contain a number of well-preserved silicified brachiopods. After etching with dilute hydrochloric acid I recovered a small faunule consisting entirely of brachiopods. The purpose of this paper is to describe several interesting new taxa discovered in this faunule. My identification of these and the other silicified brachiopod taxa in this faunule are listed below:

Rhipidomella cf. *R. dalyana* (Miller)
Perditocardinia iowensis, new species
Schuchertella sp.
Streptorhynchus sp.
"Rhynchopora" sp.
Eumetria sp.
Composita sp.
Cleiothyridina aff. *Athyris crassicardinalis* White
Planalvus, new genus
Planalvus gibberosa, new species
Unispirifer cf. *U. minnewankensis* (Shimer)
Mirifusella, new genus
Mirifusella fortunata, new species
Spirifer sp.
Verkhotomia? sp.
Punctospirifer solidirostris (White)
Beecheria sp.
Dielasma sp.

Most of the species are represented by only one or two specimens, mostly single valves, making accurate specific identification difficult. The three species described below are the most abundant elements in the faunule.

Age of the Faunule

The limestone bed of Eagle City Limestone from which most of the blocks of silicified material were taken occurs near the top of a large, actively worked quarry about one mile north of LeGrand, Marshall County, Iowa. This quarry is north and directly across the Iowa River from the abandoned quarry that yielded the famous LeGrand crinoid fauna of Laudon and Beane (1937). The silicified faunule occurs stratigraphically above that crinoid zone and probably would be placed in the "*Spiriferina* Zone" of Laudon (1931, pp. 423,

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424). The several small blocks containing silicified specimens were loosened and exposed by a bulldozer in preparation for further drilling and blasting. Additional blocks may be difficult to obtain. Small fist-size lumps containing silicified specimens were collected in the abandoned south "crinoid" quarry and similar small collections were made in a quarry two miles east of LeGrand in Tama County. Blocks of adequate size, however, were not found at any quarry other than the first one described above.

The brachiopod faunule contains no convincing horizon markers for delimiting the youngest possible age for the highest beds of the LeGrand quarries. The presence of *Eumetria* sp., *Verkhotomia?* sp., *Rhipidomella* cf. *R. dalyana,* and the new species of *Perditocardinia* in the silicified materials certainly suggests that these beds are younger than any part of the Chouteau Limestone of northeastern Missouri, and their stratigraphic position above the Maynes Creek Dolomite makes them younger than the highest Kinderhook of southeastern Iowa, the Wassonville Dolomite, which is a correlative of the Maynes Creek. Without more data I am forced to rely on the work of others and tentatively accept Laudon's (1931, p. 412) assignment of a Kinderhookian age for the upper Hampton Formation. Nevertheless, there is no evidence from the brachiopod fauna, including the nonsilicified specimens, that would preclude an early Osagian age for these beds, especially considering the possibility that the upper Hampton Formation sequence of central Iowa could conceivably represent a nearly continuous record of latest Kinderhookian-earliest Osagian sedimentation.

Preservation

This small silicified assemblage represents a thanatocoenose. Many of the spiriferid valves and some other shells are very much abraded, and no complete large shells were found with both valves intact. Many of the spiriferid pedicle valves are selectively penetrated by borings. A few of the shells have repaired boring injuries, so these brachiopods must have been alive when attacked by the boring organism. Most of the penetrated shells showed no signs of repair, however, and the large number of holes per valve suggests that the valves were bored after the death of the brachiopods.

Localities

UI (University of Illinois) locality Z–1F
Top beds exposed in SE corner of Martin-Marietta Corporation quarry, just north of Iowa River, about one mile north of LeGrand, NW¼ sec 1, T 83 N, R 17 W, Marshall County, Iowa. Eagle City Limestone.

UI locality Z–2
Upper beds exposed in abandoned quarry just south of Iowa River, about three-fourths mile north of LeGrand, SW¼ sec 1, T 83 N, R 17 W, Marshall County, Iowa. Eagle City Limestone.

UI locality Z–3
Top beds of northwest corner of B. L. Anderson Company, Montour quarry, NE¼ sec 8, T 83 N, R 16 W, Tama County, Iowa. Eagle City Limestone.

All types are in the collections of the University of Illinois, Urbana.

Phylum BRACHIOPODA Duméril, 1806

Class ARTICULATA Huxley, 1869

Order ORTHIDA Schuchert and Cooper, 1932

Suborder ORTHIDINA Shuchert and Cooper, 1932

Superfamily ENTELETACEA Waagen, 1884

Family RHIPIDOMELLIDAE Schuchert, 1913

Genus *Perditocardinia* Schuchert and Cooper, 1931

Perditocardinia iowensis, new species

PLATE 1: FIGURES 21–41; PLATE 2: FIGURES 6–11

DESCRIPTION.—Shell average size for the genus, unequally biconvex, the brachial valve being slightly to moderately more inflated than the pedicle valve; outline variable, commonly subcardiiform with a rostrate posterior or, more rarely, subcircular to subovate, and either longitudinally or transversely elongated; greatest width usually attained in the anterior half of the shell or, more rarely, at or near midlength; profile lenticular; hinge-line very narrow; cardinal extremities rounded; sulcus moderately developed, fold low and obscure; anterior commissure weakly uniplicate, anterior margin commonly slightly emarginate or gently rounded; ornament consists of numerous fine costellae and strong, irregularly spaced growth varices.

Pedicle valve thick-shelled, moderately and almost evenly convex in lateral profile; beak small, bluntly to sharply pointed and of moderate size, slightly incurved; interarea extremely small, often reduced to low ridges bounding the delthyrium, or completely absent; delthyrium filled by the cardinal process, leaving a small apical foramen; beak ridges per se poorly developed, leaving a rounded palintrope; lateral edges of valves commonly flattened and differentiated from the ventral surface by a ridge; sulcus narrow, originating in the beak region, becoming considerably impressed anteriorly.

Pedicle valve interior with stout, elongate, slightly divergent teeth; crural fossettes well developed on the anteromedial edges of the teeth; pedicle callist clearly differentiated between the tooth bases; lateral and anterior margins minutely crenulated by the inner edges of the surface costellae; muscle field large, flabellate, deeply impressed, extending anteriorly about one-half to two-thirds the length of the valve; adductor field narrow, completely enclosed by the diductor-adjustor field; low thick median ridge commonly divides the muscle field but especially prominent in anterior portion of the diductor field.

Brachial valve thinner-shelled than pedicle valve and more strongly convex in both anterior and lateral profile; beak rounded, inconspicuous; interarea obsolete; fold very weakly developed or absent; anterior commissure commonly flexed dorsad to match the small tongue of the pedicle valve sulcus.

Brachial valve interior with large thick cardinal process; myophore often appears trilobed in anterior or posterior profile; shaft not discernible, fused to brachiophores by adventitious shell tissue; brachiophores elongate, bladelike, fused to floor of valve and cardinal process, with a ventral process that articulates with the crural fossettes on the teeth of pedicle valve; short, slender, anteriorly directed crura developed on anterior edge of the brachiophores; sockets long and deep; fulcral plates not developed but the sockets may be slightly constricted anteriorly by a low ridge developed on the exterior or lateral faces of the brachiophores; dorsal adductor scars moderately impressed, separated by a wide low rounded median ridge.

Measurements (in millimeters) of the types of *Perditocardinia iowensis,* new species, from the Hampton Formation (Eagle City Limestone Member) of LeGrand, Marshall County, Iowa:

UI No.	*Length*	*Width*	*Locality*
PEDICLE VALVES			
X–3425	15.5	14.9	Z–3
X–3427	12.6	15.2	Z–3
X–3432	12.4	13.7	Z–1F
X–3426	12.5	12.7	Z–1F
X–3428	12.7	10.8	Z–1F
BRACHIAL VALVES			
X–3429	12.9	14.6	Z–3
X–3430	11.6	13.2	Z–1F
X–3431	11.2	10.5	Z–1F

HOLOTYPE.—UI No. X–3426 (Plate 1: figures 24–26; Plate 2, figure 10).

DISTINGUISHING CHARACTERS.—This species is characterized by its subcardiiform to subovate outline; poorly developed rostration; greatly reduced or obsolete ventral interareas and obsolete dorsal interareas; and narrow sulcus originating in the beak region. Internally, the large lobate cardinal process is fused to the brachiophores by a thick mass of adventitious shell tissue, and the ventral muscle field extends anteriorly about one-half to two-thirds the length of the valve.

COMPARISONS.—*Perditocardinia iowensis,* new species, is related to *P. dubia* (Hall, 1858), identified from various late Osagian and Meramecian horizons, but it can be differentiated from that species by its less rostrate, more variable outline; usually thinner-shelled valves; and narrower, shorter ventral muscle field.

Rhipidomella thiemei (White, 1860), from the Starr's Cave Limestone of Iowa and upper Chouteau Group of northeastern Missouri, often is similar in size, outline, and profile to *P. iowensis,* new species, but is never rostrate. It further differs in possessing a wider hinge-line, larger ventral interarea, and in having the sulcus originate anterior to the beak region of the pedicle valve.

REMARKS.—Since the establishment of the genus *Perditocardinia* by Schuchert and Cooper in 1931 no species, other than the type *P. dubia* (Hall), has been recognized in the Mississippian or Lower Carboniferous. That species has been reported, however, from many horizons ranging in age from Osagian through Chesterian. As Schuchert and Cooper (1932, p. 135) pointed out, the type species, as thus identified, is a composite "and it will probably prove desirable to separate it into several specific groups."

Rhipidomella Oehlert, 1890, and its close relative *Perditocardinia* represent an extraordinarily conservative stock of punctate orthids in the late Paleozoic. Tracing the unusually slow-paced morphological changes that took place in these brachiopod lineages seems to me to be possible under these circumstances. It is my view that, morphologically, *Perditocardinia dubia* is sufficiently distinct from the more typical Carboniferous rhipidomellid stock that it probably was preceded by earlier intermediate species. *Perditocardinia iowensis* seems to fit this requirement because it falls morphologically between the Meramecian rostrate forms lacking interareas and the nonrostrate rhipidomellid forms with well-developed interareas. I interpret *P. iowensis,* then, to represent an early perditocardinid offshoot from the rhipidomellid lineage, perhaps even being the direct ancestor of *P. dubia* and its unnamed younger relatives.

OCCURRENCE AND ABUNDANCE.—This is one of the commonest brachiopod species in the "*Spiriferina* Zone" of Laudon in the LeGrand vicinity. The silicified collection alone consists of several hundred disarticulated valves, many of them well preserved.

Order SPIRIFERIDA Waagen, 1883

Suborder ATHYRIDIDINA Boucot, Johnson, and Staton, 1964

Superfamily ATHYRIDACEA M'Coy, 1844

Family ATHYRIDIDAE M'Coy, 1844

Subfamily ?ATHYRIDINAE M'Coy, 1844

Planalvus, new genus

DIAGNOSIS.—Longitudinally to transversely ovate, small to medium size, unequally biconvex athyridids with weakly developed ventral sulcus and dorsal fold; pedicle valve thick-shelled, weakly convex, nearly flat posteriorly; ventral beak small, almost obsolete; beak ridges subangular, defining pseudoareas on either side of the delthyrium; pedicle foramen small, possibly obsolete in adults; dental plates lacking; surface lamellose, the lamellae being finely striated and apparently fringed with minute spines.

Brachial valve gibbous and much more inflated than the pedicle valve; dorsal beak angular, pointed, incurved, filling the delthyrium of the pedicle valve completely; cardinal plate large, athyridid, nonperforate, nearly filling the ventral umbo; brachidium unknown.

TYPE-SPECIES.—*Planalvus gibberosa,* new species.

DISTINGUISHING CHARACTERS.—This genus is characterized by its unequally biconvex valves, the brachial valve being gibbous and the pedicle valve weakly convex. The pedicle valve is thick-shelled; the ventral beak is inconspicuous; and ventral pseudoareas are developed. Internally, the pedicle valve lacks dental plates, and the cardinal plate in the brachial valve is large and nonperforate. Surface ornament consists of fine, closely spaced, striated lamellae fringed with minute spines.

COMPARISONS.—*Planalvus* occurs with *Composita* Brown, 1849, but can be differentiated externally from that genus by its weakly convex, nonrostrate pedicle valve with planareas, strongly inflated brachial valve with an extended, acute, incurved dorsal beak, and finely lamellose ornament. *Composita* is rostrate, unequally biconvex, and smooth. Internally, the pedicle valve of *Planalvus* lacks dental plates and the cardinal plate is nonperforate, whereas *Composita* has stout dental plates and a perforate cardinal plate.

Athyris M'Coy, 1844, overlaps *Planalvus* in its stratigraphic range but can be distinguished easily by its rostrate, subequally biconvex form and broad smooth lamellar frills. Internally, *Athyris* possesses dental plates and a perforate cardinal plate.

Cleiothyridina Buckman, 1906, is similar to *Athyris* except it has smooth lamellar frills fringed with well-differentiated, flattened spines.

Spirigerella Waagen, 1883, is similar to *Planalvus* in its thick shell and apparent lack of dental plates, but it differs in being smooth and having a more convex pedicle valve with a pronounced incurved beak, and the pedicle foramen is occluded by the dorsal umbo. Internally, the cardinal plate is perforate.

Actinoconchus M'Coy, 1844, is similar to *Planalvus* in possessing striated lamellar frills but the grooves or striations on the lamellae are widely spaced and do not form a spinose fringe at the margins. Furthermore, *Actinoconchus* is subequally biconvex, possesses a moderately developed ventral beak, and, internally, possesses dental plates.

REMARKS.—Although *Planalvus* probably belongs in the subfamily Athyridinae M'Coy, 1844, along with the genera mentioned above, I have assigned it to this subfamily tentatively because the brachidium is unknown. The lamellose nature of the type-species is not apparent in most of my specimens. I had thought initially that the surfaces of the valves were more or less smooth in the manner of *Composita* and, hence, that possibly *Planalvus* was a close relative of that genus.

Ultimately, however, several lamellose specimens etched out, and it became apparent that *P. gibberosa,* at least, has a more typical athyridid ornament of spine-fringed lamellae. I have not been able to determine whether *Athyris densa* possesses a lamellose ornament but place it in *Planalvus* with fair confidence due to its close similarity to the type species in most other respects.

The name is derived from the Latin *plan* (flat) and *alvus* (belly).

SPECIES ASSIGNED.—*Planalvus gibberosa,* new species; *Athyris densa* Hall and Clarke, 1894.

RANGE.—Late Kinderhookian and Meramecian of North America.

Planalvus gibberosa, new species

FIGURE 1; PLATE 1: FIGURES 1, 2; PLATE 2: FIGURES 12–41

DESCRIPTION.—Shell small for the subfamily; unequally biconvex, the brachial valve being much more inflated than the pedicle valve; longitudinally subellipsoidal to subcircular in outline, rarely wider than long; greatest width attained near midlength or slightly posterior to midlength; profile subovate; hinge-line short, curved, subterebratulid; cardinal extremities well rounded; fold and sulcus weakly developed in adult shells only; growth varices irregularly spaced; surface finely lamellose, the lamellae being finely striated and anteriorly fringed with very fine spines.

Pedicle valve thick-shelled, moderately to weakly and evenly convex in lateral profile; beak inconspicuous, with a small curved notch formed by the pedicle foramen; delthyrium almost completely filled by the dorsal umbo; beak ridges subangular, forming flattened pseudoareas on either side of the foramen; sulcus, if present, broad and shallow, giving the anterior portion of the shell a sublingual outline in many shells.

Pedicle valve interior lacking dental plates, with a moderately impressed muscle field posteriorly; teeth large, blunt.

Brachial valve thinner-shelled than pedicle valve; gibbous; much more inflated than the pedicle valve; most strongly convex in the umbo but nearly evenly curved in lateral profile; dorsum very high, the flanks sloping rapidly to the lateral margins but not forming an actual fold; beak well developed, incurved into the delthyrium of the pedicle valve.

Brachial valve interior with large nonperforate ventrally concave cardinal plate that bends posterodorsally to unite with the floor of the valve between stout socket ridges; posterior edges of cardinal plate on either side of the dorsal beak slightly recurved, forming two low flanges that may fuse medially to form a small perforation (however, this perforation is in no way homologous with the visceral perforation in *Composita, Cleiothyridina,* or *Athyris*); crural bases arise either on the outer anterior edge of the cardinal plate or on the inner anterior edges of the socket ridges (this is essentially a histological problem and can best be handled with thin section techniques applied to calcareous or essentially unaltered specimens); brachidial structures unknown; low myophragm present in posterior third of valve.

Measurements (in millimeters) of *Planalvus gibberosa,* new species, from the Eagle City Limestone Member of the Hampton Formation, LeGrand, Iowa; U.I. locality Z–1F:

UI No.	*Length*	*Width*	*Thickness*
X–3435	10. 2	9. 5	5. 6
X–3436	8. 0	7. 8	4. 0
X–3437	5. 7	6. 1	2. 8
X–3438	4. 1	4. 1	1. 9
X–3439	2. 9	3. 6	1. 5

HOLOTYPE.—UI No. X–3435 (Plate 2: figures 17–21).

DISTINGUISHING CHARACTERS.—This species is characterized by its small size, longitudinally subellipsoidal to subcircular outline, inconspicuous ventral beak, and poorly developed fold and sulcus.

COMPARISONS.—*Planalvus gibberosa,* new species, is most similar to *P. densa* (Hall and Clarke, 1894), from the Salem Limestone of Indiana and Kentucky. *Planalvus densa* is transversely subovate in outline and attains a much greater size than *P. gibberosa.* Furthermore, *P. densa* may have a weak median sulcus on the dorsal fold.

GROWTH.—Although a large collection of well-preserved pedicle valves is not available for measurement and comparison, there is a clear trend toward acceleration in length relative to width, as seen in growth lines of several of the larger well-preserved shells. These growth lines, measured for three of the types, are plotted on Figure 1. This observation is substantiated to some extent by the length-width measurements available for several well-preserved juvenile specimens. All of these specimens are transverse except for one which is equidimensional, indicating that moderate allometry probably occurs in later growth stages.

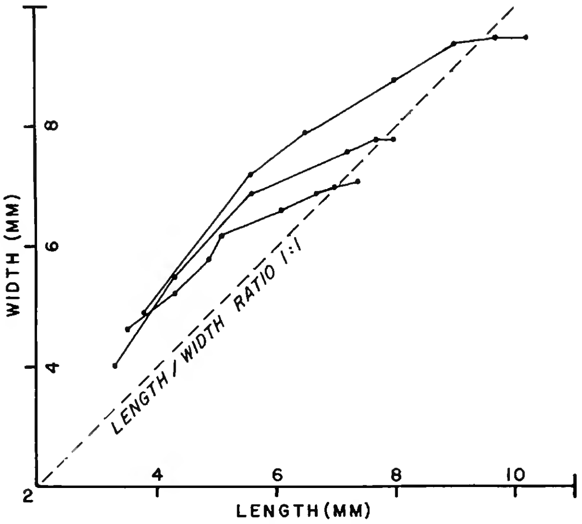

Figure 1.—Plots of length/width measurements of *Planalvus gibberosa,* new species, taken from growth varices of three pedicle valves illustrating allometric growth in late ontogenetic stages that results in elongation of the valves.

Occurrence and abundance.—Found in the upper Hampton Formation (Eagle City Limestone Member) of LeGrand, Iowa, and vicinity, and the Gilmore City Limestone of north-central Iowa. The silicified collection from the LeGrand localities consists of over 50 specimens. Only eight specimens have been recovered from the Gilmore City Limestone.

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily SPIRIFERACEA King, 1846

Family uncertain

Mirifusella, new genus

Diagnosis.—Medium size for the superfamily; mature shells often longer than wide, greatest width usually anterior to the hinge-line, often near or anterior to midlength; cardinal extremities rounded or subangular, never mucronate; outline subovate to guttate; ventral umbo long and inflated, extending posteriorly beyond the hinge-line about one-fourth to one-third the length of the valve; fold and sulcus poorly developed; hinge-line denticulate; ornament usually consists of a few simple rounded costae on the flanks, a median sulcal costa that may bifurcate anterior to the beak, and other sulcal costae, which are simple and bifurcate from the sulcus bounding costae; surface weakly capillate, forming a faintly reticulate pattern with fine growth lines; shell substance impunctate.

Type species.—*Mirifusella fortunata,* new species.

Distinguishing characters.—*Mirifusella* is characterized by its commonly elongate subovate to guttate outline and relatively narrow hinge-line (for spirifers) in mature specimens, with few low rounded simple costae on the flanks, a sulcal median costa that may bifurcate, and simple lateral sulcal costae that bifurcate from the sulcus-bounding costae.

Comparisons.—*Mirifusella* is most similar to *Fusella* M'Coy, 1844, *Anthracospirifer* Lane, 1963, *Unispirifer* Campbell, 1957, and *Imbrexia* Nalivkin, 1937. It can be distinguished from all of these genera by its elongate outline in most mature specimens. In addition, its maximum width is usually anterior to the hinge-line and the cardinal extremities are rounded or subangular. *Fusella* and *Unispirifer* are usually strongly transverse genera, commonly having angular ears and the maximum width at or very near the hinge-line. Also, *Fusella* has a simple median sulcal costa, and *Unispirifer* has numerous lateral costae. *Anthracospirifer* and *Imbrexia* commonly have rounded or subangular ears but are, nevertheless, transverse, and rarely, if ever, elongate. Further, *Anthracospirifer* has lateral costae which may bifurcate, and its median sulcal costa is consistently simple; in *Mirifusella* the lateral costae are invariably simple, but the median sulcal costa may bifurcate. *Imbrexia* (although that genus has not been properly established due to our limited knowledge of its type-species, *Spirifer imbrex* Hall, 1858) apparently has a strongly imbricate ornament covering the entire surface of the shell, except for the interareas, and a simple median costa in the sulcus.

The simple costation and tendency toward elongation of the shell of *Eochoristites* Chu, 1933, from the Kinling Limestone of northeastern China, tempt one to compare it with this new genus. However, *Eochoristites* was clearly described as possessing basal plates ("crural plates" of others) in the brachial valve, and possibly has a nondenticulate hinge, although I am not convinced of that.

Remarks.—The grouping of genera into families of spiriferid brachiopods is a particularly difficult and challenging occupation. Unfortunately, the *Treatise on Invertebrate Paleontology, Part H, Brachiopoda* (R. C. Moore, editor), which appeared in 1965, did not alleviate our miseries in this regard. The classification of the spiriferids remains a perplexing problem to the student of spiriferid systematics. This is not the time and place to attempt a new synthesis for the spiriferids. I merely want to point out the impossibility of being able to assign genera confidently to families, other than types. *Mirifusella,* new genus, possesses both spiriferid and brachythyridid characters, as do many genera assigned to one family or the other in the Treatise. Perhaps a good dose of numerical taxonomy will unsnarl the knot, perhaps not. In any case, I am unable at this time to place *Mirifusella* in a family in such a manner that the assignment in any way elucidates its true relationships.

The name is derived from the Latin *mirus* (strange) and *fusella* (little spindle).

Species assigned.—*Mirifusella fortunata,* new species, from the Eagle City Limestone Member of the Hampton Formation of south-central Iowa, and *Spirifer indianensis* Weller, 1914, from the Harrodsburg Limestone of Indiana. Weller (1914, p. 353) noted the peculiar elongation of his species and considered it to be unique. In various collections, however, I have seen undescribed representatives of that genus ascribed to be from the Keokuk Limestone and Warsaw Formation of the upper Mississippi Valley.

Range.—Late Kinderhookian through early Meramecian.

Mirifusella fortunata, new species

Figure 2; Plate 1: figures 3–20; Plate 2: figures 1–5

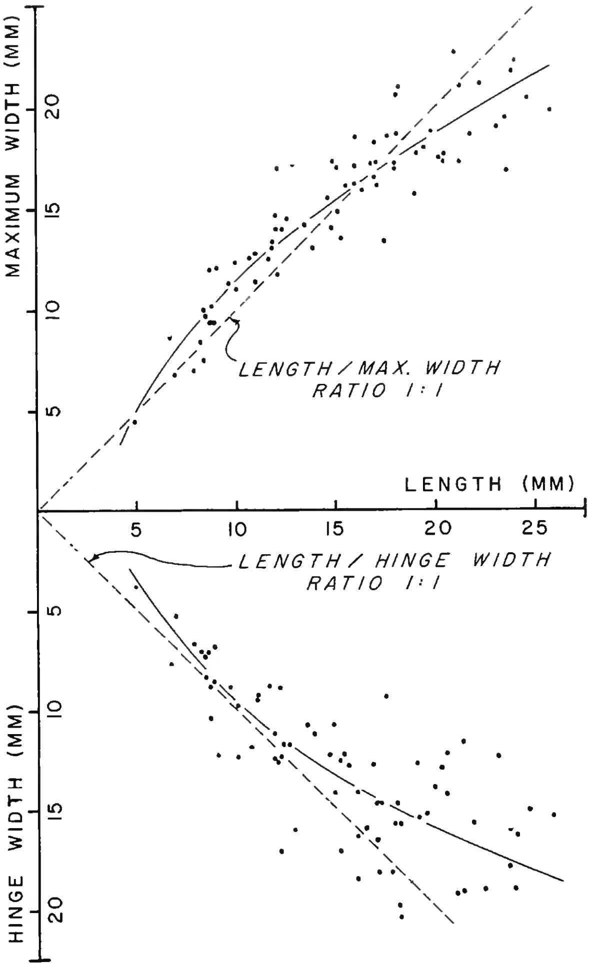

Figure 2.—Scatter diagrams of dimensions of 73 pedicle valves of *Mirifusella fortunata,* new species, from UI locality Z-1F.

Description.—Medium size for the family; subequally biconvex; moderately inflated; proportions variable due to allometry but usually considerably longer than wide in large adults; outline longitudinally guttate to transversely subovate in most specimens; hinge-line straight and less than the maximum width in most specimens, often narrow; maximum width usually near or anterior to midlength; cardinal extremites rounded in about half the known specimens, subangular in the rest; anterior commissure uniplicate; fold and sulcus of moderate width, weakly developed; macro-ornament consists of about 10 to 13 simple rounded costae per flank in adult specimens; sulcus with about 3 to 6 costae, the median costa usually bifurcating in the umbonal region and the lateral sulcal costae bifurcating from the sulcus-bounding costae; growth varices are irregularly spaced; micro-ornament consists of fine capillae and closely spaced growth lines, the latter becoming slightly imbricate near the anterior margin and forming a weak reticulate pattern.

Pedicle valve with greatest convexity near the beak, considerably more inflated than the brachial valve; beak small and incurved; umbonal region often extending posteriorly beyond the hinge-line for more than one-fourth the total length of the valve; ventral interarea apsacline, usually narrower than the maximum width, strongly concave, triangular, often vertically striated, well-defined ventrolaterally by subangular beak ridges; hinge-line denticulate; delthyrium narrow, usually forming an angle at the apex of less than 60 degrees, often partially closed in mature specimens by coalescing of the thickened dental plates; sulcus usually very shallow, or even indistinct in some specimens.

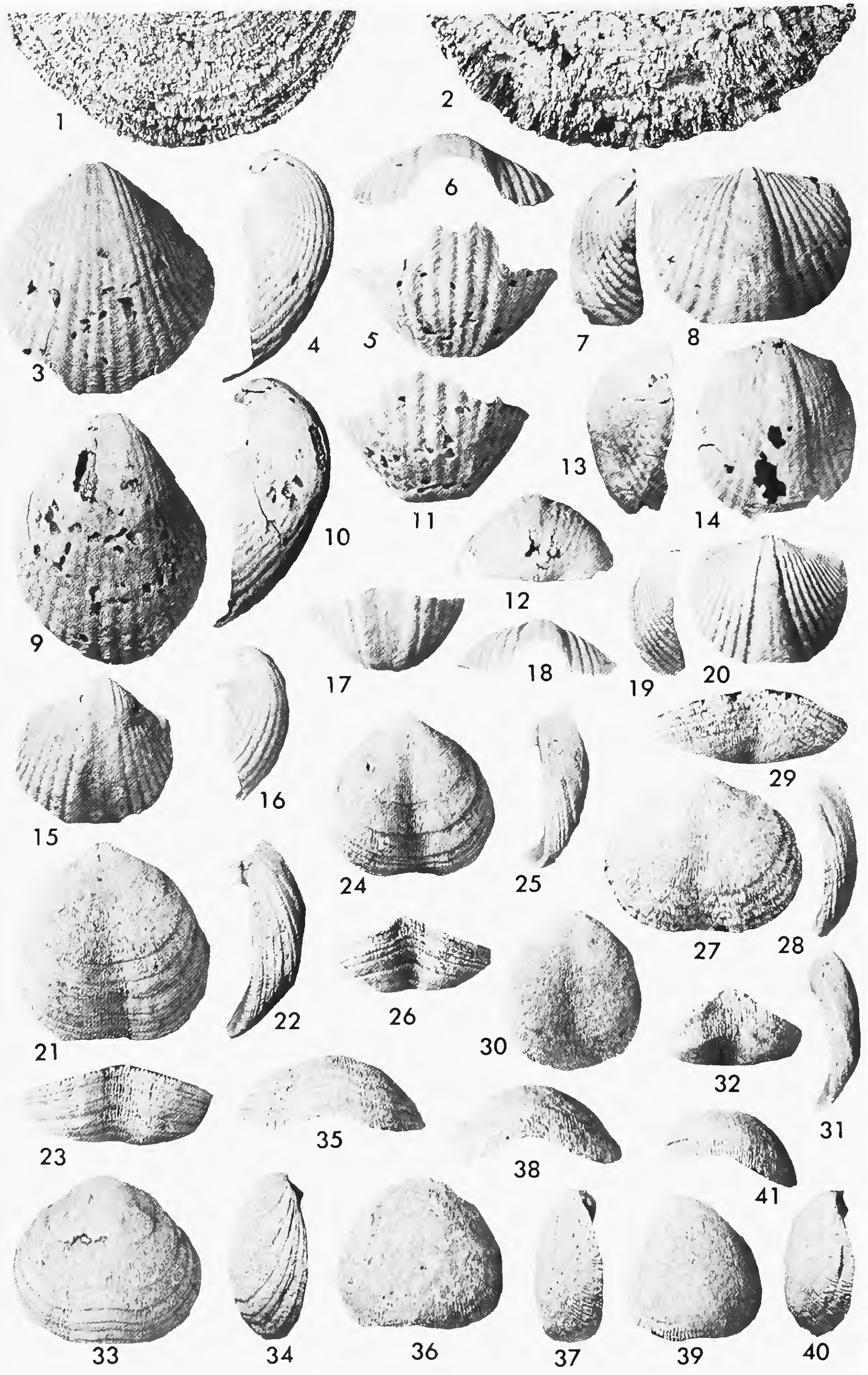
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PLATE 1

Interior of pedicle valve with strong, divergent dental plates that laterally enclose the posterior part of the muscle field; dental plates may become greatly thickened in larger specimens and often flare out anterolaterally to accommodate the muscle field; in some adults and juveniles a small subdelthyrial closure is formed in the apex of the delthyrium by the initial fusion of the thickening dental plates, however, such a closure is not a true plate; muscle field moderately impressed in large adult specimens; ovarian markings well developed between the dental plates and the posterolateral margins; teeth small, bladelike, directed laterally.

Brachial valve with greatest convexity in the umbonal region of most shells, usually moderately inflated, never as inflated as the pedicle valve; usually wider than long, much shorter than the pedicle valve, and with a subelliptical outline in most specimens; dorsal beak tiny, inconspicuous; interarea extremely low, orthocline; fold low, of moderate width, often somewhat flattened; ornament similar to and complementary with that of the pedicle valve.

Brachial valve interior with moderate-size striate cardinal process which commonly is medianly divided by a narrow groove, almost becoming bilobed in large specimens; cardinal process rests on floor of valve posteriorly but is supported laterally and anterolaterally by infolded shell tissue that wraps around the crural bases from the dorsal surfaces of the inner socket ridges (lacking thin section material, it cannot be determined at present whether this shell tissue is fibrous or columnar in nature); weak median ridge developed between the moderately impressed adductor scars; sockets wide, typically spiriferid; crura originate on the dorsolateral surfaces of the inner socket ridges but do not extend to the floor of the valve; however, they are commonly enclosed dorsally by the same shell tissue that wraps around from the inner socket ridge to support the cardinal process; other brachidial details unknown; ovarian markings present on the posterolateral portions of the valve.

Measurements (in millimeters) of the types, from the Eagle City Limestone Member of the Hampton Formation, UI locality Z–1F, near LeGrand, Iowa:

UI No.	*Length*	*Hinge Width*	*Maximum Width*
PEDICLE VALVES			
X–3451	23. 9	18. 9	21. 8
X–3445	24. 0	16. 3	22. 3
X–3447	25. 8	15. 3	19. 9
X–3452	17. 0	18. 1	18. 3
X–3449	15. 6	12. 8	16. 1
BRACHIAL VALVES			
X–3455	17. 5	16. 2	20. 3
X–3446	16. 3	17. 7	20. 6
X–3448	18. 4	11. 7	16. 3
X–3450	13. 2	14. 0	16. 3
X–3454	13. 4	13. 4	14. 9

HOLOTYPE.—UI No. X–3445 (Plate 1: figures 3–5).

DISTINGUISHING CHARACTERS.—This species is characterized by its longitudinally guttate to transversely subovate outline; usually narrow hinge-line with the maximum width at or anterior to midlength; rounded or subangular cardinal extremities; weakly developed fold and sulcus; about 10 to 13 low rounded simple costae per flank; about three to six sulcal costae, the median one usually bifurcating; capillate micro-

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PLATE 1: figures 1, 2—*Planalvus gibberosa,* new species. Micro-ornament of anterior portions of two pedicle valves, showing very finely radially striated, closely spaced lamellae fringed with minute spines at their free edges (all views ×8): 1, A medium-size pedicle valve, UI X–3433, from UI loc. Z–3, Tama County, Iowa; 2, a larger pedicle valve, UI X–3434, from the north quarry, UI loc. Z–1F, near LeGrand, Marshall County, Iowa.

Figures 3–20.—*Mirifusella fortunata,* new species, from the north quarry, UI loc. Z–1F, near LeGrand, Marshall County, Iowa (all views ×1.5): 3–5, ventral, lateral, and anterior views of a pedicle valve, the holotype, UI X–3445; 6–8, anterior, lateral, and dorsal views of a brachial valve, UI X–3446; 9–11, ventral, lateral, and anterior views of a pedicle valve, UI X–3447; 12–14, posterior, lateral, and dorsal views of a brachial valve, UI X–3448; 15–17, ventral, lateral, and anterior views of a pedicle valve, UI X–3449; 18–20, anterior, lateral, and dorsal views of a brachial valve, UI X–3450.

Figures 21–41.—*Perditocardinia iowensis,* new species (all views ×2). 21–23, ventral, lateral, and anterior views of an unusually large pedicle valve, UI X–3425, from UI loc. Z–3, Tama County, Iowa; 24–26, ventral, lateral, and anterior views of a pedicle valve, the holotype, UI X–3426, from the north quarry, UI loc. Z–1F, Marshall County, Iowa; 27–29, ventral, lateral, and anterior views of a wide pedicle valve, UI X–3427, from UI loc. Z–3, Tama County, Iowa; 30–32, ventral, lateral, and anterior views of an elongate pedicle valve, UI X–3428, from the north quarry, UI loc. Z–1F, near LeGrand, Marshall County, Iowa; 33–35, dorsal, lateral, and anterior views of a large, wide brachial valve, UI X–3429, from UI loc. Z–3, Tama County, Iowa; 36–38, dorsal, lateral, and anterior views of an emarginate brachial valve, UI X–3430, from the north quarry, UI loc. Z–1F, Marshall County, Iowa; 39–41, dorsal, lateral, and anterior views of an elongate brachial valve, UI X–3431, from the north quarry, UI loc. Z–1F, Marshall County, Iowa.

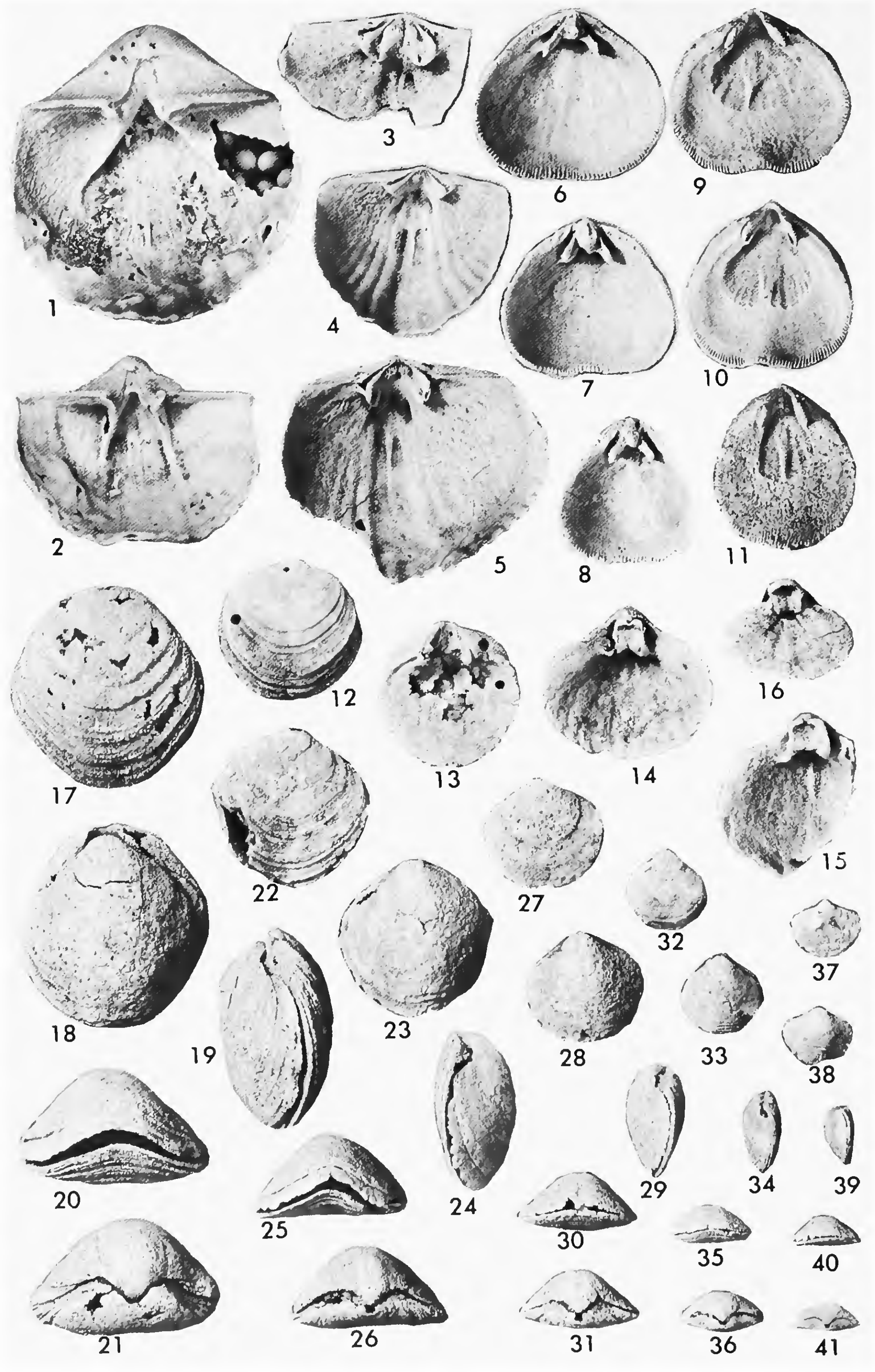
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PLATE 2

ornament; strong, divergent dental plates; and commonly in large specimens, a weakly bilobate striate cardinal process.

COMPARISONS.—*Mirifusella fortunata,* new species, is most similar and closely related to *Spirifer indianensis* Weller, 1914, from the Harrodsburg Limestone of Indiana and possibly the Keokuk and Warsaw Formations of the upper Mississippi Valley. The latter species possesses fewer but stronger lateral costae and the median costa in the sulcus rarely bifurcates. The only other discernible difference between these species is that the dorsal interarea in *M. fortunata* is orthocline, whereas in *M. indianensis* it is anacline.

Spirifer marshallensis Weller, 1914, was described from two brachial valves and, according to Weller (1914, pl. 50, figs. 13–14), is from the Kinderhook beds of LeGrand, Iowa. I have examined Weller's types and must admit that the matrix lithology can be only of the Hampton Formation, probably Maynes Creek Dolomite. As Weller noted, the types have a granulose surface ornament; hence, this species belongs to a genus other than *Mirifusella* and is probably punctate, possibly a *Punctothyris* Hyde, 1953.

GROWTH.—The allometric growth form of the pedicle valve of this species is illustrated in the scatter diagrams of Figure 2. Elongation of the shell is accelerated in relation to both hinge width and maximum width. Acceleration seems to occur when the shells are between about 7 and 15 mm long. Over 90 percent of the pedicle valves available attained maximum width anterior to the hinge-line in all observable growth stages, and elongation of the valve was evident in about two-thirds of the valves 15 mm wide and larger.

Internally, the dental plates are extremely variable in length and thickness in small and medium-size shells, the thickening that is characteristic of the larger mature shells apparently not being related to shell size alone. The cardinal process in the smaller brachial valves is usually small, not well supported by callus. In larger valves, however, the lateral edges of the process grow anteriorly, and, in conjunction with deposition of callus, give the process a decidedly bilobed appearance.

REMARKS.—Many of the pedicle valves and several brachial valves in the silicified collection were penetrated by boring organisms, possibly sponges. Some of these borings were sealed by secretion of additional shell tissue, indicating that the boring organism attacked the shell while the brachiopods were still alive. However, many of the holes penetrate the valves completely. These borings either were fatal or were made on already lifeless shells.

OCCURRENCE AND ABUNDANCE.—*Mirifusella fortunata* is one of the most common species in the Eagle City Limestone Member in the vicinity of LeGrand, Iowa. The silicified collections consist of several hundred disarticulated valves, and unaltered or weakly silicified shells are common in the beds just below the highest bed exposed in the LeGrand quarries.

PLATE 2: figures 1–5.—*Mirifusella fortunata,* new species, from the north quarry, UI loc. Z-1F, near LeGrand, Marshall County, Iowa (all views × 2): 1, 2, slightly oblique views of the interiors of two pedicle valves, UI X-3451–2, respectively; 3, interior of large dorsal umbo, UI X-3453, showing the thickened bilobed cardinal process; 4,5, interior views of two brachial valves, UI X-3454–5, respectively.

Figures 6–11.—*Perditocardinia iowensis,* new species (all views ×2): 6, interior view of a large wide brachial valve, UI X-3429, from a quarry, UI loc. Z-3, Tama County, Iowa; 7,8, interior views of two brachial valves, UI X-3430–1, respectively, from the north quarry, UI loc. Z-1F, near LeGrand, Marshall County, Iowa; 9–11, interior views of three pedicle valves, UI X-3432, 3426 (holotype), and 3428, respectively, from the north quarry, UI loc. Z-1F, near LeGrand, Marshall County, Iowa.

Figures 12–41.—*Planalvus gibberosa,* new species, from the north quarry, UI loc. Z-1F, near LeGrand, Marshall County, Iowa (all views × 3): 12, 13, exterior and interior views of a pedicle valve, UI X-3440; 14, 15, interior views of two brachial valves, UI X-3441–2, respectively; 16, oblique anterior view of a pedicle valve, UI X-3443, with the cardinalia of the dorsal umbo articulated with the teeth; 17–41, ventral, dorsal, lateral, anterior, and posterior views of a growth series of five complete specimens, UI X-3435–9, respectively, including the holotype (figures 17–21).

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Mackenzie Gordon, Jr.

Carlinia, a Late Mississippian Genus of Productidae from the Western United States

ABSTRACT

Carlinia, new genus (type-species: *Productus phillipsi* Norwood and Pratten, 1855) occurs in rocks of late Chester age in Nevada, Utah, and Wyoming. It is a late derivative of *Diaphragmus* Girty in which the multiple diaphragms and trails in the brachial valve become modified into a series of concentric frills, very closely spaced along the valve margin. The diaphragm area is not differentiated within the interior of the brachial valve. *Carlinia* also differs from *Diaphragmus* in lacking spines on the brachial valve and in having a thicker shell. Besides the type-species, two other species, *Carlinia amsdeniana*, new species, and *C. diabolica*, new species, are described. All three species have a limited stratigraphic range near the top of the Mississippian System. *Diaphragmus cestriensis* (Worthen), *D. fasciculatus* (McChesney), and *D. montesanae* Ulrich are discussed in relation to *Carlinia* and its species.

Three distinctive species of diaphragm-bearing productoids have a limited stratigraphic range near the top of the Mississippian System. These shells have characters in common that differentiate them from other members of the family Productidae and are believed to belong in a new genus, herein named *Carlinia* for its occurrence in Carlin Canyon, Nevada. The relatively short time-span of this genus renders these species useful for stratigraphic correlation in that part of the western United States where they occur.

In the United States the family Productidae ranges through the upper part of the Meramec Series to the top of the Chester Series (see Table 1). Its earliest known representative is *Productus tenuicostus* Hall, which occurs in the St. Louis Limestone and in the Arroyo Peñasco Formation of northern New Mexico. This species bears a single diaphragm along the margin of the visceral disc in the brachial valve. It is succeeded, in the St. Genevieve Limestone and in early Chester beds, by *Diaphragmus montesanae* Ulrich, a small, finely costellate species with two or three diaphragms and delicate trails.

In middle early Chester time the familiar and widespread *D. cestriensis* (Worthen), the type-species of the genus *Diaphragmus* Girty, appeared along with the closely related *D. fasciculatus* (McChesney). In middle and late Chester time these species spread from the Mississippi Valley and ranged rather widely over the United States. *D. cestriensis* is recognized from western Wyoming to northern Alabama. Several other species of *Diaphragmus* also can be recognized in various parts of the United States, but they have more restricted geographic ranges than *D. cestriensis*.

The tendency in the evolution of the brachial valve in *Diaphragmus* was for the initial disc to become proportionately smaller, the diaphragm area wider, and individual diaphragms and trails more numerous. Typical *Diaphragmus* has as many as seven diaphragms and trails in the brachial valve. The outer surface of the initial trail is commonly covered with scattered spines along costae and costellae; spines generally are most numerous on the brachial valve opposite the spine patch commonly present on the flanks and umbonal slopes of the pedicle valve.

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TABLE 1.—*Distribution of species of the family Productidae in the Upper Mississippian of the United States.*

Species	Meramec			Chester		
	Lower	Middle	Upper	Lower	Middle	Upper
Productus tenuicostus		X				
Diaphragmus montesanae			X	X –		
D. cestriensis				– X	X	X – –
D. fasciculatus				– X	X	X – –
Carlinia diabolica						X X –
C. phillipsi						– X –
C. amsdeniana						– X –
Diaphragmus, undescribed species						– – X

In fairly late Chester time the modified form herein designated as *Carlinia* appeared on the scene in the western United States. The multiple diaphragms and trails of this genus are more numerous than in *Diaphragmus* but seem to have served mainly as external ornamentation rather than having the function of separating the visceral cavity from the trail, as in *Diaphragmus*. The trails in *Carlinia* do not appear to have grown to any appreciable length, and the diaphragms were covered with callus internally so that they cannot be distinguished on the interior of the shell. The spines on the ventral valve became sparser and coarser in *Carlinia* and those on the brachial valve disappeared entirely.

The acme of the genus *Carlinia* was near the end of Chester time. Nevertheless, the youngest member of the Productidae in the Great Basin, in the highest Mississippian beds along the Nevada-Utah border, is a species of *Diaphragmus* as yet undescribed. *Carlinia* is not found in these highest beds. The family Productidae, as such, appears to have died out suddenly at the end of Chester time, but probably gave rise to other forms in the later Carboniferous.

I thank A. J. Unklesbay and R. L. Etherington of the Department of Geology of the University of Missouri for the loan of Branson and Greger's figured specimens, which herein are designated holotype and paratype of *Carlinia amsdeniana*, new species. I am grateful also to J. T. Dutro, Jr., and R. E. Grant for their review of this paper and helpful suggestions.

The following abbreviations are used in this paper: USGS, United States Geological Survey; USNM, United States National Museum; UM, University of Missouri; UW, University of Wyoming.

Superfamily PRODUCTACEA Gray, 1840

Family PRODUCTIDAE Gray, 1840

Carlinia, new genus

DIAGNOSIS.—Productids with rather coarse uneven costation, bearing scattered spines on pedicle valve. Brachial valve nearly flat to moderately concave, with large diaphragm area bearing numerous concentric frills externally; spines absent. Diaphragm area not clearly delimited internally.

DESCRIPTION.—Shell of moderate size, somewhat elongate. Pedicle valve fairly evenly arched longitudinally; curvature decreasing gradually from umbo anteriorly; venter elevated, somewhat flattened medially, with or without sulcus; flanks fairly steep; valve flaring rather widely toward anterior margin.

Pedicle valve ornamentation of costae and costellae, weak indistinct rugae, and spines. Costae and costellae somewhat irregular in strength, with subequal to narrow intercostal sulcae; spines normally rather coarse, suberect, occurring: (1) scattered over shell on costae and commonly disposed in rows along thicker costae, directed forward on anterior slope; (2) in random group on flanks and on ears; and (3) usually sparsely and weakly along hinge.

Pedicle valve interior having narrow, shallow muscle scar platform flanked by relatively small weak diductor muscle scars; without identifiable endospines.

Brachial valve having small concave initial part bounded by narrow concentric ridge; diaphragm area large, concentric frills spaced 2 to 3 mm apart posteriorly and bunched anteriorly. Costae weak over initial unfrilled part of valve, absent over diaphragm area except locally on frills; spines absent on valve.

Brachial interior having visceral disc not clearly divided into prediaphragm and diaphragm areas; cardinal ridges moderately strong; median septum stout posteriorly; posterior platform supporting short sessile cardinal process, like that of *Diaphragmus*. Anterior and posterior pairs of adductor muscle scars well differentiated, on prominent raised platforms at either side of median septum, quadrilobate in overall aspect; brachial ridges enclosing slightly raised areas; no identifiable endospines.

TYPE-SPECIES.—*Productus phillipsi* Norwood and Pratten, 1855.

DISCUSSION.—This genus differs from *Diaphragmus* in having a very short trail, in having more irregular and usually coarser costation, in lacking a well-defined spine cluster on the flanks, in lacking spines on the brachial valve, and in having more than 10 concentric frills over the diaphragm area becoming more numerous and bunched together anteriorly.

Carlinia is a late offshoot of *Diaphragmus,* in which the trails developed so fast and so weakly that they never extended very far beyond the floor of the brachial valve but either broke off or just did not grow long. Spines also failed to develop on the brachial valve. This genus appears to have been a mud-lover and is generally found in calcareous shale and siltstone, rarely in impure limestone.

The name *Carlinia* is derived from Carlin Canyon near Carlin, Nevada, which is almost certainly the type-locality of its type-species, and where a second species, *Carlinia diabolica,* new species, is fairly common.

STRATIGRAPHIC CONSIDERATIONS.—This genus is restricted largely, and perhaps entirely, to late Chester rocks in the western United States. It is particularly abundant in those Late Mississippian rocks that overlie the *Caninia excentrica* coral zone (K zone of Dutro and Sando, 1963). In the Great Basin region of Utah and Nevada, however, *Diaphragmus* ranges a little higher than *Carlinia.*

Carlinia phillipsi (Norwood and Pratten)

PLATE 1: FIGURES 1–8, 21

Productus phillipsi Norwood and Pratten, 1855, p. 8, pl. 1, figs. 2a–c.

Productus(?) *phillipsi* Norwood and Pratten. Sutton, 1938, p. 559.

DIAGNOSIS.—Slightly elongate-oval *Carlinia* with hinge-line equal to three-fourths to four-fifths greatest width of shell; 20 to 26 costae and costellae on pedicle valve.

DESCRIPTION.—Shell generally slightly longer than wide, subcircular to suboval in plan; widest at or just anterior to middle. Pedicle valve strongly curved posteriorly; curvature lessening gradually anteriorly; umbo protruding 1 or 2 mm across hinge, moderately inflated, its sides diverging initially at approximately a right angle; flanks steep. Venter flattened, either with or without broad shallow sulcus on anterior slope; ears rather small, set off weakly from umbonal slopes by broad sulci. Valve somewhat flattened and tending to flare anteriorly.

Pedicle valve ornamentation consisting typically of 7 or 8 coarse ribs with wide and fairly deep intercostal sulci over ventral part of valve, commonly with narrower costellae between and on flanks, increasing by bifurcation; 20 to 26 costae and costellae present near anterior margin; considerable variation in arrangement and strength of costation among specimens. Rugae very indistinct, confined to posterior third of valve. Spine bases fairly prominent, suberect: (1) distributed in alternating pattern on stronger costae, 7 to 15 mm apart on single costa, (2) scattered in weak row or rows along hinge, strengthening toward ears, and (3) in two or three diagonal rows on ears and along base of umbonal slope, forming group of 6 to 9 spines just anterior to ears and on flanks.

Interior of pedicle valve having slightly raised midventral adductor muscle scar platform, about 9 mm long and 3½ mm wide, beginning 5 mm in front of umbo. Posterior pair of adductor muscle scars elongate, lenticular, weakly dendritic behind and smooth in front, separated by shallow median groove; anterior pair of adductor muscle scars indistinct, occupying V-shaped area enclosing anterior end of posterior pair and joining in oval area at anterior end of muscle scar platform. Diductor muscle scars occupying short fan-shaped areas at either side of adductor muscle scar platform, beginning 7 mm in front of umbo, rather coarse posteriorly, weaker and more finely radial anteriorly. No endospines observed.

Brachial valve gently concave; initial disc slightly more so, extending to approximately one-half the length of valve, edged by narrow raised ridge or lamella; broad shallow medial ridge arising anterior to initial disc, strongest near margin of valve. Part of valve outside of initial disc, valve consisting of frilled multiple diaphragm area, frills becoming more closely spaced anteriorly and crowded near margin. Costae narrow, weak, indistinct on initial disc, even weaker over diaphragm area but expressed by radial rows of frill convolutions. Trail very short on most brachial valves but moderately long and curving from visceral disc on some.

Interior of brachial valve with initial disc not differentiated from diaphragm area; ears pointed and set off from rest of valve by marginal embayment just in front of them. Cardinal ridges[1] prominent, acute, continuing outward and forward in curve across ear to valve margin, separating ear from visceral disc. Posterior platform massive, supporting cardinal process of marginiferid type; shaft short; myophore bifid above, divided by narrow median groove, trifid posteriorly. Median septum stout posteriorly, narrowing suddenly between adductor muscle scar platforms and extending about three-fifths of way across valve. Adductor muscle scars on prominent elevated subtriangular platforms; posterior pair dendritic, sprawling, anterior pair smooth, on club-shaped elements with narrow ends converging slightly anteriorly. Brachial ridges rather obscure, given off from middle of anterior pair of adductor muscle scars at angle of 25 degrees to hingle-line, curving outward, then inward and backward to enclose two subtriangular areas about 5 by 7 mm across, their farthest anterior extremities along line 7 mm behind anterior edge of valve.

Dimensions (in millimeters) of two hypotypes, both occurring near the top of the Chainman Shale, are as follows:

Dimension	*USNM 144014**	*USNM 144015†*
Maximum length	28. 5	30. 8
Length along arch	51. 0	59. 0
Maximum width	26. 0	24. 6
Width of hinge	19. 0‡	17. 8
Depth	15. 0	17. 5

*From USGS loc. 20460–PC.
†From USGS loc. 17217–PC.
‡Twice the half-width.

DISCUSSION.—The description and illustrations of *Carlinia phillipsi* are based upon specimens from the upper part of the Chainman Shale at Conger Spring in the Confusion Range and at Jensen Wash in the Burbank Hills, both in Millard County, Utah. As the partially silicified specimens at these localities did not yield well-preserved interiors suitable for illustration, the brachial valve interior is illustrated by a specimen from the type section of the Manning Canyon Shale in Soldier Canyon, Oquirrh Mountains, Tooele County, Utah (Plate 1: figure 21).

Norwood and Pratten's type-specimen, the whereabouts of which is not known to the writer, was well illustrated in the original report and shows the characteristic sculpture of this species. The specimens from Conger Spring have about the same relative proportions as those given for the holotype but tend to be coarsely costate. Those from Jensen Wash tend to be narrower than normal and ornamented by alternating costae and costellae. Those at Soldier Canyon are broad and tend to have costae of subequal strength. In general, the very coarse ribs and spines of this species are its identifying characters.

TYPE-LOCALITY.—According to Norwood and Pratten (1855, p. 8) the holotype of this species came from "Big Canyon of Humboldt River, Utah Territory." Only two large canyons are present along the Humboldt River: Carlin Canyon, a few miles east of the town of Carlin, and Palisades Canyon, a few miles southwest of Carlin. No upper Paleozoic rocks are exposed in Palisades Canyon, but in the eastern part of Carlin Canyon, near Tonka Siding, limestone of Late Mississippian age in the upper part of the Diamond Peak Formation crops out on both sides of the Humboldt. Light gray limestone in three fault blocks on the south side of the river has yielded fossils normally associated with *Carlinia phillipsi*. In two of the fault blocks, at the west side of a small north-trending tributary valley, 0.1 and 0.2 mile south of the river, respectively, *Carlinia diabolica,* new species, is included in this association. Although the writer has not found *C. phillipsi* in Carlin Canyon, he believes that the holotype must have come from these beds.

TYPES.—Hypotypes, USNM 144014–144020, inclusive (7 specimens).

DISTRIBUTION.—*Carlinia phillipsi* ranges from near Stockton, Utah, to near Eureka, Nevada. It is limited to a stratigraphic zone roughly 50 to 60 feet thick in the upper part of the Chainman Shale and stratigraphically equivalent beds in Utah in the lower part of the Manning Canyon Shale and in Nevada in the upper part of the Diamond Peak Formation. The top of this zone lies at levels of from roughly 60 to 150 feet below the top of the Mississippian System.

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[1] The term "cardinal ridges" is used in preference to "lateral ridges."

Occurrence.—Chainman Shale, upper part, USGS loc. 17217–PC, fossils weathering from calcareous shale on slope in measured section in Jensen Wash, Burbank Hills, 80 to 135 feet below top of Chainman Shale in SW¼SE¼NW¼ sec 35, T 22 S, R 18 W; USGS loc. 20460–PC, fossils in 5-foot calcareous shale bank, 100 feet north of Conger Spring, Confusion Range, Millard County, Utah. Manning Canyon Shale, USGS loc. 14515–PC, 10-foot platy limestone bed 405 feet above base in measured section in Soldier Canyon, one-half mile upstream from mouth, Oquirrh Mountains, Tooele County, Utah.

Carlinia amsdeniana, new species

Plate 1: figures 9–13, 22, 23

Diaphragmus phillipsi (Norwood and Pratten). Branson and Greger, 1918, p. 314, pl. 19, figs. 5, 6.

Marginifera muricatina Dunbar and Condra. Burk, 1954 p. 10, 11, pl. 1, figs. 26–28.

Diagnosis.—Rounded-subpentagonal *Carlinia* of subequal length and width; pedicle valve normally having V-shaped median sulcus, surface ornamented by 24 to 35 costae and costellae and numerous scattered spines including about 20 in area of hinge and ear. Brachial valve transversely subrectangular.

Description.—Pedicle valve having greatest width usually at ears just in front of hinge. Valve convex throughout longitudinal profile; curvature greatest at umbo and decreasing a little unevenly but gradually toward anterior margin. V-shaped median sulcus (not quite central in lectotype) present in some specimens, commonly beginning less than 5 mm in front of umbo, which protrudes slightly across hinge; in other specimens, area of sulcus is merely flattened or slightly depressed. Anterior and lateral slopes diverging toward margins; umbonal slopes steep and curving gradually outward so that ears are only moderately set off by broad diagonal sulci. Umbonal slopes diverging anteriorly at angle of roughly 110 degrees.

Surface of pedicle valve ornamented by somewhat irregular and subequal costae interspersed locally with costellae, averaging 30 in all but ranging from 25 to 35 in various specimens. Costae increase by bifurcation and some tend toward fasciculation anteriorly. Rugae absent or merely suggested by two or three faint concentric ridges in umbonal region of some specimens; concentric growth lirae not prominent. Spine bases abundantly scattered over valve: (1) on top of costae, commonly 1 to 2 mm apart over anterior slopes and 2 to 2¼ mm apart along individual costae; (2) in two rows of 6 to 7 spine bases at either side of umbo, one along hinge margin, other just in front at a very low angle diagonal to hinge and extending on to ears, merging with (3) cluster of about 12 to 15 spines scattered over umbonal and lateral slopes near ears.

Interior of pedicle valve with low medial platform-like structure beginning 2 to 3 mm anterior to umbo and up to 3 mm wide, consisting of two elongate smooth lobes divided by low median ridge; adductor muscle scar area begins at its anterior end, occupying space 4 mm long and 1.3 to 1.7 mm wide between diductor muscle scars. Posterior pair of adductor muscle scars narrowly dendritic, diverging slightly posteriorly; anterior pair nearly smooth, situated in elongate parallel depressions opposite anterior parts of diductors. Diductor muscle scars transversely oval, longitudinally lirate, 4 mm by 5 mm across, beginning 4 to 5 mm in front of umbo. Rest of pedicle interior weakly costate; no endospines visible.

Brachial valve transversely subrectangular in outline, gently concave medioposteriorly, somewhat less concave in lateral areas just in front of ears; also concave near anterior margin, except at shallow fold, commonly present, corresponding to sulcus of pedicle valve. Surface ornamentation of fine radial costellae limited to initial part of valve, bounded by single tiny concentric frill approximately at middle of valve. Two or three more such frills having wide but gradually narrower interspaces outward surrounding first one; band of 7 to 10 concentric wavy frills just within valve margin; all appear to represent trails that never fully developed. Interior of brachial valve not known.

Dimensions (in millimeters) are as follows:

Dimension	*Holotype UM 2645*	*Paratype USNM 163760*	*Paratype UM 2645*
Length	25. 1	23. 5	18. 5
Length along curvature	41. 0	40. 5	32. 5
Greatest width	25. 0	23. 5	20. 9
Width of hinge	22. 5	18. 5	19. 2
Depth	13. 3	12. 5	9. 7

Discussion.—Branson and Greger (1918) described and figured this species as *Diaphragmus phillipsi* (Norwood and Pratten). Their two figured specimens (UM 2645) have been examined and are refigured (Plate 1: figures 9–13, 22, 23) in this report. The larger has been selected as the holotype of *Carlinia amsdeniana* and the smaller has been designated a paratype. Dimensions of these two specimens are given above.

Included among the paratypes is a lot of 23 specimens collected by Keyte near Lander, Wyoming. The dimensions of one of these specimens (USNM 163760) are given above.

Burk (1954) described and figured two broken specimens from South Pass, Fremont County, Wyoming, as *Marginifera muricatina* Dunbar and Condra. Both specimens (UW IT–197 and IT–198) have been compared with the primary types of *Carlinia amsdeniana* and are judged to be conspecific.

Carlinia amsdeniana is a distinctive species that differs from *C. phillipsi* (Norwood and Pratten) in having a slightly wider shell, commonly with a V-shaped median sulcus in the pedicle valve; a larger number of costae; much wider hinge and ears; a much greater number of spine bases scattered over the surface, particularly along the hinge and near the ears; and a transversely subrectangular brachial valve.

Carlinia diabolica, new species, differs from *C. amsdeniana* in lacking a V-shaped median sulcus, in its finer surface ornamentation of 35 to 50 costellae, and in having fewer and coarser spine bases.

TYPES.—Holotype, UM 2645 (part); paratypes, UM 2645 (part, 1 specimen); paratypes, USNM 163760–3.

DISTRIBUTION.—*Carlinia amsdeniana* apparently is restricted to the *Spirifer welleri* zone of Shaw (1955), which is very late Chester (Late Mississippian) in age, in Fremont County, Wyoming.

OCCURRENCE.—Amsden Formation, Horseshoe Shale Member, near middle; UM 2645 (USGS loc. 19283–PC), Cherry Creek, sec 19, T 31 N, R 99 W; USNM 163760–1, near Lander, Fremont County, Wyoming.

Carlinia diabolica, new species

PLATE 1: FIGURES 14–20, 24, 25

Productus elegans Norwood and Pratten. Hall and Whitfield, 1877, p. 268, 269, pl. 5, figs. 3, 4.

Diaphragmus elegans (Norwood and Pratten). Girty, 1920, pl. 53, fig. 8.

DIAGNOSIS.—Subcircular to subpentagonal *Carlinia* with greatest width near hinge. Pedicle valve ornamented by 35 to 50 costae and costellae; coarse spines scattered sparsely over surface, 6 to 7 on each flank near ear. Brachial valve subtrapezoidal in plan.

DESCRIPTION.—Shell subcircular in plan, except for protruding ears giving subpentagonal aspect; visceral cavity of moderate depth. Pedicle valve moderately arched; curvature decreasing rather gradually from umbo, except for slight geniculation 7 to 8 mm in front of umbo. Venter and flanks merging in gradual convex curve, venter either rounded or somewhat flattened; some specimens possessing broad shallow median sulcus on anterior slope. Ears rather large, not well differentiated from sloping lateral and umbonal slopes but merging in broad concavity. Umbo narrow, pointed, protruding not quite 2 mm in front of hinge, sides diverging anteriorly at approximately a right angle; umbonal region somewhat depressed.

Pedicle valve ornamented by fine irregular costae or costellae, weak rugae, and scattered spines. Costae low, rounded, with narrow intercostal sulci, increasing by bifurcation and tending toward fasciculation, particularly near spine bases; some costae pairs merging into single costa anteriorly; normally 14 to 15 costae occurring in space of 10 mm in middle of

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PLATE 1.—All views natural size unless otherwise indicated. Figures 1–8, 21.—*Carlinia phillipsi* (Norwood and Pratten): 1–3, Pedicle, side, and brachial views of USNM 144015, from USGS loc. 17217–PC, Burbank Hills, Utah; 4, enlarged posterior view (× 1½) of USNM 144017, from the same locality; 5–7, pedicle, side, and brachial views of USNM 144014, from USGS loc. 20460–PC, Confusion Range, Utah; 8, interior of pedicle valve from rubber cast of an internal mold (× 1½); USNM 144016, from USGS loc. 17217–PC; 21, interior of brachial valve from USNM 144019, from USGS loc. 14515–PC, Oquirrh Mountains, Utah.

Figures 9–13, 22, 23.—*Carlinia amsdeniana*, new species: 9–11, 22, 23, pedicle, side, and brachial views and enlarged posterior and side views (× 2) of the holotype UM 2645, Wind River Range, Wyoming; 12, 13, pedicle and side views of a paratype, UM 2645, from the same locality.

Figures 14–20, 24, 25.—*Carlinia diabolica*, new species: 14–16, 25, pedicle, side and brachial views and enlarged side view (× 2) of the holotype USNM 144021, from USGS loc. 16993–PC, Confusion Range, Utah; 17, enlarged interior view of a specimen collected by the 40th Parallel Survey and paratype, USNM 144024, from USGS loc. 20460–PC, Confusion Range, Utah: 18, 19, side and pedicle views of a paratype, USNM 144025, from USGS loc. 16993–PC; 20, pedicle view of a specimen collected by the 40th Parallel Survey and figured by Hall and Whitfield (1877, pl. 5, figs. 3, 4) as *Productus elegans* and by Girty (1920, pl. 53, fig. 8) as *Diaphragmus elegans*, from Oquirrh Mountains, Utah; 24, enlarged view (× 1½) of interior of a brachial valve, a rubber cast from a paratype, USNM 144024, from USGS loc. 20460–PC.

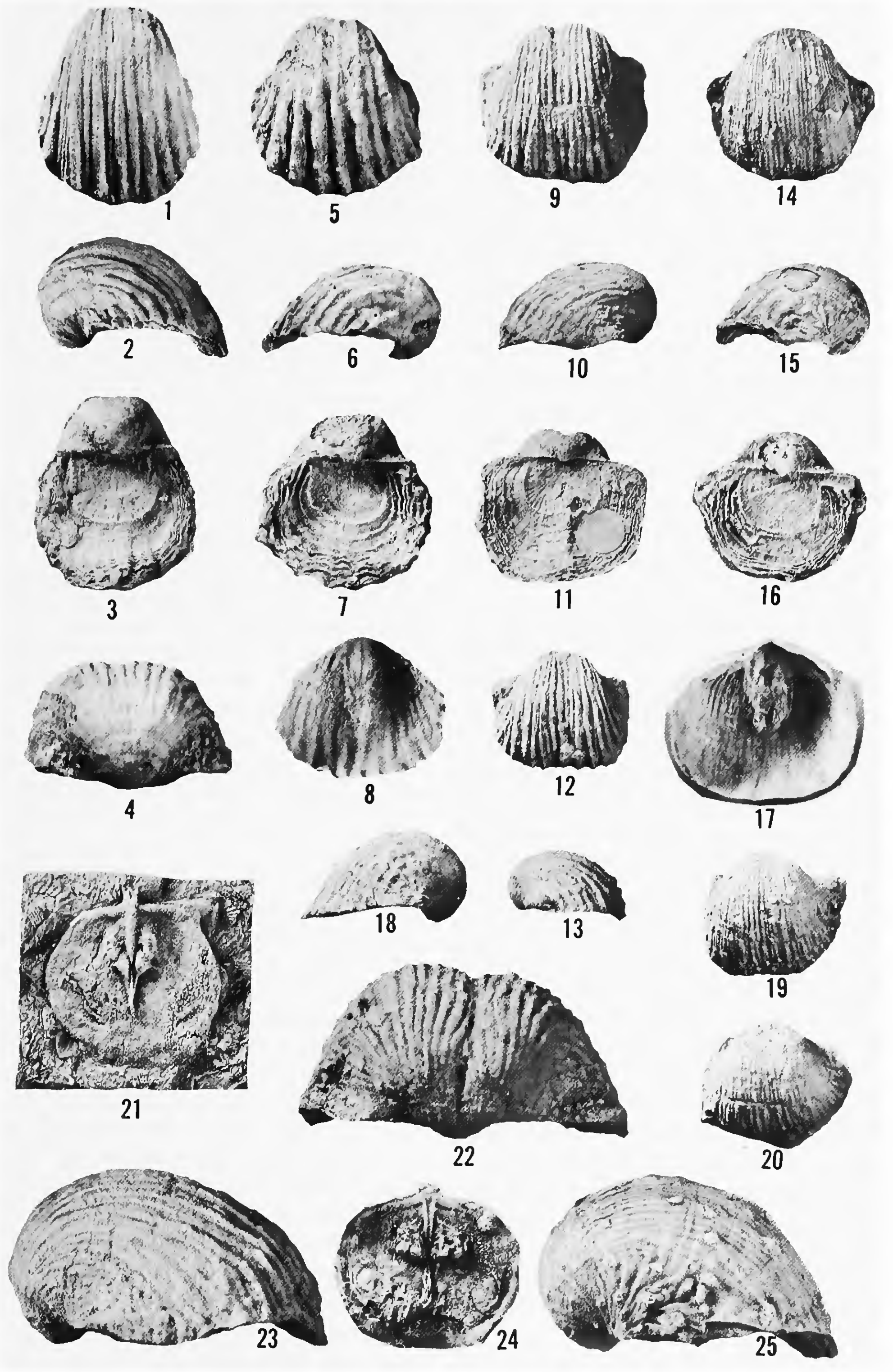

PLATE 1

anterior slope; costae averaging about 40 in all, weak to absent near ears. Rugae fine, weak, confined to flanks and ears on posterior half of valve. Spines rather stout, suberect; spine bases occur: (1) scattered over venter and anterior and lateral slopes, 2 to 7 mm apart, mainly along rows of costae where fasciculation is greatest, 3 to 11 mm apart on single rows; (2) in row of 5 or 6 along hinge margin at either side of umbo and generally two vague rows of 2 or 3 in sulcus at base of ear and also on ear at considerable angle to hinge; and (3) in group of 5 or 6 large spines on flanks in front of ears.

Interior of pedicle valve having prominent bilobate raised adductor muscle scar platform beginning 5 mm in front of umbo, 4 mm wide and 8 mm long; posterior and anterior adductor scar pairs dendritic. Diductor scars deeply grooved, fan-shaped, beginning 7 mm in front of umbo and extending about 6 mm. Anterior part of valve interior finely and irregularly lirate, with numerous tiny endospines.

Brachial valve very shallowly concave; initial part of valve shallowly concave, bordered with acute raised ridge; area along hinge about 2 mm wide, smooth from ear to ear; rest of valve consisting of multiple diaphragm area, ornamented by concentric frills 1 or 2 mm apart near initial part and becoming ever more closely spaced anteriorly; frilled area with broad shallow medial ridge anteriorly. Fine costae and rugae indistinct but present on initial part of valve; some costae discernible in diaphragm area.

Interior of brachial valve having rather thick rounded cardinal ridges supporting short sessile cardinal process, weakly bifid above and trifid posteriorly and externally; posterior part of septum fairly thick, marked by shallow median groove; septum narrowing markedly in front of adductor muscle scar platforms and extending to point about two-thirds of way across valve. Pair of adductor muscle scar platforms forming four pear-shaped lobes standing in low relief anteriorly and sloping posteriorly; posterior pair of muscle scars dendritic, anterior pair appearing smooth. Brachial ridges anterior to and at either side of muscle scars enclosing suboval areas roughly 3 mm by 4 mm across near lateral margins of valve and behind line 4 mm from anterior end of valve.

Dimensions (in millimeters) of holotype and a paratype:

Dimension	*Holotype USNM 144021*	*Paratype USNM 144022*
Length	23. 6	23. 5
Length along arch	45. 0	45. 0
Maximum width	25. 7	*28. 0
Width of hinge	24. 0	*25. 0
Depth	14. 0	14. 5

*Twice the half-width

Discussion.—The description of the external characters of this species is based on specimens from Wallet Gulch on the west slope of the Confusion Range, Utah. The internal characters are from a paratype from Conger Spring, two miles southeast of Wallet Gulch, where this species occurs in association with *C. phillipsi* (Norwood & Pratten).

Variation in *Carlinia diabolica* most frequently involves the number of costae and costellae, number and distribution of spines, and presence or absence of a shallow ventral sulcus. The number of costae and costellae on individual specimens ranges, roughly, from 35 to 50. Those with finer costation generally have more rows of spines. Some specimens have more spines along the hinge and also on the flanks near the ears, but the spines are distributed randomly and never form an isolated spine cluster as in species closely related to *Diaphragmus cestriensis* (Worthen).

Carlinia diabolica can be mistaken for shells of *Diaphragmus cestriensis* because the number and strength of the costae are similar; it may be distinguished, however, by its wide ears, less steeply sloping flanks, less protruding umbonal region, absence of a prominent spine cluster on the flanks just in front of the ears in the pedicle valve, the absence of a long tail or of spines on the brachial valve and the presence, in their stead, of concentric frills on the brachial valve.

A productid from the Oquirrh Mountains, Utah, described and illustrated by Hall and Whitfield (1877) as *"Productus elegans* Norwood and Pratten" [=*Diaphragmus cestriensis* (Worthen)] has been compared with the primary types of *C. diabolica* and found to be conspecific. The same specimen was figured by Girty (1920). This specimen, recorded by geologists of the 40th Parallel Survey as coming from north of Snowstorm Hill, Dry Canyon, Oquirrh Mountains, is refigured here (Plate 1: figure 20).

The new species is readily distinguished from *C. phillipsi* by its finer sculpture, wider hinge, and prominent ears. This species can be distinguished from *C. amsdeniana* by its more numerous costae and costellae, fewer and coarser spines, and by its general lack of a narrow median sulcus in the pedicle valve.

TYPES.—Holotype, USNM 144021; paratypes, USNM 144022-5, inclusive (7 specimens). Figured specimen, USNM 14216.

DISTRIBUTION.—This species is recognized in the Great Basin from the Oquirrh Mountains, at the east, to the Carlin region, Nevada, at the west. It is found throughout at least 150 feet of the section at Wallet Gulch in the upper part of the Chainman Shale. In the Oquirrh Mountains it probably comes from the Manning Canyon Shale, and in the Carlin region it has been collected in the upper part of the Diamond Peak Formation.

OCCURRENCE.—Primary types from the Chainman Shale, upper part (USGS loc. 16993-PC), 50 feet stratigraphically below and east of base of Ely Limestone. Additional paratypes from 5-foot calcareous shale bank (USGS loc. 20460-PC) 100 feet north of Conger Spring, Confusion Range, Millard County, Utah. Figured specimen from unidentified formation, probably the Manning Canyon Shale, Dry Canyon, Oquirrh Mountains, Utah.

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M. J. S. Rudwick

The Functional Morphology of the Pennsylvanian Oldhaminoid Brachiopod *Poikilosakos*

ABSTRACT

The morphology of *Poikilosakos,* the earliest known oldhaminoid, is analyzed functionally. It is inferred that (1) much of the ventral mantle tissue was permanently exposed beyond the edge of the pinnate dorsal valve; (2) the normal external growth lines on the dorsal valve indicate that it was not sheathed in mantle tissue but (3) it grew according to the same morphogenetic "rules" as later oldhammoids; (4) the hinge, although aberrant, indicates habitual movement of the dorsal valve rotating vertically; (5) the right diductor was atrophied except in a rare variant form; (6) the axis of a ptycholophe was borne near the edge of the dorsal valve; and (7) the feeding mechanism may have been of a rhythmic type analogous to that known in septibranch mollusks and inferred in richthofeniid brachiopods. The phyletic significance of this functional reconstruction is considered briefly; it is concluded that the oldhaminoids may have been derived neotenously (and hence cryptogenetically) from davidsoniacean ancestors, and that their extinction should not be attributed too readily to over-narrow adaptive specialization.

The oldhaminoids are of exceptional interest in the study of brachiopod evolution. In form and structure they are more peculiar and aberrant than any other members of the phylum, and they seem to indicate the fullest extent to which the basic organization of the brachiopod body has ever been modified in the course of evolution. Their structural peculiarities suggest that their mode of life may have been correspondingly unusual; therefore, they are important in any functional or adaptive interpretation of brachiopod evolution.

Such aberrant fossils have naturally attracted much attention, and interpretations of their structure and mode of life have been varied and controversial. Papers by Williams (1953) and Stehli (1956) summarize some of the points at issue, and refer to earlier works. An evaluation of divergent views has been hampered, however, by the small number of well-preserved specimens which have been adequately illustrated. For the later, Permian, members of the group this will no doubt be rectified by the publication of Dr. G. A. Cooper's description of the magnificent silicified material from the Glass Mountains in western Texas. Meanwhile, it seems worthwhile to analyze the earliest member of the group, which is simplest in structure and, by common consent, likely to be the ancestor of all later members; for in its functional interpretation there may be found a key to the understanding of the aberrant structure of the group as a whole.

Poikilosakos was first described half a century ago by D. M. S. Watson (1917), from 20 specimens collected in the Graham Group (late Pennsylvanian) of north-central Texas. These specimens are now in the British Museum (Natural History), abbreviated herein as BMNH. They came from "a well-known locality in the west bank of the Salt Creek at Graham, Young County, Texas." This was probably in the Wayland Shale, the topmost member of the Graham Group, which consists of clay shales with partings of earthy limestone. In the United States National Museum

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(USNM) there are other specimens from the Wayland Shale, from Gunsight, Stephens County, Texas, and also specimens from the Gonzalez Formation, in the lower part of the Graham Group, from near Finis, Jack County, Texas. Also, I have restudied the specimens described by Dunbar and Condra (1932) from the base of the Plattsmouth Limestone Member of the Douglas Group, near Lawrence, Kansas, and now in the Peabody Museum, Yale University (YPM 13559); and a single important specimen from the same limestone at Williamsburg, Kansas, in the United States National Museum (USNM 137498). All these localities are at approximately the same horizon in the late Pennsylvanian.

Poikilosakos was cemented throughout life to some hard material, on a substrate which must have been predominantly muddy. The surfaces used for attachment include large fragments of a massive shell with prismatic structure, productoid shells, large cylindrical corals, and crinoid stems. These organisms merely provided debris suitable for the attachment of the spat of *Poikilosakos:* there is no evidence to suggest that any of them were alive at the time of attachment.

I am grateful to Dr. H. Brunton and Dr. G. A. Cooper for access to specimens of *Poikilosakos* in the British Museum (Natural History) and in the United States National Museum, respectively, and for the loan of some specimens. Most of this work was done under a grant from the Science Research Council of Great Britain.

Shell and Mantle

General morphology of the shell (Figures 1, 4a).—*Poikilosakos* is the earliest and structurally the simplest of the oldhaminoids. But it already possessed most of the peculiar characteristics of the group, and has little immediate resemblance to most ordinary brachiopods.

The ventral valve consists of a very thin sheet of calcite. Generally its outer surface is entirely adherent to the substratal surface, and the shell material is so thin that in parts of some specimens it is almost transparent. Its outer edge, therefore, is difficult to locate precisely, except where it has grown a little away from the substrate. For this reason, the true size of the valve is difficult to determine in most specimens.

This thin sheet of shell material is thickened locally into a long sinuous ridge, termed by Watson as the "flange," which coalesces posteriorly with a short transverse "hinge ridge." The sinuous course of the flange marks out a series of blunt-ended "lobes" separated by narrower "indentations." There is a long and relatively conspicuous "median indentation," projecting backwards towards the hinge ridge. The "lateral indentations" are much less regular. Generally, the course of the flange is highly variable and shows only a very rough approximation to bilateral symmetry (Figure 2). Its irregularity is not due to that of the surface of attachment, since many highly irregular specimens are attached to almost smooth plane surfaces.

Both outside and inside the flange, the surface of the valve is marked faintly with fine pustules (Plate 1: figure 8; Plate 2: figure 5). These probably indicate a pseudopunctate shell structure, as on other oldhaminoid brachiopods. The area outside the flange may be termed the "peripheral zone" on the valve; the area inside, the "inner zone."

The dorsal valve[1] is also a very thin plate, almost flat, and with a pinnate outline corresponding to the course of the flange on the ventral valve. Watson's specimens included no dorsal valves at all, but he correctly inferred that its pinnate edge would be found to rest on the narrow "shelf or rabbet" which runs around the inner side of the flange. Specimens since discovered, in which the dorsal valve is preserved in place, show that there is a tight fit between the edge of the valve and the shelf on which it rests. This may be termed a "secondary commissure": there is no true commissure, since the ventral valve extends on all sides beyond the edge of the dorsal. Between the dorsal valve and the inner zone of the ventral valve, within the flange, there is a very shallow "shell cavity." When

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[1] Williams (1953) has argued that the dorsal valve of oldhaminoids was, in fact, an "internal plate," homologous with the internal "lophophore platform" of some earlier brachiopods, and that the true dorsal valve is vestigial. But the term "dorsal valve," as ordinarily understood, includes not merely the external surface of the valve (generally covered with primary-layer shell) but also all its various internal modifications and processes, such as the cardinalia, and including any so-called "lophophore platform." Even if Williams' anatomical reconstruction is correct, it is therefore legitimate to continue to use the conventional term "dorsal valve" for oldhaminoids, rather than the confusing and overinterpretative term "internal plate." Similarly, I prefer to use the clearly understood term "ventral valve" rather than "pedicle valve" for a structure in which no trace of a pedicle is known.

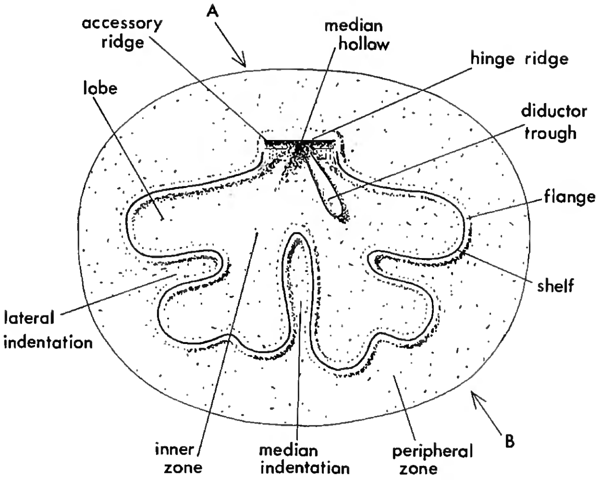

FIGURE 1.—Ventral valve of *Poikilosakos,* diagrammatic, to illustrate morphology. A–B, Approximate line of section shown in Figure 4A.

the dorsal valve is resting on the shelf, the shell cavity is completely isolated from the exterior.

On the posterior side of the dorsal valve, there is a broad rectangular projection. Its straight posterior edge abuts against the anterior face of the hinge ridge. No specimen in which the internal surface of the dorsal valve is exposed has been available to me.

RECONSTRUCTION OF MANTLE.—In order to secrete the peripheral zone, the ventral mantle must have extended outwards beyond the edge of the dorsal valve and mantle. Williams (1953, and in Moore, 1965) has argued convincingly that the ventral mantle of some later oldhaminoids, which was responsible for secreting a complex "posterior flap" in the peripheral zone, must have been highly contractile. If the tissue of *Poikilosakos* shared this property, the ventral mantle might normally have been retracted within the flange, and thus protected by the dorsal valve; and it might have been extended periodically to secrete new increments to the peripheral zone. But it is difficult to imagine how the ventral mantle could have been retracted from the posterior sector of the peripheral zone, because its retraction across the hinge ridge would have been barred by the abutting posterior edge of the dorsal valve. It is more satisfactory to conclude, with Williams, that the ventral mantle, although perhaps somewhat contractile, was permanently exposed beyond the edge of the dorsal valve. The dorsal valve would thus have lost its normal—and probably original—function of protecting all the soft tissues from the external environment (cf. Sarycheva, 1964). In this respect *Poikilosakos* and other oldhaminoids resemble richthofeniids: the spines developed in the peripheral zone ("outer shell cavity") of *Prorichthofenia* would have prevented the ventral mantle from retracting within the protection of the dorsal valve (Rudwick 1961a).

Williams (1953) postulated that the dorsal valve of oldhaminoids was entirely sheathed in mantle tissue, covering its external as well as its internal surface. This reconstruction was based on the known relation between the mantle edge and the external primary-layer shell in living brachiopods, and on the absence of primary-layer (except a small area at the hinge) on the dorsal valve of oldhaminoids. This was criticized

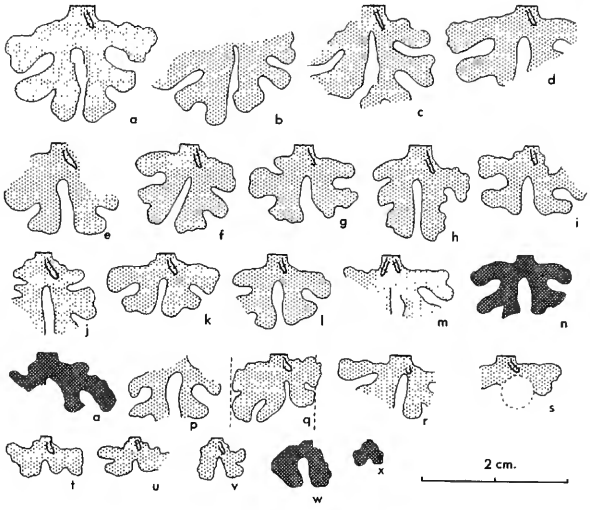

FIGURE 2.—Outlines of dorsal valves of *Poikilosakos,* arranged in approximate order of size, to show variability, and correlation of complexity with size. In most specimens (lightly stippled) the dorsal valve is not preserved, and its outline is inferred from the course of the shelf on the ventral valve flange. Specimens with dorsal valve preserved are more darkly stippled. The diductor troughs also are shown where visible. Key to specimen numbers: *a,* BMNH BB.11266 (holotype, as in Plate 1: figure 1); *b,* USNM 148051d; *c,* YPM 13559a; *d,* BMNH BB.11267a (as in Plate 2: figure 3); *e,* BMNH BB.54734a; *f,* BMNH BB.11269a (as in Plate 2: figure 6); *g,* BMNH BB.11269b; *h,* BMNH BB.54734b; *i,* USNM 148051c; *j,* USNM 165838; *k,* USNM 165839 (as in Plate 1: figure 4); *l,* BMNH (unnumbered); *m,* USNM 148051b (as in Plate 1: figure 5; note paired diductor troughs); *n,* USNM 137498 (as in Plate 1: figure 7 and Plate 2: figures 1, 2); *o,* YPM 13559b; *p,* YPM 13559c; *q,* USNM 165840 (as in Plate 1: figure 3 and Plate 2: figure 5; lateral lobes foreshortened by being curved around crinoid stem, outlined by dashed lines); *r,* USNM 148051e; *s,* USNM 165841 (as in Plate 1: figure 8; outline modified by circular base of crinoid cirrus); *t,* USNM 165842; *u.* USNM 148051a; *v.* BMNH BB.11267b (as in Plate 1: figure 2); *w,* USNM 165843 (as in Plate 1: figure 6); *x,* USNM 165844 (as in Plate 1: figure 4).

by Stehli (1956), who suggested that the absence of primary-layer more probably reflected some differences in the physiology of shell secretion in the oldhaminoids. To some extent this criticism has been justified by the discovery, emphasized recently by Williams (in Moore, 1965; 1968), that primary-layer is sporadically developed, and sometimes absent, on strophomenide and other early brachiopods. Yet, Williams' interpretation is strongly supported, in my opinion, by the distinctive pustular external surface of the dorsal valve of most oldhaminoids (Rudwick and Cowen, 1968). This surface closely resembles the adjacent internal surface of the ventral valve. It is quite different from the external surface of the ventral valve, which, like the external valve surfaces of most other brachiopods, is marked with strong growth lines.

In this context the presence of pustules or of growth lines on a valve surface may be a more reliable criterion than the absence or presence of primary-layer for determining which surfaces were covered with mantle tissue and which were not. It would hardly be doubted that the criterion is valid for the ventral valve of oldhaminoids, so it may also be valid for the dorsal.

There is a striking difference between the dorsal valve of *Poikilosakos* and that of later oldhaminoids such as *Leptodus* and *Oldhamina.* In the later oldhaminoids, as already mentioned, the external surface of the dorsal valve is pustular, and resembles the adjacent internal surface of the ventral valve. In *Poikilosakos* it is not pustular but smooth, and shows clear growth lines, indicating the course of its development during ontogeny (Plate 1: figures 6, 7; Plate 2: figures 1, 2, 4). It closely resembles the external surface of the ventral valve of other oldhaminoids (the ventral valve of *Poikilosakos* itself cannot be used for comparison, since its external surface is wholly adherent to the substratum). On any less-aberrant brachiopod, such a surface with growth lines would be accepted without hesitation as a true external surface, which was not covered by mantle tissue. Specimens of *Poikilosakos* are too rare to justify sectioning a dorsal valve to determine its shell structure; but it appears to have primary-layer on its external surface. Even if primary-layer is absent, the clear growth lines indicate that the surface grew only by peripheral accretion, and this is strong circumstantial evidence that it was not covered by mantle tissue.

It therefore is probable that the dorsal valve of *Poikilosakos* was lined with mantle tissue only on its internal surface, as in any normal brachiopod, and that it was not wholly sheathed in mantle tissue. If Williams's interpretation is correct for some later oldhaminoids, as I believe it is, the dorsal valve must have become sheathed with mantle tissue at some point in oldhaminoid evolution later than the stage represented by *Poikilosakos.*

GROWTH-PATTERN OF THE DORSAL VALVE.—The growth lines on the dorsal valve show that fairly early in ontogeny it had a bilobed outline (Plate 2: figure 4): the earliest stages of all are not clearly preserved. Beyond this stage the analysis rests perforce on a single good specimen. In this specimen (Plate 1: figure 7), the bilobed outline developed by differential secretion into a four-lobed form. In detail (Plate 2: figures 1, 2), each lobe can be seen to have grown principally by a somewhat irregular addition of arcuate increments at its distal end; there was little or no accretion on the sides of the lobe, with the result that it maintained a fairly uniform width while growing in length.

The posterior pair of lobes grew laterally almost parallel to the hinge-axis; the anterior pair grew parallel to the posterior, maintaining a uniform width of indentation between them. At some point in the growth of these four lobes, a third pair seems to have been initiated by the budding of new accretionary material from the anteromedian corners of the anterior pair. These new lobes, like their predecessors, seem to have grown in such a way as to maintain slits of uniform width both medially and anterolaterally.

This growth-pattern has been analyzed elsewhere, in conjunction with evidence from later and more complex oldhaminoids, as the result of the operation of simple morphogenetic "rules" (Rudwick, 1968b). These "rules" would include two basic parameters, a standard lobe-width width (W) and a standard slit-width (S). The valve would develop, probably from an initial subcircular form, in such a way as to maintain those parameters, each lobe growing parallel to a pre-existing lobe. There may then have been a critical lobe-length (K), on attaining which the anterior lobes would produce anteromedian buds, thus initiating further lobes. On the assumption of parameters such as these, the growth of a wide variety of oldhaminoid dorsal valves can be simulated realistically.

The dorsal valve of *Poikilosakos* is amenable to analysis in these terms. In particular, the widths of the lobes and slits (or indentations) are comparable to those of all later oldhaminoids, and the dorsal valve growth lines show positive evidence for localized "budding," which can only be inferred circumstantially in other genera. But *Poikilosakos* is distinctive in two important respects: the dorsal valve is both simpler and more irregular in form than in most later genera. These features can be interpreted as the result of the same morphogenetic "rules" as in later genera, operating on a valve of smaller absolute size, and also operating with much less precision.

Reconstruction of body and mantle cavities.—The limits of the body cavity or coelom of *Poikilosakos* can be reconstructed approximately by homology with living brachiopods. In living articulates the body wall is closely wrapped around the anterior and lateral surfaces of the muscles, and the coelom is confined to a very small posteromedian portion of the shell cavity. The muscles of *Poikilosakos* are difficult to interpret (see below), but they almost certainly were confined to the posteromedian portion of the shell cavity. In any case the coelom must have been greatly confined by the extreme shallowness of the space available between the valves (Figure 3).

The remainder of the shell cavity would have formed an equally shallow "mantle cavity." When the dorsal valve was closed and resting on the shelf, the tight secondary commissure would have insured that the mantle cavity was completely isolated from the exterior. Thus, the dorsal valve must have retained at least a part of its original protective function. When closed it would have sealed off from the external environment not only the "body" of the brachiopod (i.e., muscles, gut, etc.) but also the lophophore and any other organs in the mantle cavity. Only the peripheral tissue of the ventral mantle would have been permanently exposed, and unprotected by the dorsal valve.

Hinge and Musculature

Structure of the hinge (Figure 3).— The posterior edge of the dorsal valve abuts the anterior face of the hinge ridge. This anterior face is sharply defined and concave in the vertical plane (Plate 2: figure 6). Ventrally, it curves around into a very fine sharp ridge that runs parallel to the hinge ridge itself. This may be termed the "accessory ridge" (Plate 1: figure 8; Plate 2: figure 3). Dorsally, it curves around to the crest of the hinge ridge, behind which the ridge slopes away gradually and merges into the posterior sector of the peripheral zone.

Although no dorsal valve interior has been seen in the course of this study, an isolated dorsal valve (USNM 137498) shows that the posterior edge is convex in the vertical plane, so that it could have fitted accurately against the concave surface of the hinge ridge. This implies that the actual articulation of the valves occurred between these cylindrical surfaces. Thus, the hinge axis of the rotation of the dorsal valve during its movements would have passed through the posterior edge of the dorsal valve.

The anterior surface of the hinge ridge is marked with faint growth lines (Plate 2: figure 6) which show that during ontogeny it increased in size only by marginal accretion. This suggest that it was not covered by mantle tissue. If it was an articulating surface, as it appears to have been, it is not surprising that it should have been an area of naked shell.

The anterior face of the hinge ridge of *Poikilosakos* was identified by Watson as the vestigial "area," i.e., ventral interarea. This homology seems to be difficult to sustain. A true interarea is a part of the external surface of the valve, modified by being the growth track of the hinge line during ontogeny. The homologous area in *Poikilosakos* would be the posterior sec-

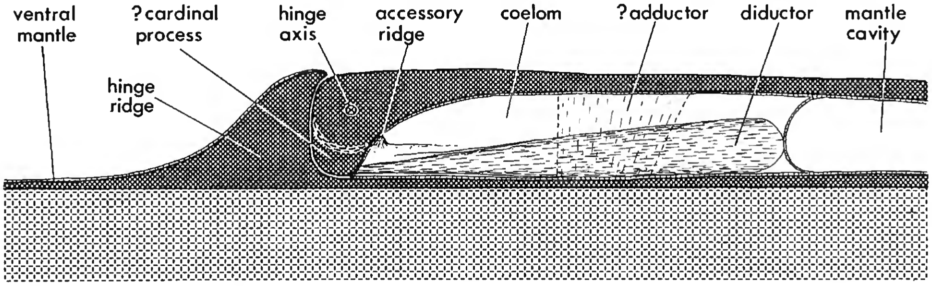

Figure 3.—Reconstruction of hinge mechanism and muscles of *Poikilosakos:* left side of hinge region, cut in median section and seen from right. Form of cardinal process and position of adductor muscle hypothetical.

tor of the peripheral zone of the ventral valve, but this is adherent to the substratum and has lost all functional and spatial connection with the hinge mechanism. Likewise, a faint median notch in the hinge ridge of some specimens was identified by Watson as the homologue of the delthyrium, but it too can only be regarded as an analogue.

Anterior to the hinge ridge is a relatively deep depression, which may be termed the "median hollow." It is deepest and also narrowest immediately in front of the hinge ridge, where it interrupts the fine accessory ridge (Plate 3: figure 3). Anteriorly it becomes broader and shallower, and merges into the rest of the inner zone of the ventral valve surface.

The posterior part of the median hollow probably is occupied fully by the cardinal process. Since no dorsal valve interior has been seen, the form of the cardinal process is uncertain.

Flanking the median hollow laterally are the two triangular areas which Watson termed "dental areas." By giving them that name, he evidently regarded them as homologues, or at least analogues, of normal teeth and sockets. He noted that they are very slightly concave (not convex as stated by Williams in Moore, 1965), but it is not known whether there are corresponding convex areas on the dorsal valve. In any case they do not make convincing homologues for the convex teeth of normal brachiopods. Watson noted that they are marked with faint longitudinal striations (Plate 2: figure 5). These cannot be equivalent to the striations of the teeth of some other brachiopods, nor can they be vestigial denticles. Anteriorly they can be seen in some specimens to swing laterally, following the course of the rest of the flange; and this indicates that they are merely growth lines showing the stages of growth of the most posterior part of the shelf and flange.

Watson inferred, from the asymmetrical muscle attachments (see below), that the dorsal valve did not rotate vertically but slewed laterally. But the edge of the dorsal valve, when closed, rests on the shelf within the flange. Therefore no lateral movement would have been possible unless the valve were first raised vertically enough to bring its edge clear of the crest of the flange. Even after this slight vertical rotation, a subsequent lateral movement seems highly improbable. Any such movement must have been centered around some secondary, vertical pivotal axis, which would surely be reflected in some asymmetry of the hinge ridge and dental areas. In fact, the symmetrical and strictly transverse structure of the hinge region suggests strongly that the pivotal axis was exclusively horizontal and transverse in orientation, and that the movement was strictly vertical, as in any normal articulate brachiopod. In any case, as both Williams and Stehli have pointed out, no lateral movement would have been possible in most of the later oldhaminoids, for in these brachiopods the peripheral zone of the ventral valve generally curves upwards on either side of the dorsal valve and would have confined its movement strictly to the vertical plane.

The degree to which the dorsal valve of *Poikilosakos* habitually opened cannot easily be inferred. Judging by the orientation of the articulating surfaces, the maximum possible angle of opening might have been as great as 45 degrees, but the usual angle may have been much less. In some later oldhaminoids, e.g., *"Lyttonia conica,"* the ventral valve developed into a narrow cone within which the maximum possible angle of opening was certainly quite small (Rudwick and Cowen, 1968).

The articulation of *Poikilosakos* is highly modified from the hinge structures of more normal brachiopods, but it does not support Williams' suggestion that the dorsal valve of oldhaminoids was immobile. Given the existence of suitably arranged muscles, the dorsal valve of *Poikilosakos* would have been physically capable of rotating vertically through a small or large angle. The valves were not locked together by teeth and sockets, but in this respect the oldhaminoids merely resemble the many productoids in which teeth and sockets were lost.

RECONSTRUCTION OF MUSCLES.—On a ventral valve of *Poikilosakos,* one muscle attachment is conspicuous. It is generally a narrow parallel-sided trough with raised margins, extending obliquely forwards from the posterior part of the median hollow. In detail its form is variable, but its outer edge is generally overhanging, so that the opening of the trough faces obliquely inwards (Plate 2: figures 3, 6). Within the trough there are faint growth lines (Plate 2: figure 5), showing the stages of its enlargement away from the hinge region during ontogeny.

Watson identified this trough as the ventral attachment of an adductor muscle, but in form and position it more closely resembles a diductor attachment and generally has been accepted as such. From the apex of the median hollow, where the cardinal process would have been situated, the muscle would have extended obliquely along the axis of the trough as a slender bundle of fibers. The raised margins of the trough would have increased the area for attachment of the fibers without increasing the area occupied on the floor of the valve, thus saving space in the confined body cavity.

This attachment invariably lies on the anatomical left side of the ventral valve (i.e., right side of illustrations in conventional orientation). With one important exception (to be discussed below), there is no trace of any corresponding attachment on the anatomical right side. Watson marked two small areas on this side as being muscle scars, but I have been unable to detect them on his original specimens or on any others. In well-preserved specimens the whole of this area is covered uniformly with a finely pustular surface (Plate 1: figure 8; Plate 2: figure 5). It is difficult to avoid the conclusion that the right diductor muscle of *Poikilosakos* had atrophied altogether. If so, it is likely that when a specimen with cardinal process is discovered it will be found to have corresponding asymmetry, i.e., a single lobe instead of the usual bilobed structure.[2]

This conclusion is supported by the existence of a single specimen in which the left diductor attachment is matched by another attachment of equal size on the right side. That specimen is from the same locality as other specimens having the usual single asymmetrical attachment. It may be interpreted as a variant, evidently rare, in which the right diductor was not atrophied. No specimen has been found in an intermediate condition, with a right diductor attachment reduced in size. Though the available sample is small, this suggests that the atrophy of the right diductor may have affected the population in an all-or-none manner.

The pull of the diductor during contraction would have been nearly horizontal, but on a line running ventral to the inferred hinge-axis (Figure 3). This would have enabled the animal to rotate and open the dorsal valve by the normal leverage, provided only that the posterior edge of the dorsal valve was constrained from sliding forward. In most brachiopods this constraint is given by the interlocked teeth and sockets. In *Poikilosakos* the accessory ridge may have been able to hold the posterior edge of the dorsal valve in position; less probably, there may have been some specially toughened strip of mantle tissue along the inner side of the hinge line. Provided that the hinge was in some way held in position, the asymmetrical pull of a single diductor would not have affected the vertical nature of the rotation of the dorsal valve. Only the forwardly directed component of the contractile power would have been effective; the minor lateral component, although unbalanced by an equal and opposite component from a right diductor, could have been held by the articulation of the cardinal process against the side of the median hollow. As in most brachiopods, the moment of the diductor's leverage on the dorsal valve would have been extremely small.

The extremely restricted shell cavity of *Poikilosakos* suggests a functional explanation for the atrophy of the right diductor muscle. A comparison with the unique symmetrical specimen shows that this atrophy was not accompanied by any substantial increase in the size of the remaining muscle (compare figures 5 and 4 of Plate 1). Therefore the power available for raising the dorsal valve must have been almost halved. On the other hand, the atrophy of one diductor would have made available an appreciably greater space within the very small body cavity. Apart from the muscles, the organ of greatest bulk within the coelom of a living brachiopod is the digestive tube, and, in particular, the stomach and its associated ramifying digestive diverticula ("liver"). The atrophy of the right diductor in *Poikilosakos* could have enabled the digestive tube to spread from its usual medial position into the whole of the right half of the coelom, and might have allowed it to increase in size with a corresponding increase in its metabolic efficiency.

The evidence for adductor muscles in *Poikilosakos* is circumstantial. By homology with more normal brachiopods, a pair of small attachments, perhaps fused into a single scar, should be found in the midline on the ventral valve. If the right adductor had atrophid like the right diductor, a small scar might still be expected on the medial side of the left diductor attachment. No clear trace of any such scar can be seen, but the attachment might not be visible on such a thin shell. Most scars owe their visibility to a slightly lower rate of shell thickening of the site of the muscle attachment, relative to the rate on the surrounding surface. On a very thin shell there is little chance of such a differential becoming apparent. The diductor attachment is conspicuous only because it has strongly raised edges.

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[2] Since completing this paper, I have been informed by Dr. Cooper that he has found specimens with a single-lobed asymmetrical cardinal process, as predicted here.

By itself, the absence of any visible scar would suggest that the adductors of *Poikilosakos* were atrophied This is possible, but the existence of definite adductor scars on the dorsal valves of other oldhaminoids makes it more likely that adductors (or at least a left adductor) were present in *Poikilosakos*. Circumstantial evidence for the existence of an adductor can also be derived from the form of the hinge ridge. The chief resistance to the contraction of an adductor would have been the resistance of the water that had to be expelled from beneath the dorsal valve. This would have produced a backward thrust on the dorsal valve itself. If part of the adductor consisted of "quick" fibers for rapid closure of the shell, as in living articulates (Rudwick, 1961b), this thrust might have been quite considerable, relative to the size of the shell, but it would have been countered effectively by the apposition of the hinge ridge. The articulating anterior face of the hinge ridge is buttressed strongly from behind by the mass of the ridge itself, sloping away posteriorly. With this form, the hinge ridge would have been well adapted to counter the thrust of the dorsal valve during its closure.

Lophophore and Feeding Mechanism

Ever since oldhaminoids were first recognized as aberrant brachiopods, it has been commonly agreed that their lophophore was probably schizolophous to ptycholophous. The pinnate outline of the oldhaminoid dorsal valve has an obvious resemblance to the pinnate grooves on the inner surface of thecideoid dorsal valves. In living thecideoids (*Thecidellina, Lacazella*) these grooves are known to accommodate the brachial axes of a schizolophous to ptycholophous lophophore.

The interior of the dorsal valve of *Poikilosakos* is unknown, but in other oldhaminoids there is a fine ridge running parallel to the pinnate outline of the valve, separated from the valve edge by a narrow groove. This submarginal ridge has been identified by Stehli (1956) and Sarycheva (1964) as the site of attachment of the brachial axes; but the marginal groove is a more probable site, for it is closely analogous to the axis-bearing grooves of thecideoids (Rudwick, 1968a). But in any case the brachial axis of *Poikilosakos* may be reconstructed in a submarginal position, near the edge of the valve on its inner side (Figure 4B, C). Then, by homology with the ptycholophes of living brachiopods, the growing tips of the brachial axes would have been situated at the tip of the median indentation. Proximally, the brachial axes would have left the edge of the dorsal valve, probably at the base of the rectangular hinge projection, and would have joined each other at the mouth, in the midline on the anterior side of the coelom. The frontal side of the axes would have faced inward, and the abfrontal side outward, all around the lobate course of the brachia.

The outline of the dorsal valve evidently increased in relative complexity with increasing absolute size during ontogeny; it is not practicable to express this quantitatively, but in qualitative terms the allometric relation between the overall shell size and the length of the dorsal valve edge (or of the shelf) is obvious enough (Figure 2). If the edge of the dorsal valve in fact represents the course of the brachial axes, this allometry becomes intelligible: in living brachiopods the relative complexity of the brachia increases in the same way during increase in absolute size. This is a necessary consequence of the dimensional relation between the linear brachia and the metabolic requirements of the body (cf. Rudwick, 1962).

Although the morphology of oldhaminoids is aberrant, it is methodologically important to assume, as a provisional working hypothesis, that their feeding mechanism was comparable to that of living brachiopods. Only if their morphology proves difficult to explain on this assumption should an aberrant feeding mechanism be postulated.

On this provisional assumption, therefore, lateral cilia on the lophophoral filaments would have driven water from the frontal side to the abfrontal whenever the dorsal valve was raised and the filaments relaxed. Food particles colliding with the frontal surfaces of the filaments would have been enmeshed in mucus and conveyed by frontal cilia to the food groove at the base of the filaments, and thence by other cilia along the groove to the mouth (cf. Rudwick, 1962, and references therein).

The most effective orientation of the filaments would be for all of them to project obliquely outward and ventrally all around the edge of the dorsal valve. Then the tips of the filaments on either side of each indentation would meet and interlock, covering each indentation with a complete screen of filaments. A similar interlocking of filaments occurs in each indentation of the ptycholophe of the living *Megathiris* (Atkins, 1960). Thus, if the dorsal valve of *Poikilosakos* was habitually opened through some moderately

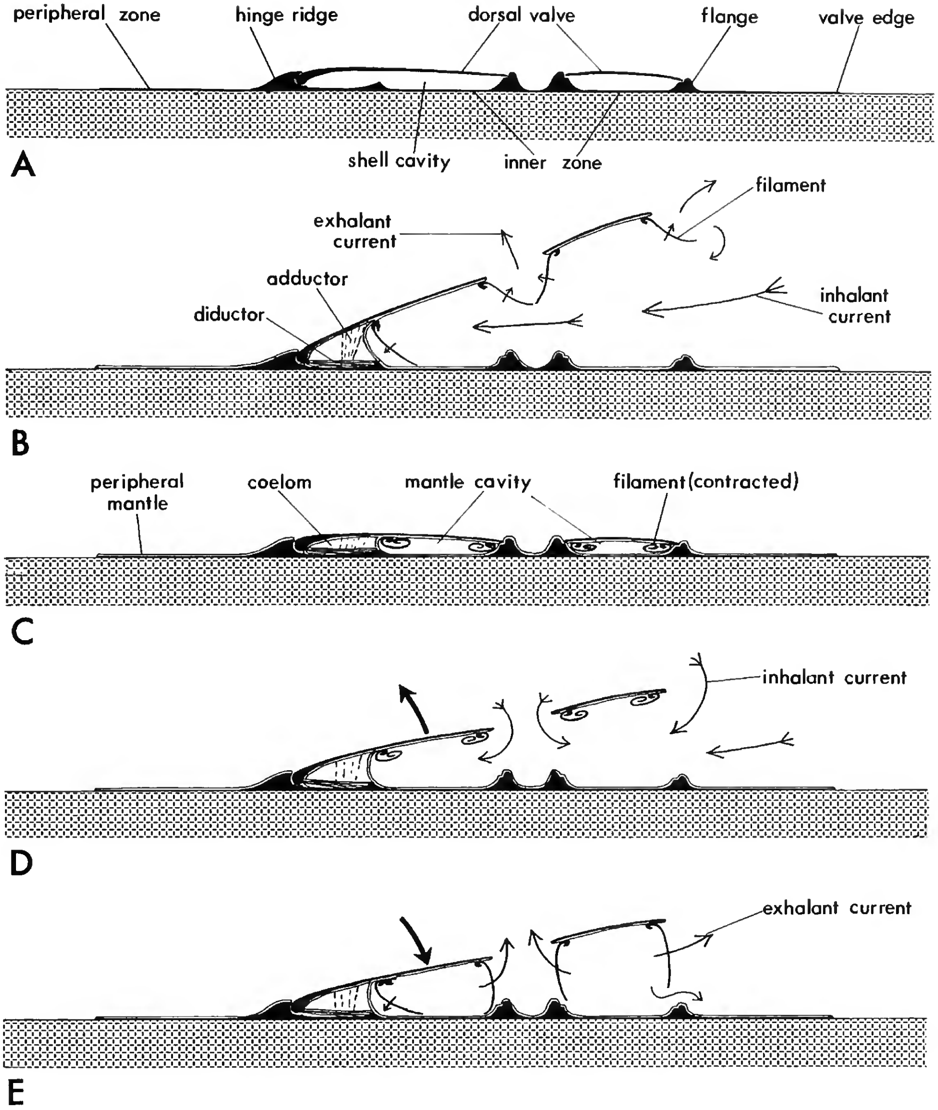

FIGURE 4.—Possible feeding mechanisms of *Poikilosakos*. A, Oblique longitudinal section through shell (along line A–B in Figure 1), as preserved, to illustrate morphology. B, C, Steady-flow feeding mechanism with brachial axis reconstructed submarginally on dorsal valve: B, dorsal valve open, filaments in feeding position; C, dorsal valve closed, filaments contracted. Orientation and action of filaments reconstructed by analogy with living megathirids. C–E, Rhythmic-flow feeding mechanism: C, dorsal valve closed, filaments contracted; D, diductor contracting, dorsal valve rising, water drawn into mantle cavity; E, adductor contracting, dorsal valve falling, water expelled from mantle cavity through screen of filaments.

small angle, the pumping action of the lateral cilia would have drawn an inhalant water current inward under the edge of the dorsal valve and then dorsally through the screen of filaments. The water, thus filtered, would have been released as an exhalant current from the dorsal side of the dorsal valve (Figure 4B). When feeding ceased temporarily, or the brachiopod was disturbed, all the filaments would have been quickly contracted inward, and the dorsal valve would have snapped shut (Figure 4C). In living articulate brachiopods this reaction is due to the contraction of "quick" muscle fibers on the frontal side of each filament, followed immediately by the contraction of the similar fibers in the posterior adductor muscles.

This hypothetical feeding mechanism provides a reasonable functional explanation of the morphology of *Poikilosakos,* but it is not without difficulties. Most living brachiopods are able to operate similar steady-flow filtering systems with great effectiveness, but only because the filaments are so arranged that they divide the mantle cavity into separate inhalant and exhalant chambers, and also divide the gape between the valve edges into separate inhalant and exhalant apertures. By this means, recirculation of water around the tips of the filaments is reduced to a minimum, and the filtered exhalant water is thrown clear of the shell as a fairly strong exhalant jet from the exhalant aperture. But with the steady-flow system postulated for *Poikilosakos,* on the other hand, a high proportion of all the filaments would have projected freely, and recirculation around their tips might have detracted seriously from the effectiveness of the filtering; there would have been no clear channeling of exhalant water away from the shell. It is true that there is a similar lack of effectively separate apertures in the living *Megathiris,* but it is noteworthy that this genus and its relatives are invariably much smaller in size than even the simplest oldhaminoids such as *Poikilosakos.*

The thecideoids probably operate a system similar to megathirids, although they are not closely related; but they too are always small in size, even in fossil representatives with ptycholophes almost as complex as those of later oldhaminoids (Rudwick, 1968a). This disparity in the absolute size of the lobate outlines of thecideoids and megathirids on the one hand and of oldhaminoids on the other is strong evidence for a functional discontinuity between them. There are other strong contrasts in the morphology of the two groups. The dorsal valves of thecideoids and megathirids are always moderately thick, and sometimes massive, and are clearly protective in function. In oldhaminoids, as already mentioned, the prime protective function seems to have been lost, and the dorsal valve is extremely thin and delicate; yet the muscle scars, where they are visible at all, show that the musculature was not correspondingly reduced.

A similar combination of strong musculature with a very light dorsal valve exists in another aberrant group of late Paleozoic age, the richthofeniids; this has been interpreted as evidence for a rhythmic-flow feeding system comparable to that of living septibranch bivalves, and the feasibility of this reconstruction has been confirmed by experiments with working models of richthofeniids (Rudwick, 1961a). Without prejudging the question of the phyletic relation between richthofeniids and oldhaminoids, it is worth considering whether a rhythmic-flow system might be applicable to *Poikilosakos.*

Such a system need not have been exactly analogous to that of richthofeniids: indeed, there are enough differences in morphology to make a close similarity unlikely. In particular, there is no evidence for the form or even the existence of a lophophore in richthofeniids; whereas in oldhaminoids, as already argued, the lobate dorsal valve probably reflects the course of a ptycholophous lophophore. But both groups have a notably thin and delicate dorsal valve, resting on a shelf within a larger ventral valve, and both groups combine aberrant hinge mechanism with a relatively strong musculature. This suggests that both groups might have derived the motive power for feeding from a rhythmic movement of the dorsal valve, even if their means of food collection were different. In living brachiopods the lophophore performs two distinct functions: it creates the movement of water for filtering, and it catches the particles out of the current so created. There is no reason *a priori* why *Poikilosakos* should not have lost the first of these functions while retaining the second.

A possible rhythmic-flow system for *Poikilosakos* can be reconstructed as follows. The feeding cycle would have begun with the dorsal valve resting on the ventral (Figure 4C). A strong contraction of the diductor muscle would have raised the dorsal valve (Figure 4D). Since the valve was light, most of the resistance would have come from the water displaced. Because the moment of leverage was very small, the movement could have been fairly rapid, even if the diductor was a "slow" muscle (as in living brachiopods), provided only that it was powerful enough. With this upward movement, water would have swirled under the edge of the dorsal valve, past the contracted filaments. The mantle cavity would then have been entirely filled with unfiltered water, apart from the very small volume remaining from the phase when the valve was closed (this would give functional advantage to the exceptionally shallow mantle cavity). If the filaments then relaxed and projected ventrally, they could have surrounded this mass of unfiltered water with a complete screen. The contraction of the adductor muscle (or muscles) would then have forced this water outwards through the screen of filaments as the dorsal valve closed toward the ventral (Figure 4E). The resistance of this water would tend to thrust the dorsal valve backward; but as already mentioned, this thrust would have been held against the buttressing posterior ridge of the ventral valve. As the water was forced through the screen of filaments, suspended particles would have been caught on their frontal surfaces and transported to the mouth in the usual way.

The most important feature of this hypothetical feeding cycle is that the relatively powerful though intermittent inhalant current could have swept relatively large suspended particles into the mantle cavity. *Poikilosakas* might therefore have been able to exploit a wider range of food material than more normal brachiopods living in the same environment. Even those particles (including small animals) that were too large to pass to the mouth in the normal way might have been utilized. They would have been trapped within the mantle cavity when the dorsal valve closed at the end of the cycle. The small and tightly sealed mantle cavity would have been highly effective as a site for external digestion of such material, if digestive juices were extruded from the gut through the mouth. The living septibranchs provide a very close analogue here (Yonge, 1928), and such a mechanism of external digestion would also help to explain the tight closure of the secondary commissure of *Poikilosakos*. It might also explain the exceptionally flat form of *Poikilosakos*, which was so closely adherent to its substrate that it must have been highly inconspicous. Small animals crawing across the ventral mantle edge (which in living brachiopods is highly sensitive) might have activated the contraction of the diductor and have been swept inward into the mantle cavity. It is also possible that the peripheral zone of the ventral valve might have acted as a subsidiary site of particle collection, if it was covered in ciliated mucus-secreting mantle tissue like that of living brachiopods: in richthofeniids the homologous zone often developed fluted spines projecting into the path of the strongest currents (Rudwick, 1961a, Rudwick and Cowen, 1968).

These suggestions are unavoidably hypothetical, but they are based on homologies with the mantle and muscles of living brachiopods and on analogies with the quasi-carnivorous habits of living septibranchs; and they do provide a coherent functional explanation of most of the peculiar morphological features of *Poikilosakos*. On the whole, a conventional steady-flow mechanism seems a less satisfactory explanation of the morphology than an aberrant rhythmic-flow system, notwithstanding a proper methodological bias in favor of the former.

Evolution and Phylogeny

The ancestor of *Poikilosakos,* and hence of the oldhaminoids as a whole, must be sought among other Pennsylvanian brachiopods sharing at least some of the same distinctive characters. Among the characters which should be taken into account are (1) its cemented attachment and lack of pedicle, (2) its lack of tubular spines assisting attachment, (3) its loss of a true commissure, and extension of the ventral valve beyond the edge of the dorsal, (4) its peculiar hinge without true teeth, sockets, or denticles, and (5) its probably marginal or submarginal sessile lophophore. Other important characters, not positively demonstrable in *Poikilosakos* itself but which have rightly been stressed in earlier discussions of oldhaminoid affinities, are (6) the pseudopunctate shell and (7) the small bilobed cardinal process.

The cemented attachment of *Poikilosakos* was retained by all later oldhaminoids, at least for the earlier part of their ontogeny. In articulate brachiopods there are no well-authenticated instances of cemented attachment except among the Strophomenida (Cowen and Rudwick, 1967). (The pseudopunctate shell structure also points to the Strophomenida.) It has been argued that within that order cementation may have been evolved several times, but it seems unnecessary to postulate that the oldhaminoids had evolved it separately. Contemporary groups with cementation include the strophalosiaceans and the davidsoniaceans. The strophalosiaceans, however, are characterized by their tubular, external spines, some varieties of which (the "rhizoid" spines of Muir-Wood and Cooper, 1960) are used to supplement the cemented attachment of the ventral valve itself. Some strophalosiaceans resembled *Poikilosakos* in being adherent to the substrate by almost the whole external surface of the ventral valve. Yet, even in these, rhizoid spines were developed, spreading out across the surface of attachment. The total absence of such spines in *Poikilosakos* and almost all later oldhaminoids is, as Williams and Stehli stressed, suggestive evidence that they were not derived from strophalosiacean ancestors; and a davidsoniacean origin seems more probable.

But Sarycheva (1964) has described the new genus *Spinolyttonia,* in which rhizoid spines are said to be developed, from the late Permian of Transcaucasia; and she argues that this discovery points to a strophalosiacean affinity for all oldhaminoids. If this is so, it is curious that such an important and effective functional device was held in abeyance throughout the earlier history of the group and only developed in one species of late date. It might be argued that *Spinolyttonia* more probably represents an independent development of the ability of the mantle edge to secrete tubular spines—if, indeed, the spines are genuinely growing out of the oldhaminoid, and are not merely productoid spines fortuitously attached to it.

On the other hand, there are some features of *Poikilosakos* and later oldhaminoids that might favor a strophalosiacean affinity. Sarycheva has pointed to the resemblance between oldhaminoids and the richthofeniids, suggesting that both were derived from teguliferinid ancestors. This suggestion is supported by the extension of the ventral valve beyond the dorsal, the lack of teeth and sockets and development of an aberrant "internal" articulation, and by the form of the cardinal process.

In any case, the distinctive pinnate dorsal valve of oldhaminoids would be derived most simply from an ancestral form having a circular or bilobed dorsal valve similar to the early growth stages of *Poikilosakos.* A paedomorphic origin of the oldhaminoids may thus account for their cryptogenetic appearance in the fossil record.

Functionally, the feeding mechanism postulated for *Poikilosakos* could have been derived by gradual stages from a normal mechanism. Rapid closure of the dorsal valve could have been purely a cleansing mechanism at first, as it is in living brachiopods. It could have taken over the motive function of the lateral cilia by very gradual stages; in an intermediate stage it would be possible for the water to be driven between the filament partly by the cilia and partly by the closure of the shell.

The existence of one specimen of *Poikilosakos* in which the right diductor attachment is as large and conspicuous as the left is of great interest. It suggests that in this population the atrophy of the right diductor muscle may have been controlled by a gene with simple all-or-none effect. There are two possible explanations for its occurrence as a rare variant: (a) it may be a surviving representative of a condition that was general in the population at an earlier time but which had become submerged by the selective advantage of the asymmetrical form, or (b) the asymmetrical condition may have long been stabilized in the population; but the gene for symmetrical muscles may have been held latent in the gene pool, and may have been actualized phenotypically from time to time as a rare variant. This would be analogous to the occasional narwhal with paired "unicorn's horns" at the present day, as a sporadic variant from the normal form with only a single hypertrophied incisor. (I owe this analogy to Dr. K. A. Joysey.)

The latter alternative seems the more probable, in view of the later history of the oldhaminoids. Later oldhaminoids, as Stehli has stressed, can be divided into those with symmetrical diductor scars and those in which one diductor is missing. In the asymmetrical group it is always the right diductor that has atrophied, and not the left; yet these two conditions would be

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PLATE 1.—*Poikilosakos petaloides* Watson, Pennsylvanian. All views × 3 except figure 8.

Figure 1.—Ventral valve (holotype), showing broad lobes and narrower indentations of flange, hinge ridge, and asymmetrical diductor sheath (BMNH BB.11266: "*P. petaloides* Watson, West bank of the Salt Creek at Graham, Young Co., Texas"; figured by Watson (1917, fig. 1). Photo courtesy E. F. Owen.

Figure 2.—Ventral valve of small (?juvenile) specimen with roughly bilobed flange (BMNH BB.11267b; "*P. petaloides* Watson, West bank of the Salt Creek at Graham, Young Co., Texas").

Figure 3.—Ventral valve of specimen with unusually irregular flange, attached to a crinoid stem (USNM 165840; "*P.* sp., Graham (Wayland), 1.2 m S. of Gunsight, Texas").

Figure 4.—Ventral valve of specimen showing edge of valve, probably broken (USNM 165839; "*P.* sp., Graham (Gonzales Creek Shale), roadside, 3.9 m. N.W. of Finis, Young Co. [actually, Jack Co.], Texas").

Figure 5.—Ventral valve of specimen with paired diductor sheaths (USNM 148051b; "*P. petaloides* Watson, Gonzales Shale, 6 m. N.E. of Finis, Jack Co., Texas").

Figure 6.—Specimen with bilobed dorsal valve, crushed but showing clear growth lines, preserved in position resting on the ventral valve flange. (USNM 165843; "*P.* sp., Graham (Wayland), 1.2 m. S. of Gunsight, Texas").

Figure 7.—Dorsal valve with external growth lines (USNM 137498; "*P.* aff. *petaloides* Watson, basal Plattsmouth limestone, 1 m. S. of Williamsburg, Kansas").

Figure 8.—Part of a ventral valve (× 6) showing detailed structure of hinge ridge, diductor sheath, flange, and pustular valve surface both within and outside the flange (USNM 165841; "*P.* sp., Graham (Wayland), 1.2 m. S. of Gunsight, Texas").

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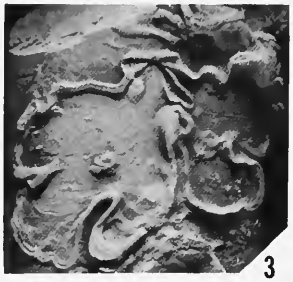

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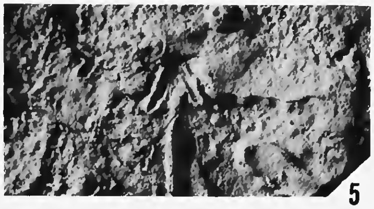

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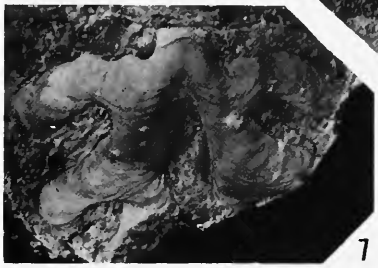

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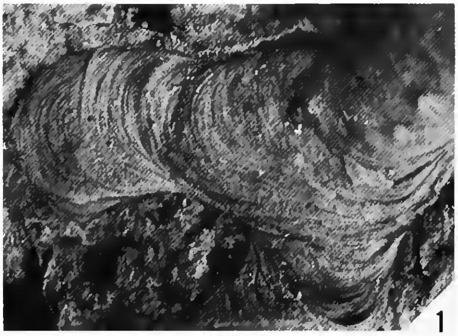
PLATE 1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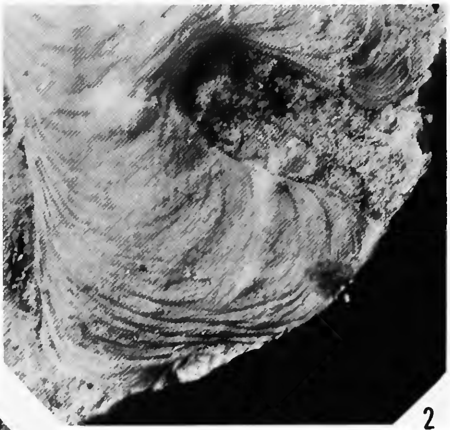
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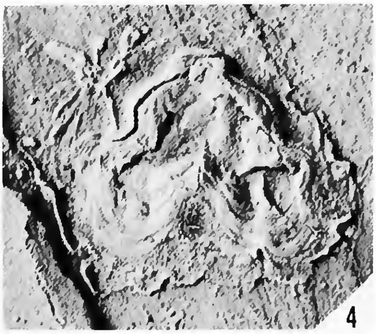
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PLATE 2

functionally identical, and probably also selectively equivalent. This is strong evidence that all species in the asymmetrical group are derived from *Poikilosakos*. But the occurrence of oldhaminoids with symmetrical diductors is more difficult to interpret. On the alternative (a) above, it would be necessary to postulate that these symmetrical oldhaminoids were derived from a *Poikilosakos* population, at present undiscovered, in which the symmetrical condition had survived. Unless and until such a species is discovered in late Pennsylvanian strata, it seems preferable to postulate that the symmetrical oldhaminoids evolved in the Permian from an ancestral population that was predominantly asymmetrical, under conditions which gave the rare symmetrical variants a selective advantage.

If the asymmetrical condition originally had an advantage in relation to the very shallow shell form of *Poikilosakos,* the evolution of populations in which the symmetrical condition predominated could have been connected with the abandonment of that shell form for other forms adapted to other environments: the diversity of later oldhaminoids strongly suggests a minor adaptive radiation of this kind.

The evolution of the later oldhaminoids can be interpreted in terms of the further development of the postulated aberrant feeding mechanism. Although some later species are no larger than *Poikilosakos,* there was a general trend towards a larger overall size, coupled with an increase in the number of lobes on the dorsal valve. The lobes and indentations retained the same standard dimensions throughout, but increased in number with increasing overall shell size. This implies a further relative increase in the complexity of the ptycholophe, similar to that which occurs in the ontogeny of *Poikilosakos* itself. As in *Poikilosakos,* it would be due to the necessary dimensional relation between the collecting capacity of the linear brachia and the metabolic requirements of the whole body.

The later evolution of the group is not, however, wholly explicable in terms of adaptation to enlarging body size. There is also evidence of increasingly effective overall adaptation: the irregularly lobate outline of *Poikilosakos* was replaced by a more highly organized system of regular lobes and indentations. These would have served to arrange the maximum length of filament-row, and hence the maximum filtering capacity, within a shell of any given size.

The extinction of the oldhaminoids in late Permian time was relatively sudden in geological terms. Although it is part of a much larger problem, affecting many other groups of brachiopods and many other phyla, it is important that it should be explained and not merely explained away. A functional analysis of some of the later oldhaminoids does not suggest that they were so narrowly adapted as to be ecologically vulnerable (Rudwick and Cowen, 1968). On the contrary, they seem to have acquired extremely "promising" new features, both anatomically and physiologically. These innovations might have been expected to open up new and less restricted possibilities in brachiopod evolution, and to lead to some new phase of adaptive radiation. Their failure to do so, or even to survive at all, must be given a convincing and not merely facile explanation.

PLATE 2 —*Poikilosakos petaloides* Watson, Pennsylvanian. All views × 9.

Figures 1, 2.—Enlargements of parts of external surface of a dorsal valve, to show growth lines indicating localized "budding." (Specimen as in Plate 1: figure 7.)

Figure 3.—Hinge region of a ventral valve, showing thick hinge ridge, slender accessory ridge, and diductor sheath (BMNH BB.11267a; "*P. petaloides* Watson, West bank of the Salt Creek at Graham, Young Co., Texas").

Figure 4.—Small (?juvenile) specimen showing dorsal valve with clear growth lines, preserved in position on ventral valve (USNM 165844; "*P.* sp., Graham (Gonzales Creek Shale), roadside, 3.9 m. N.W. of Finis, Young Co. [actually, Jack Co.], Texas").

Figure 5.—Hinge region of a ventral valve, showing accessory ridge, so-called dental areas, growth lines within diductor sheath, and pustular valve surface. (Specimen as in Plate 1: figure 3.)

Figure 6.—Oblique view of hinge region of a ventral valve, showing growth lines on anterior face of hinge ridge, and oblique medial orientation of diductor sheath. (BMNH BB.11269a; "*P. petaloides* Watson, West bank of the Salt Creek at Graham, Young Co., Texas"; figured by Watson, 1917, fig. 4.)

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PERMIAN

Robert M. Finks

Sponge Zonation in the West Texas Permian Type Section

ABSTRACT

Five sponge zones are recognized, corresponding to the Neal Ranch-Lenox Hills, Skinner Ranch, Cathedral Mountain-Road Canyon, Word-Cherry Canyon, and Capitan Formations. The second and third zones can be subdivided into two subzones each: the Decie Ranch and post-Decie Ranch parts of the Skinner Ranch Formation, and the Cathedral Mountain and Road Canyon Formations. The most pronounced turnover of species is at the base of the Cathedral Mountain Formation, or about 100 feet above the base of the Bone Spring Formation. It is characterized by radiation of the sphinctozoan lineages of *Stylopegma* and *Guadalupia,* as well as by extinction of *Heliospongia* and *Stereodictyum.* The base of the Skinner Ranch is also an important datum, marked by the apparent immigration of the earliest pharetronid calcisponges. Eight "acme-associations" are also recognized, each characterized by a unique combination of species that reach a simultaneous peak of abundance.

The type section of the Permian, in western Texas, is unusually rich in fossil sponges. Such abundance raises the hope that they may prove useful in correlation, and the present article is an essay in that direction. The conclusions presented here are based on a monographic study of the late Paleozoic sponges of Texas, now nearing completion, in which thousands of specimens from several hundred localities have been examined. It is my hope that stratigraphers working in the Permian of the Southwest may be able to test the proposed zone fossils in a practical way.

The richest sponge collections of the lower part of the section, from the base of the Permian to the middle of the Word Formation, are from the Glass Mountains. Most of the collections were silicified specimens removed en masse by means of acid from blocks of limestone. Supplementary collections of calcified specimens showed no striking differences in faunal composition and the silicified faunas seem to be representative. The upper part of the section, the Cherry Canyon and Capitan Formations, is known almost entirely from the Guadalupe Mountains, 150 miles to the northwest, from both silicified and calcified faunules. The nearby Sierra Diablo has provided a considerable series of faunules, mostly weathered material off the outcrop, from the Hueco, Bone Spring, and Victorio Peak Formations, which correspond to the Glass Mountains section. Some interesting differences in sponge faunas are apparent, between the Sierra Diablo and the Glass Mountains, due either to environmental differences, geographic separation, or both. Nevertheless, the main outline of the Glass Mountains sponge zonation is recognizable, and sustains the hope that the zonal distribution will be recognizable over a wider area.

Ideally, biostratigraphic zones should completely subdivide a span of time and have contiguous boundaries. Even on a worldwide basis, however, there are likely to be gaps in the sedimentary and fossil record. Moreover, one is unlikely to find coterminous ranges of zonal guide species; they either overlap or are separated by gaps. The ideal is approached when one has a maximum of worldwide information, but this is probably never quite reached. Nevertheless, the present paper attempts a complete subdivision of the type section in terms of sponges. The species chosen as guides do seem to have coterminous ranges in many instances, though it remains for future work to test to what extent this is due to insufficient information,

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to gaps in the section, or to truly simultaneous immigration, evolution, and extinction of species.

Without the vast treasures of fossils from the Texas Permian gathered over the last three decades by Dr. G. Arthur Cooper at the Smithsonian Institution, and gathered by Dr. Norman D. Newell at the American Museum of Natural History, this attempt at a comprehensive sponge zonation would not have been possible. The very large samples from many localities are the primary data on which this study has been based, and the stratigraphic framework provided by the field studies of these men has been absolutely essential. It is a pleasure to acknowledge my indebtedness to them also in a more personal way: to Dr. Newell who started me on the study of fossil sponges when I was his student, and to Dr. Cooper who has been a friend, guide and mentor over the years at the United States National Museum. I am pleased to be able to dedicate this paper to Dr. Cooper.

The large collections of fossils from the Sierra Diablo made by S. J. Kříz, then of Princeton University, and by P. B. King and J. B. Knight of the United States Geological Survey, have also formed a major part of the data presented here. Continued access to the collections of the United States National Museum, the United States Geological Survey, the American Museum of Natural History, the Yale Peabody Museum, and Princeton University, have been an essential element in the pursuit of this study. I can only thank my colleagues at these institution en masse for the many stimulating discussions, material aid, and bits of advice during the past 16 years. They are, of course, not to be blamed for my mistakes.

Evolution and Zonation

Species that form part of a single lineage and its branches, undergoing progressive evolutionary change, are at once the most reliable for stratigraphic zonation and the most difficult to use. They are reliable because a continuously evolving lineage makes it more likely, though it does not prove, that we are dealing with a true sequence in time and not with contemporaneous, environmentally controlled species that merely succeed one another locally by the chances of distribution. Lineages that show a progressive change at a more or less constant rate also favor the conclusion that no major time gaps are present in the record. For these reasons I have chosen, insofar as possible, zonal guide species from such continuously developing lineages.

At the same time, such species are difficult to use because, being part of a gradually changing lineage, they are difficult to separate from one another. Boundaries between species are therefore somewhat arbitrary, and the sharpness of resolution of the corresponding zonal boundary is thereby diminished. This is somewhat mitigated by using concurrent overlapping ranges of species from different lineages. For a given zonal boundary a second lineage may show a sharper break between species or, better still, a species may begin or end at the boundary by immigration or extinction, thereby avoiding problems of transitional forms. The existence of a lithologic break can also be used to provide a precise point of division between zonal species in a lineage, though of course it must coincide approximately with a recognizable morphologic change in the fossils themselves. Needless to say, the species must be initially sorted out and delimited without reference to their stratigraphic position if they are to be at all useful in correlation. The known stratigraphic sequence, however, must be used subsequently to choose which morphological differences are significant in terms of time. Such methods have been used here.

The principal evolutionary lineages among the Texas Permian sponges are two. One is a line of development that seems to stem from the Pennsylvanian sphinctozoan calcisponge *Maeandrostia,* which was already present in the Texas area. Two species of the genus *Stylopegma* in the Neal Ranch Formation seem to have arisen from it. The more advanced of the two, *S. stenaulos,* is found in the reefy facies, the other in the shales. *Stylopegma stenaulos* seems to have given rise to the Skinner Ranch species, *S. dulcis* by a continuation of the same trends that brought it out of *Maeandrostia.* The Cathedral Mountain and later species, *S. wordensis,* continues the same trend still further. Two other Cathedral Mountain species, *S. isopora* and *Polysiphonella flabellata,* represent quite different lines of development, but are clearly related morphologically to the *S. dulcis* type. Partly contemporary with *S. dulcis,* but appearing slightly later in the upper Skinner Ranch, is the rather different *S. annulata.* It could have arisen from *S. dulcis* by a more abrupt transition, in a direction parallel to that of *S. wordensis.* Early Word (China Tank) representatives of *S. annulata* show a greater resemblance to the later *S. getawayensis* of the Cherry Canyon, and could have developed into it, though one might also regard *S. getawayensis* as a further development of *S. wordensis.* The major adaptive radiation of the *Stylopegma* lineage appears to have taken place around the Skinner Ranch–Cathedral Mountain boundary.

This same period seems to be that at which the initial radiation of the second lineage took place, namely, that of the sphinctozoan calcisponge *Guadalupia.* Unlike the *Maeandrostia—Stylopegma* lineage, that of *Guadalupia* has no known Pennsylvanian history in the area, unless it be derived from the related, but rather different, Pennsylvanian genus *Cystauletes. Guadalupia* first appears as the species *G. williamsi* in the middle of the Skinner Ranch Formation, long after the last known *Cystauletes,* and it seems more likely to have evolved elsewhere and migrated into the Texas region during Skinner Ranch time. By late Skinner Ranch time a second species, *G. auricula,* has appeared, which is closely related to a complex of species in the Cathedral Mountain and Road Canyon Formations, and in the China Tank Member of the Word Formation; namely, *G. lepta, G. cupulosa, G. ramescens* and *G. vasa.* These forms, including *G. auricula,* intergrade with one another and they may well be environmentally controlled growth forms of one species, but they show a certain stratigraphic separation, and for this reason I have given them separate names. They also show a progressive trend in the sequence *G. auricula* through *G. cupulosa* to *G. vasa,* which is directly continued into the Cherry Canyon and Capitan species *G. cylindrica.* Meanwhile, at the base of the Cathedral Mountain Formation two other species of Guadalupia appear, *G. zitteliana* and *G. "Polyphymaspongia" explanata,* which like *G. auricula* may have arisen from *G. williamsi. Guadalupia zitteliana* may have given rise in turn to the Word species *G. cystauletoides* and probably did give rise to the Word species *Cystothalamia nodulifera.* The last is almost certainly ancestral to the Capitan *C. megacysta.* Another Word species, *G. microcamera,* was probably derived from *G. cupulosa* (transitional forms occur in the Road Canyon Formation), and in turn leads to the Capitan *G. favosa.*

The *Guadalupia* family tree is more continuously branching than that of *Stylopegma,* but both show a marked radiation at the beginning of Cathedral Mountain time, and both show progressive trends that reassure one concerning temporal sequences.

Systematics of Zonation

The boundaries between the zones have been drawn at horizons of major turnover in the sponge faunas. They have also been chosen, insofar as possible, so that the overlapping ranges of at least two common and easily recognizable species will identify the zone.

It is convenient to arrange the zones in a hierarchical scheme according to the magnitude of the faunal breaks between them and according to the apparent breadth of distribution of the zonal guide fossils. One may assess the magnitude of the faunal breaks by comparing what may be called the *turnover index* of the useful zonal species, that is, the sum of species disappearing and appearing at that boundary. One may also examine turnover indices for genera (first and last appearance of genera at the zonal boundary) as well as for families and for the Class or Order level. The indices for the formational boundaries of the type section are given in Table 1.

The principal breaks (apart from the base of the Neal Ranch) are at the top of the Neal Ranch and the base of the Skinner Ranch, at the base of the Cathedral Mountain, at the base of the Word (as revised by Cooper and Grant, 1966), and at the base of the Capitan. They are marked not only by a high turnover index for species, but also for the higher categories. These breaks serve to delimit five biostratigraphic zones of sponges.

If one judges them further according to the breadth of geographic distribution of the zonal guides, and their ease of recognition, one of these breaks is somewhat more prominent than the rest; namely, that at the base of the Cathedral Mountain Formation, or the top of the Skinner Ranch Formation. At his horizon, the widespread, abundant, large, and easily recognizable genera *Heliospongia* and *Stereodictyum* disappear from West Texas, and so far as is now known, from the earth. This horizon is recognizable not only in the Glass Mountains but also in the Sierra Diablo-Guadalupe Mountains area, where the equivalent horizon lies about 100 feet above the base of the Bone Spring Limestone. This horizon may serve to delimit two *megazones.*

The remaining breaks can be arranged so as to define subzones within the major zones, and what may be called *microzones* within some of the subzones. The two megazones can be defined on the range of a single species each within the Glass Mountains. The zones, subzones, and microzones are best identified on the basis of numerous concurrent, overlapping ranges (shown on Figures 1 and 2) and may take their names, but not their ultimate definition, from two of the species whose concurrent overlapping ranges help to fix the zone.

The complete classification of the zones is as follows:

Zones	*Formations of type section*
Top of Section	
II. *Stylopegma isopora* Megazone	
5. *megacysta-cylindrica* Zone (*Cystothalamia megacysta* and *Guadalupia cylindrica*)	Capitan
4. *microcamera-zitteliana* Zone (*Guadalupia microcamera* and *G. zitteliana*)	Word and Cherry Canyon
4b′. *nodulifera-typicale* Microzone (*Cystothalamia nodulifera* and *Stromatidium typicale*)	Cherry Canyon
4a′. *vasa-dunbari* Microzone (*Guadalupia vasa* and *Girtyocoelia dunbari*)	China Tank Member of Word
3. *flabellata-robusta* Zone (*Polysiphonella flabellata* and *Virgola robusta*)	Cathedral Mountain and Road Canyon
3b. *ramescens-cupulosa* Subzone (*Guadalupia ramescens* and *G. cupulosa*)	Road Canyon
3a. *auricula-lepta* Subzone (*Guadalupia auricula* and *G. lepta*)	Cathedral Mountain
I. *Heliospongia vokesi* Megazone	
2. *vokesi-defuncta* Zone (*Heliospongia vokesi* and *Defordia defuncta*)	Skinner Ranch
2b. *williamsi-vokesi* Subzone (*Guadalupia williamsi* and *Heliospongia vokesi*)	post-Decie Ranch Member
2b′. *vokesi-auricula* Microzone (*Heliospongia vokesi* and *Guadalupia auricula*)	base of Taylor Ranch Member of Hess to top of Skinner Ranch
2a. *megalochetus-agaricus* Subzone (*Haplistion megalochetus* and *Catenispongia agaricus*)	Decie Ranch Member of Skinner Ranch
1. *vokesi-prosseri* Zone (*Heliospongia vokesi* and *Amblysiphonella prosseri*)	Neal Ranch (and Lenox Hills?)
Base of Section	

The megazones, zones, and subzones are intended to completely partition the sequence and to have contiguous boundaries. The microzones lie wholly within zones or subzones, and their boundaries are not necessarily contiguous with other units. The two microzones within the *microcamera-zitteliana* Zone may ultimately prove to be regular subzones with contiguous boundaries.

TABLE 1.—*Indices for the formational boundaries of the type section as recognized by Cooper and Grant (1966) and based on the ranges shown in Figures 1 and 2.*

Formational Boundary	*Turnover Indices*			
	Species	*Genera*	*Families*	*Classes or Orders*
(1) Base of Neal Ranch	12	7	0	0
(2) (a) Top of Neal Ranch	7	3	1*	1*
(b) Base of Skinner Ranch	4	2	1	1
Combined	11	5	2*	2*
(3) Top of Decie Ranch	6	2	1	0
(4) Base of Taylor Ranch	2	0	0	0
(5) Base of Cathedral Mountain	12	4	3	0
(6) Base of Road Canyon	5	0	0	0
(7) Base of Word (China Tank)	10*	2*	1*	0
(8) Top of China Tank	3*	1*	1*	0
(9) Base of Willis Ranch	1*	1*	0	0
(10) Base of Cherry Canyon	4	1	1	0
(11) Base of Capitan	10	1	0	0

*Includes taxon whose range may extend farther elsewhere.

The *vokesi-prosseri* Zone

This is the fauna of the Neal Ranch Formation. Besides *Amblysiphonella prosseri,* which ranges up from the Virgilian, and *Heliospongia vokesi,* which continues into higher beds, the zone contains a number of other species which are restricted to this horizon, mainly occurring in the reefy facies, and mainly constituting a radiation of the family Fissispongiidae and to a lesser extent of the Maeandrostiidae. Reefy faunas of sponges are not well known from the Virgil. It is possible that some of these species were already present in Virgilian reefs; it is reasonably certain, however, that they are not present in post-Wolfcampian reefs.

The base of the Neal Ranch Formation is marked by the disappearance of the common Pennsylvanian genera *Coelocladia, Girtycoelia* (but not *Girtyocoelia!*), and *Maeandrostia.* The first appears to have died without issue. *Girtycoelia* seems to have died out locally, but Ott (1967) considers the Triassic *Colospongia* Laube to be a senior synonym of *Girtycoelia.* They are indeed very similar, and probably related, but in view of the time difference, of the absence of *Girtycoelia* from the Texas Permian, and of certain differences in form, the possibility of homeomorphy is suggested, and I believe the two genera should not be combined at the present time. The Permian *Steinmannia* Waagen and Wentzel, from the Salt Range of Pakistan, is also considered by Ott to be a synonym of *Girtycoelia,* but it is at present very poorly known.

The third Pennsylvanian genus, *Maeandrostia,* appears to have evolved into the genus *Stylopegma,* of which two species characterize the *vokesi-prosseri* Zone. One of these, *S. turbinata,* occurring in the shaly, or nonreefy, beds is very close indeed to *Maeandrostia,* and could be included in that genus if it was interpreted broadly. *Wewokella* (*Talpaspongia*) also disappears at the base of the Neal Ranch in the Glass Mountains, but is extremely common in the southern calcitic facies (Finks, in King, 1965) of the Hueco Formation of the Sierra Diablo and Hueco Mountains, which contains *Heliospongia vokesi* and appears to lie within the *vokesi-prosseri* Zone. The distribution of *Wewokella* appears to be environmentally controlled.

Stereodictyum orthoplectum, another common sponge of the *vokesi-prosseri* Zone, extends into the overlying *vokesi-defuncta* Zone, and has also been found in reefy facies of the Virgilian Holder Formation of New Mexico (J. M. Parks, J. L. Wilson, and D. F. Toomey, personal communications).

It is not clear whether the Lenox Hills Formation, which directly overlies the Neal Ranch in the Glass Mountains, falls within the *vokesi-prosseri* Zone because the only sponges so far found in it are *H. vokesi* and *Fissispongia* species, neither of them diagnostic.

The diagnostic sponge association of the *vokesi-prosseri* Zone is as follows (Page 292):

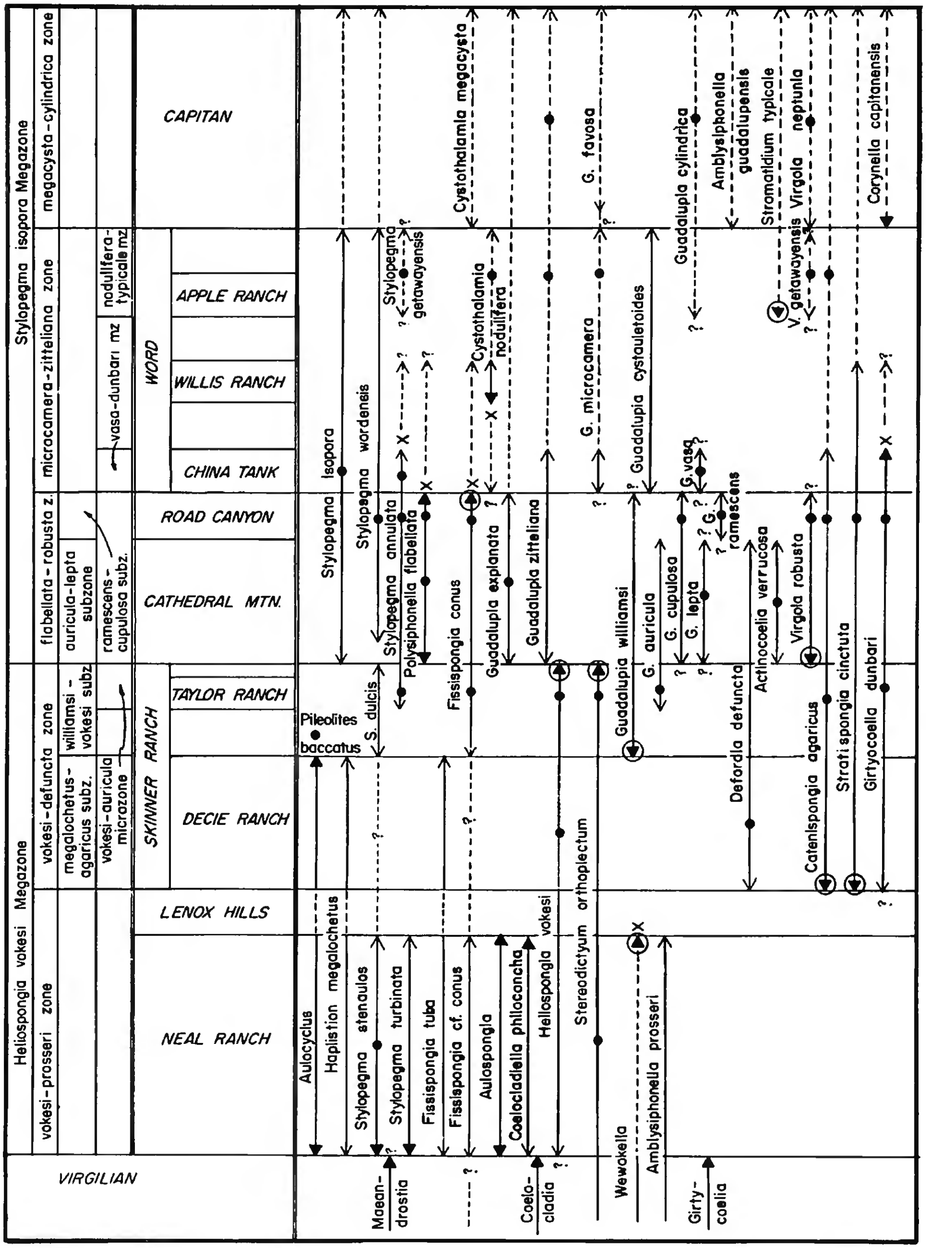

FIGURE 1.—Distribution of sponge zonal-guide taxa in the standard section of the Permian in the Glass Mountains, Texas, showing sponge zones and key rock units. Symbols: < first appearance of a genus; > last appearance of a genus; ○, first or last appearance of a family; ?, limit of range not clear-cut because of intergradation with related species; X, range may extend farther elsewhere; - - -, known range outside this area, absent here due to lack of collecting or facies difference; ●, horizon of unusual abundance (acme).

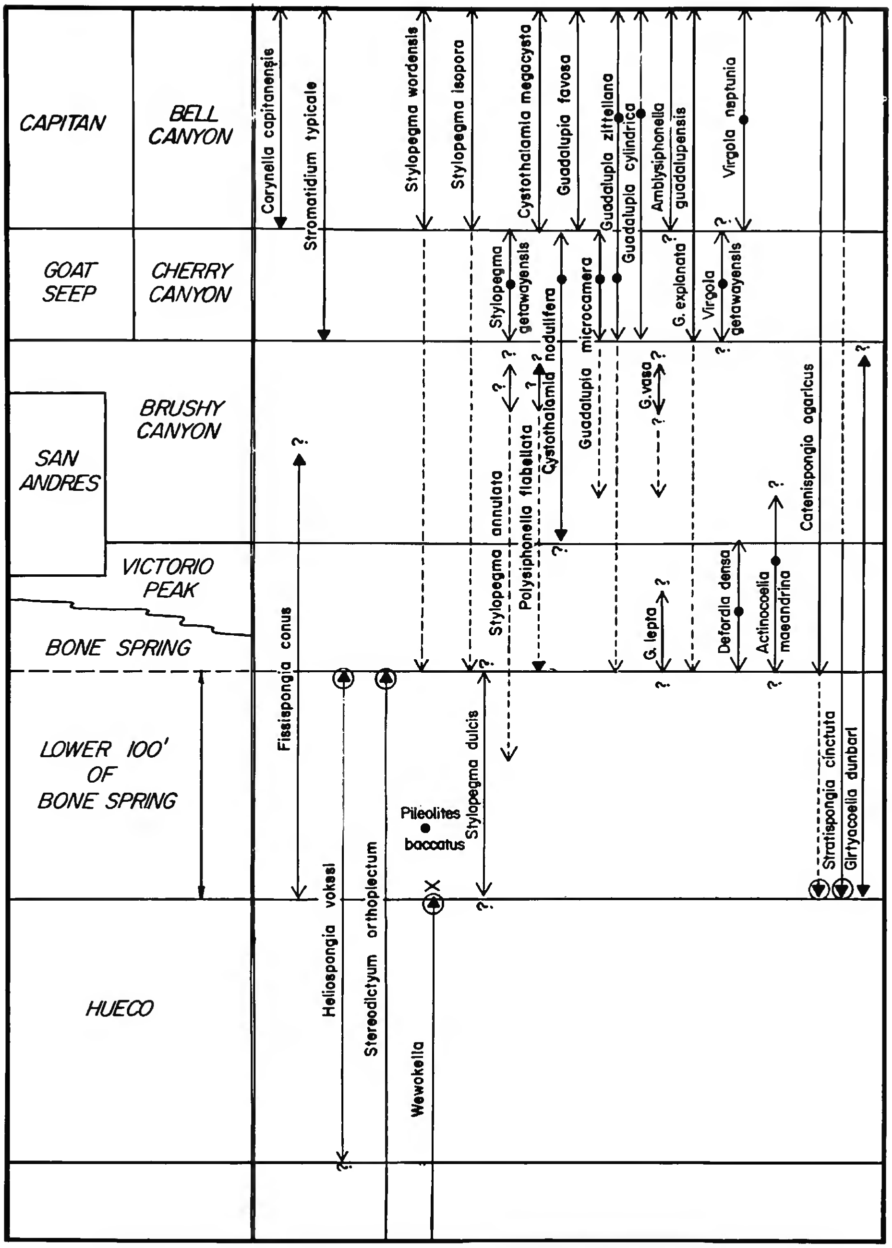

FIGURE 2.—Distribution of sponge zonal-guide taxa in the Permian section of the Sierra Diablo-Guadalupe Mountains area, including the standard section of the Guadalupian. Symbols as in Figure 1.

Calcarea
Sphinctozoa
Fissispongiidae
Fissispongia tuba Finks
Fissispongia species cf. *F. conus* Finks
Aulocyclus Finks
Aulospongia Finks
Maeandrostiidae
Stylopegma stenaulos Finks
S. turbinata Finks
Sebargasiidae
Amblysiphonella prosseri Clarke
Heteractinida
Wewokellidae
Wewokella (*Talpaspongia*) *clavata* (King)
Demospongea
Heliospongiidae
Heliospongia vokesi King
Coelocladiella philoconcha Finks
Haplistiidae
Haplistion megalochetus Finks
Hexactinellida
Stereodictyidae
Stereodictyum orthoplectum Finks

Base of the *vokesi-prosseri* Zone:

Last appearances:	
By local extinction:	*Coelocladia* *Girtycoelia*
By evolution:	*Maeandrostia* (into *Stylopegma*)
First appearances:	
By immigration:	*Autocyclus* (or by evolution from *Fissispongia*) *Haplistion megalochetus* (or by evolution from other *Haplistion*)
By evolution:	*Stylopegma stenaulos* (from *Maeandrostia*) *S. turbinata* (from *Maeandrostia*) *Heliosponga vokesi* (from *H. ramosa*)
Exclusive to zone:	*Stylopegma stenaulos* *S. turbinata* *Aulospongia* *Coelocladiella philoconcha*
Species having acmes within zone:	*Stylopegma stenaulos* *Stereodictyum orthoplectum*

Recognition of the base of the *vokesi-prosseri* Zone may be rendered somewhat difficult by the fact that the boundary between *H. vokesi* and the earlier *H. ramosa* is somewhat arbitary, and the two may occur together (Finks, 1960, p. 45). The presence of *vokesi*, rather than the absence of *ramosa*, should be considered diagnostic. The whole association of species is the best guide to this zone. The top is best placed at the incursion of the characteristic species of the overlying *vokesi-defuncta* Zone. In the present state of our knowledge this occurs at the base of the Skinner Ranch Formation in the Glass Mountains, and at the base of the Bone Spring in the Sierra Diablo. The entire Hueco of the Sierra Diablo will thus fall into this zone, as will the Neal Ranch and Lenox Hills in the Glass Mountains. It should be noted that the exclusion of both the Hueco and Lenox Hills Formations from the higher *vokesi-defuncta* Zone is based only on negative evidence.

The *vokesi-defuncta* Zone

This zone coincides with the Skinner Ranch Formation of the Glass Mountains and with approximately the lower 100 feet of the Bone Spring Formation in the Sierra Diablo. It is defined by the co-occurrence of *Heliospongia vokesi* or *Stereodictyum orthoplectum*, which become extinct at the top, with *Catenispongia agaricus*, *Stratispongia cinctuta* or *Defordia defuncta*, which start at the base. *Catenispongia* and *Stratispongia* appear to represent the first pharetronid calcisponges in the fossil record (they are the "Pharetronid Genera A and B" of Finks, 1960). The top of this zone is the last appearance of the families Heliospongiidae and Stereodictyidae as well as the first appearance of many new forms of the succeeding zone. The upper and lower boundaries of the *vokesi-defuncta* Zone are the most clear-cut breaks in the sequence of sponge faunas of the Texas Permian.

In the Glass Mountains a lower subzone (*megalochetus-agaricus*) can be recognized, bearing an attenuated fauna (*Aulocyclus*, *Haplistion megalochetus*, *Fissispongia tuba*) from the preceding *vokesi-prosseri* Zone, along with the new elements. This lower subzone is coincident with the Decie Ranch Member of the Skinner Ranch Formation. It is marked by a strong abundance of *Defordia defuncta* and *Heliospongia vokesi*.

Immediately above it, in the middle of the Skinner Ranch Formation, the first *Guadalupia* appears, and defines the base of the upper, or *williamsi-vokesi* Subzone. Towards the top of this subzone, the Taylor Ranch Member of the Hess Formation has a very characteristic faunal association, described below under the section on "Acme-associations," and seems to be marked by the first appearances of *Guadalupia auricula* and *Stylopegma annulata*. Because of these first appearances it may have a time significance, and has been named the *vokesi-auricula* Microzone. On the other hand, this may be merely a richer fauna of the *vokesi-williamsi* Subzone.

In the Sierra Diablo area, the known sponge fauna is much less varied and the subzones and microzone cannot be recognized. Nevertheless, the lower part of the Bone Spring contains *Heliospongia vokesi, Stereodictyum orthoplectum,* and *Stratispongia cinctuta,* which together are sufficient to diagnose the *vokesi-defuncta* Zone. The correlation is strengthened by the occurrence in both the mid-Skinner Ranch and the lower Bone Spring of *Stylopegma dulcis,* which is intermediate in an evolutionary progression between the Neal Ranch *S. stenaulos* and the Cathedral Mountain and the later *S. wordensis.* Also the peculiar hexactinellid *Pileolites baccatus* is known, and rather abundantly, from but two localities; one in the middle of the Skinner Ranch, the other at the base of the Bone Spring.

Wewokella (*Talpaspongia*) *clavata* is common in the Clyde Formation of central Texas, which has been correlated approximately with the Skinner Ranch horizon on the basis of the presence in it of *Pseudoschwagerina crassitectoria* (Dunbar and others, 1960, p. 1789). *Wewokella,* absent from the Glass Mountains Permian entirely, is not present in the Sierra Diablo above the Hueco Formation. It may be that its absence from the Sierra Diablo at the Skinner Ranch horizon is due to environmental differences, or, perhaps, the Clyde is actually older than the Skinner Ranch, or perhaps again, the Clyde correlates with only the *lower* part of the Skinner Ranch of the Glass Mountains, and that in turn with the post-Hueco, pre-Bone Spring erosion interval in the Sierra Diablo, or even with the upper Hueco. In connection with the last possibility, a *Defordia* species in the Upper Hueco suggests Skinner Ranch affinities. In any case, *Wewokella* is not presently known to be a part of the fauna of the *vokesi-defuncta* Zone of western Texas.

The diagnostic faunal association of the *vokesi-defuncta* Zone is as follows:

- Calcarea
  - Sphinctozoa
    - Fissispongiidae
      - *Fissispongia conus* Finks
      - *F. tuba* Finks (lower subzone only)
      - *Aulocyclus* Finks (lower subzone only)
    - Maeandrostiidae
      - *Stylopegma dulcis* (King)
      - *S. annulata* Finks (uppermost microzone only)
    - Celyphiidae
      - *Girtyocoelia dunbari* King
    - Guadalupiidae
      - *Guadalupia williamsi* King (upper subzone only)
      - *G. auricula* Finks (uppermost microzone only)
  - Pharetronida
    - Stellispongiidae
      - *Catenispongia agaricus* Finks
      - *Stratispongia cinctuta* Finks

- Demospongea
  - Helispongiidae
    - *Heliospongia vokesi* King
  - Chiastoclonellidae
    - *Defordia defuncta* King

- Hexactinellida
  - Stereodictyidae
    - *Stereodictyum orthoplectum* Finks
  - Pileolitidae
    - *Pileolites baccatus* Finks

Base of *vokesi-defuncta* Zone:
- Last appearances (top of Neal Ranch):
  - By local extinction: *Aulospongia*; *Coelocladiella*; *Amblysiphonella prosseri*; *Wewokella* (*Talpaspongia*) *clavata* (in Hueco only; persists in Clyde Formation of central Texas); *Stylopegma turbinata*
  - By evolution: *Stylopegma stenaulos* (into *S. dulcis* and possibly *S. annulata*)
- First appearances (base of Skinner Ranch):
  - By immigration: *Catenispongia*; *Stratispongia*; *Defordia defuncta* (or by evolution)

Base of *williamsi-vokesi* Subzone (upper subzone):
- Last appearances:
  - By local extinction: *Aulocyclus*; *Haplistion megalochetus*; *Fissispongia tuba*
- First appearances:
  - By immigration: *Guadalupia williamsi*; *G. auricula* (base of uppermost microzone) (or by evolution from *G. williamsi*)
  - By evolution: *Stylopegma annulata* (base of uppermost microzone) (from *S. stenaulos*?); *S. dulcis* (possibly earlier) (from *S. stenaulos*)

Exclusive to *vokesi-defuncta* Zone: *Stylopegma dulcis*; ?*Pileolites baccatus*

Acmes within *vokesi-defuncta* Zone:

- *Heliospongia vokesi* (lower subzone and uppermost microzone)
- *Defordia defuncta* (lower subzone)
- *Pileolites baccatus*
- *Stereodictyum orthoplectum* (uppermost microzone)
- *Fissispongia conus* (uppermost microzone)
- *Girtyocoelia dunbari* (uppermost microzone)
- *Catenispongia agaricus* (uppermost microzone)

The *flabellata-robusta* Zone

This zone includes the Cathedral Mountain and Road Canyon formations of the Glass Mountains and the upper part of the Bone Spring and Victorio Peak Formations of the Sierra Diablo. Its base is marked by a great expansion of the *Guadalupia* and *Stylopegma* lineages, giving rise to four new species of *Guadalupia* and two new species of *Stylopegma,* as well as the related genus *Polysiphonella.* It marks also the first appearance of the genus *Virgola.* Most of the new forms persist into higher zones, but progressive changes in a group of species seemingly descended from *Guadalupia auricula* give some assurance of temporal continuity and progression.

The extinction of the formerly abundant *Heliospongia vokesi* and *Stereodictyum orthoplectum* at the base of this zone, together with the appearance of the new forms cited above, makes this boundary an important punctuation in the sequence of sponge faunas. For this reason, it has been selected as the break between two megazones.

Many forms persist from earlier zones so that the total sponge fauna of the *flabellata-robusta* Zone is perhaps the richest in the entire section of the Texas Permian. This is particularly true when one includes the many hexactinellid and lithistid species that have been omitted from the lists of zonal guides because their ranges are either too great or too poorly known.

The top of this zone is less well defined than the base. It is probably best defined by the appearance of the diagnostic species of the succeeding zone: *Guadalupia microcamera, G. vasa,* and *G. cystauletoides,* although a transitional form to the first species is present in the Road Canyon Formation (the upper subzone) and may give trouble. In the Glass Mountains the genera *Fissispongia* and *Polysiphonella* are not known above this zone, but in the Sierra Diablo—Guadalupe Mountains area they are associated with species of the succeeding zone.

Several species appear to be confined to this zone; namely, *Guadalupia cupulosa, G. lepta, G. ramescens, Actinocoelia verrucosa, Defordia densa,* and *Virgola robusta.* The *Guadalupia* species appear to be the most reliable guides because they form part of a general evolutionary progression extending from the preceding zone to the following one. Within the zone, *Guadalupia lepta* appears to be confined to the lower (Cathedral Mountain) part and *G. ramescens* to the upper (Road Canyon) part, permitting the recognition of two subzones in the Glass Mountains. The disappearance of *Guadalupia auricula, Defordia defuncta,* and *Actinocoelia verrucosa* at the boundary between the two subzones tends to reinforce it.

The two subzones have distinctive associations of species that have acmes within the subzone. The lower subzone (*auricula-lepta*) is characterized by the abundant occurrence of *Guadalupia lepta, G. explanata, Polysiphonella flabellata,* and *Actinocoelia verrucosa.* The upper subzone (*ramescens-cupulosa*) is characterized by the acmes of *Stylopegma wordensis, S. annulata, Polysipnonella flabellata, Fissispongia conus, Guadalupia cupulosa, G. ramescens, Virgola robusta, Catenispongia agaricus, Stratispongia cinctuta,* and *Girtyocoelia dunbari.*

The two subzones cannot be recognized in the Sierra Diablo region. The distinctive lower subzonal species *Defordia defuncta* and *Actinocoelia verrucosa* are replaced by *Defordia densa* and *Actinocoelia maeandrina.* They occur with *Guadalupia lepta,* but the upper subzonal guide, *G. ramescens,* is unknown. It may be that tthe entire upper Bone Spring and Victorio Peak are equivalent only to the lower subzone (Cathedral Mountain). The lower part of the San Andres has provided the holotype of *Actinocoelia maeandrina,* which ties it to the Victorio Peak. It does not contain *Guadalupia ramescens,* though nothing in the lower San Andres sponge fauna would rule out an upper subzone age. The presence of *Cystothalamia nodulifera* suggests an even later age, for this is a species of the next higher zone, but at the same time the presence of *Fissispongia,* which in the Glass Mountains lies wholly beneath *Cystothalamia,* issues a warning that the Glass Mountains picture, at least as presently known, is not always applicable elsewhere.

Actinocoelia maeandrina is one of the most widely distributed of the Permian sponge species, and is a common sponge in the Kaibab Formation of Arizona, and its equavalents in Nevada and Utah. Since publication of an article calling attention to its wide distribution (Finks, Yochelson, and Sheldon, 1961), it has been reported in Kaibab equivalents from other localities in southern Arizona and in Utah (various personal communications). It also is known from the top of the Franson Member of the Park City Formation in western Wyoming, possibly out of line with its stratigraphic position in western Texas. An occurrence reported from the Goat Seep Formation of the Sierra Diablo (Finks, in P. B. King and others, 1965, p. 76) may be a different species of *Actinocoelia* having finer trabeculae.

The diagnostic sponge association of the *flabellata-robusta* Zone is as follows:

Calcarea
Sphinctozoa
Fissispongiidae
Fissispongia conus Finks
Maeandrostiidae
Stylopegma isopora Finks
S. wordensis Finks
S. annulata Finks
Polysiphonella flabellata Finks
Guadalupiidae
Guadalupia williamsi King
G. auricula Finks (lower subzone only)
G. cupulosa Finks
G. lepta Finks (lower subzone only)
G. ramescens Finks (upper subzone only)
G. zitteliana Girty
G. explanata (King)
Celyphiidae
Girtyocoelia dunbari King
Pharetronida
Stellispongiidae
Catenispongia agaricus Finks
Stratispongia cinctuta Finks
Virgola robusta Finks
Demospongea
Chiastoclonellidae
Defordia defuncta King (lower subzone only)
D. densa Finks
Actinocoelia verrucosa Finks (lower subzone only)
A. maeandrina Finks

Base of the *flabellata-robusta* Zone:
Last appearances:
By local extinction: *Heliospongia*
Stereodictyum
By evolution: *Stylopegma dulcis* (into *S. wordensis* and *S. isopora*)
First appearances:
By immigration: *Virgola robusta*
By evolution: *Stylopegma isopora* (from *S. dulcis*?)
S. wordensis (from *S. dulcis*)
Polysiphonella flabellata (from *S. dulcis* or by immigration)
Guadalupia zitteliana (from *G. williamsi* or by immigration)
Guadalupia (*Polyphymaspongia*) *explanata* (from *G. zitteliana* or by immigration)
G. cupulosa (from *S. auricula*)
G. lepta (from *G. auricula*)
?*Actinocoelia maeandrina* (related form known from preceding zone)
?*A. verrucosa* (from *A. maeandrina*?)
?*Defordia densa* (from *D. defuncta*?)

Base of the *ramescens-cupulosa* Subzone:
Last appearances:
By local extinction: *Defordia defuncta*
Guadalupia auricula
By evolution: *G. lepta* (into *G. ramescens*?)
First appearances:
By evolution: *Guadalupia ramescens* (from *G. cupulosa* or *G. lepta*)

Species confined to the *flabellata-robusta* Zone:
Guadalupia lepta (lower subzone)
G. ramescens (upper subzone)
G. cupulosa
Virgola robusta
?*Actinocoelia maeandrina* (may extend into zone above)
A. verrucosa
Defordia densa
?*Polysiphonella flabellata* (in Glass Mountains)

Acmes within *flabellata-robusta* Zone:
Stylopegma wordensis (upper subzone)
S. annulata (upper subzone)
Polysiphonella flabellata
Fissispongia conus (upper subzone)
Guadalupia explanata (lower subzone)
G. lepta (lower subzone)
G. cupulosa (upper subzone)
G. ramescens (upper subzone)
Actinocoelia verrucosa
A. maeandrina
Defordia densa
Virgola robusta (upper subzone)
Catenispongia agaricus (upper subzone)
Stratispongia cinctuta (upper subzone)
Girtyocoelia dunbari (upper subzone)

The *microcamera-zitteliana* Zone

This zone includes the sponge faunas of Word Limestones 2, 3, and 4 in the Glass Mountains and of the

Getaway and Goat Seep Limestones in the Guadalupe Mountains. It is coextensive with the range of *Guadalupia microcamera,* which is an easily recognizable species and has been found in both the Glass Mountains and the Guadalupe Mountains. Transitional forms between it and *G. cupulosa* occur in the Road Canyon Formation, however, and may give a bit of trouble. *Guadalupia cystauletoides* occupies all of this zone in the Glass Mountains, but has not been found outside that area. The distinctive species *Cystothalamia nodulifera* is abundant in the Getaway Limestone of the Guadalupe Mountains, and so far has not been found below the Willis Ranch Member of the Word (Word 3) in the Glass Mountains. There is a possibility, however, that its range may extend to the base of this zone, or even lower, because it occurs in the lower part of the San Andres Formation along with *Fissispongia conus, Stylopegma annulata,* and *Girtyocoelia dunbari.* In the Glass Mountains, *Fissispongia conus* goes no higher than Road Canyon; the other two species no higher than the China Tank. Consequently, either the range of *Cystothalamia* must be lowered or those of the other three raised, or both.

The best guide for temporal relationships within this zone may prove to be the lineage *Guadalupia cupulosa-G. vasa-G. cylindrica. Guadalupia vasa* of the China Tank Member of the Word (Word 2) appears to be a direct development out of *G. cupulosa* of the preceding zone and to lead into *G. cylindrica* of the Getaway, Goat Seep, and higher formations. *Guadalupia vasa, Stylopegma annulata,* and the genus *Girtyocoelia,* seem to disappear at the top of the China Tank Member. The fauna of the China Tank is a distinctive assemblage of some temporal significance, and may be identified at the *vasa-dunbari* Microzone.

The fauna of the Cherry Canyon Formation (Getaway Limestone and Goat Seep Limestone in particular) is also distinctive, and includes two species possibly peculiar to it (*Stylopegma getawayensis* and *Virgola getawayensis*) as well as the first appearances of *Guadalupia cylindrica* and *Stromatidium typicale,* both of which continue into the overlying zone. This fauna, at least partly of temporal significance, is set off here as the *nodulifera-typicale* Microzone. Future collecting, especially in the upper part of the Word, from which relatively few sponge-bearing collections have been available for study, may ultimately show that the two microzones have a contiguous boundary, in which case they could serve as regular subzones.

The genera *Fissispongia, Polysiphonella,* and *Girtyocoelia* disappear from the Texas Permian record somewhere within the *microcamera-zitteliana* Zone. The first two genera are absent in the Glass Mountains above the top of the preceding zone and *Girtyocoelia* is absent above the China Tank Member. In two localities the Guadalupe Mountains–Delaware Mountains area, however, one or another of them occurs together with *Cystothalamia.* Either the last-named genus ranges lower than it does in the Glass Mountains or the first three range higher, or both. This question cannot be settled at the moment. *Polysiphonella* occurs in one of these localities with *Guadalupia vasa.* If we are to use the *Guadalupia* evolutionary lineage as an Ariadne-thread in this labyrinth of incompatible ranges, then at least the range of *Polysiphonella* must be raised somewhat, and the range of *Cystothalamia* perhaps, but not necessarily, lowered. In the very large etched collections from the Getaway Limestone, there is no trace of *Fissispongia, Polysiphonella,* or *Girtyocoelia,* nor are they known from the Goat Seep, Capitan, or Bell Canyon Formations. It is likely, therefore, that they disappear before the beginning of Cherry Canyon time (the *nodulifera-typicale* Microzone).

The diagnostic faunal association of the *microcamera-zitteliana* Zone is as follows:

- Calcarea
  - Sphinctozoa
    - Maeandrostiidae
      - *Stylopegma isopora* Finks
      - *S. wordensis* Finks
      - *S. annulata* Finks (China Tank only)
      - *S. getawayensis* Finks (Getaway Limestone only)
    - Guadalupiidae
      - *Guadalupia zitteliana* Girty
      - *G. microcamera* Finks
      - *G. explanata* (King)
      - *G. cystauletoides* Finks
      - *G. vasa* Finks (China Tank only?)
      - *G. cylindrica* Finks (Getaway-Goat Seep only)
      - *Cystothalamia nodulifera* Girty (post-China Tank only?)
    - Celyphiidae
      - *Girtyocoelia dunbari* King (China Tank only?)
  - Pharetronida
    - Stellispongiidae
      - *Catenispongia agaricus* Finks
      - *Virgola getawayensis* Finks (Getaway only)
- Hexactinellida
  - Stromatidiidae
    - *Stromatidium typicale* Girty (Getaway only)

Base of the *microcamera-zitteliana* Zone:
- Last appearances:
  - By local extinction:
    - *Polysiphonella flabellata* (or higher)
    - *Fissispongia* (or higher)
    - *Guadalupia ramescens*
    - *G. williamsi* (or higher)
  - By evolution:
    - *Guadalupia cupulosa* (into *G. vasa* and *G. microcamera*)
    - *Virgola robusta* (into *V. getawayensis*)
- First appearances:
  - By evolution:
    - *Guadalupia vasa* (from *G. cupulosa*)
    - *G. microcamera* (from *G. cupulosa*)
    - *G. cystauletoides* (from *G. zitteliana*)

Top of the *vasa-dunbari* Microzone:
- Last appearances:
  - By local extinction:
    - *Girtyocoelia* (or higher)
  - By evolution:
    - *Stylopegma annulata* (into *S. getawayensis*)
    - *Guadalupia vasa* (into *G. cylindrica*)

Base of the *nodulifera-typicale* Microzone:
- First appearances:
  - By immigration:
    - *Stromatidium typicale*
  - By evolution:
    - *Stylopegma getawayensis* (from *S. annulata* or *S. wordensis*)
    - *Guadalupia cylindrica* (from *G. vasa*)
    - *Virgola getawayensis* (from *V. robusta*)

Exclusive to the *microcamera-zitteliana* Zone:
- *Guadalupia microcamera*
- *G. cystauletoides*
- *G. vasa* (China Tank only?)
- *Cystothalamia nodulifera* (post-China Tank?)
- *Stylopegma getawayensis* (Getaway only?)
- *Virgola getawayensis* (Getaway only?)

Acmes within the *microcamera-zitteliana* Zone:
- *Stylopegma isopora* (China Tank)
- *S. annulata* (China Tank)
- *S. getawayensis* (Getaway)
- *Cystothalamia nodulifera* (Getaway)
- *Guadalupia zitteliana* (Getaway)
- *G. microcamera* (Getaway)
- *G. vasa* (China Tank)
- *Virgola getawayensis* (Getaway)

The *megacysta-cylindrica* Zone

The Bell Canyon, Capitan, and Carlsbad Formations of the Guadalupe Mountains have a distinctive sponge fauna which constitutes this zone, the highest recognizable in the section. In it *Cystothalamia megacysta* replaces *C. nodulifera*, *Guadalupia favosa* replaces *G. microcamera*, and *Virgola neptunia* replaces *V. getawayensis*.

These would all seem to be evolutionary developments and suggest that the lower boundary of the zone may ultimately prove to be difficult to place exactly. *Amblysiphonella guadalupensis* Girty and *Corynella capitanensis* (formerly *Anthracosycon ficus* var. *capitanense* Girty, 1909) are distinctive species now seemingly confined to this zone. In a practical way the zone may be recognized by the great abundance of *Guadalupia cylindrica* and *Virgola neptunia* together with the diagnostic *Cystothalamia megacysta*. On the whole, the difference between this zone and the preceding, especially the reefy facies of the Goat Seep, in which *Guadalupia cylindrica* has already become prominent, is less than between the earlier zones.

The diagnostic species of the *megacysta-cylindrica* Zone are as follows:

- Calcarea
  - Sphinctozoa
    - Maeandrostiidae
      - *Stylopegma isopora* Finks
      - *S. wordensis* Finks
    - Guadalupiidae
      - *Guadalupia zitteliana* Girty
      - *G. explanata* (King)
      - *G. cylindrica* Girty
      - *G. favosa* Girty
      - *Cystothalamia megacysta* Finks
    - Sebargasiidae
      - *Amblysiphonella guadalupensis* Girty
  - Pharetronida
    - Stellispongiidae
      - *Catenispongia agaricus* Finks
      - *Stratispongia cinctuta* Finks
      - *Virgola neptunia* (Girty)
      - *Corynella capitanensis* (Girty)
- Hexactinellida
  - Stromatidiidae
    - *Stromatidium typicale* Girty

Base of the *megacysta-cylindrica* Zone:
- Last appearances:
  - By local extinction:
    - ?*Stylopegma getawayensis*
    - ?*Guadalupia cystauletoides*
  - By evolution:
    - *Guadalupia microcamera* (into *G. favosa*)
    - *Cystothalamia nodulifera* (into *C. megacysta*)
    - *Virgola getawayensis* (into *V. neptunia*)
- First appearances:
  - By immigration:
    - ?*Amblysiphonella guadalupensis*
    - ?*Corynella capitanensis*
  - By evolution:
    - *Guadalupia favosa* (from *G. microcamera*)
    - *Cystothalamia megacysta* (from *C. modulifera*)
    - *Virgola neptunia* (from *V. getawayensis*)

Exclusive to the *megacysta-cylindrica* Zone: All species listed under first apperaances.

Acmes within the *megacysta-cylindrica* Zone:
Guadalupia zitteliana
Guadalupia cylindrica
Virgola neptunia

Acme-Associations

Many of the longer-ranging species show distinct periods of markedly greater abundance, not necessarily at the midpoints of their ranges, and often at more than one horizon (see Figures 1 and 2). Such flowerings can usually be recognized in more than one locality at the same horizon, and therefore are not a strictly local matter. The environment undoubtedly played a major part in determining the time and place of a bloom of a particular species. At the same time, an evolutionary, and therefore a temporal, element is also present, as can be seen by examining those species that have more than one period of abundance, such as *Heliospongia vokesi* or *Catenispongia agaricus*. Each of their blooms is accompanied by the bloom of a somewhat different set of other species (see Figures 1 and 2). At particular horizons, the association of species enjoying a period of florescence gives a characteristic stamp to the sponge fauna. Such an association may prove to be more useful for correlation within a limited area than the zonal-guide fossils. The characteristic acme-associations (I use the word "acme" perhaps somewhat loosely) are listed below. I use the same type of two-species name for the acme-associations as are used for the other biostratigraphic units.

1. The *stenaulos-orthoplectum* acme-association (Neal Ranch reef facies):
   Stylopegma stenaulos
   Stereodictyum orthoplectum
2. The *defuncta-vokesi* acme-association (Decie Ranch Member of the Skinner Ranch Formation):
   Defordia defuncta
   Heliospongia vokesi
3. The *vokesi-dunbari* acme-association (Taylor Ranch Member of the Hess Formation):
   Stylopegma annulata
   Fissispongia conus
   Heliospongia vokesi
   Stereodictyum orthoplectum
   Guadalupia auricula
   Catenispongia agaricus
   Girtyocoelia dunbari
4. The *lepta-flabellata* acme-association (Cathedral Mountain Formation):
   Polysiphonella flabellata
   Guadalupia explanata
   G. lepta
   Actinocoelia verrucosa
5. The *wordensis-robusta* acme-association (Road Canyon Formation):
   Stylopegma wordensis
   S. annulata
   Polysiphonella flabellata
   Fissispongia conus
   Guadalupia cupulosa
   G. ramescens
   Virgola robusta
   Catenispongia agaricus
   Stratispongia cinctuta
   Girtyocoelia dunbari
6. The *isopora-vasa* acme-association (China Tank Member of the Word Formation):
   Stylopegma isopora
   S. annulata
   Guadalupia vasa
7. The *nodulifera-zitteliana* acme-association (Getaway Limestone Member of the Cherry Canyon Formation):
   Stylopegma getawayensis
   Cystothalamia nodulifera
   Guadalupia zitteliana
   Guadalupia microcamera
   Virgola getawayensis
   Catenispongia agaricus
8. The *cylindrica-neptunia* acme-association (Capitan Limestone):
   Guadalupia cylindrica
   G. zitteliana
   Virgola neptunia

Extinction and Immigration

The introduction of new forms by apparent immigration may be suspected when they appear without known relatives in the area in earlier deposits. The principal such cases occur at the base of the *vokesi-defuncta* Zone, when the pharetronids appear for the first time in the form of *Catenispongia* and *Stratispongia*. This may also be the first appearance of the pharetronids anywhere. The related pharetronid *Virgola* appears at the base of the next higher *flabellata-robusta* Zone. It is sufficiently different from the other two for it to be likely to have evolved outside the area and to have entered by immigration. The genus *Guadalupia* appears at the base of the *williamsi-vokesi* Subzone of the *vokesi-defuncta* Zone. It is seemingly without antecedent in the area and also appears to have entered as an immigrant. It has undergone a considerable adap-

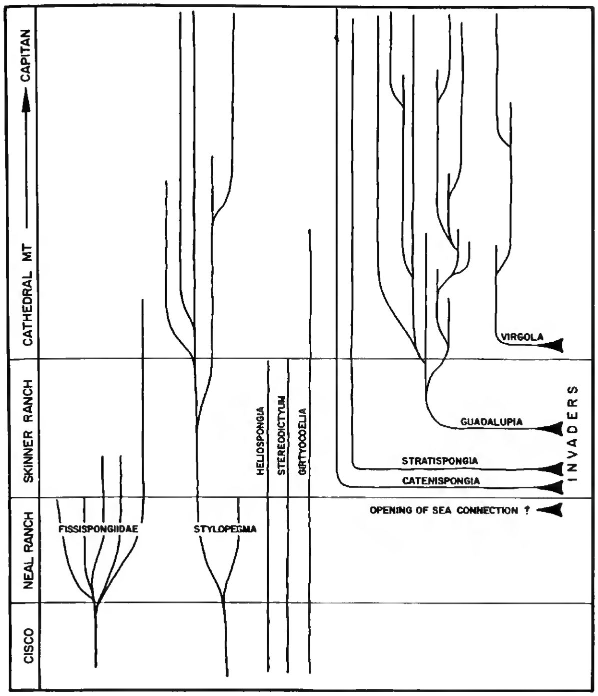

FIGURE 3.—Immigration, radiation and extinction of selected sponges in the shoal-water facies of the west Texas Permian section.

tive radiation in higher beds which may well have taken place within the Texas Permian basin.

Disappearances by extinction seem more widely dispersed in the section, but a slightly higher concentration of them occurs at the base of the *vokesi-defuncta* Zone, chiefly due to the disappearances of Neal Ranch forms. The base of the *flabellata-robusta* Zone marks the apparent extinction of the genera *Heliospongia* and *Stereodictyum* and, outside the area, possibly that of *Wewokella* (and with it the Class Heteractinida) as well. Thus, from the point of view of both immigrations and extinctions, the base and the top of the *vokesi-defuncta* Zone appear to be datum planes of more than usual significance.

Paleoecologic Considerations

The new elements of the Neal Ranch Formation can be derived almost entirely from Pennsylvanian predecessors in the area. Most of the newer forms are associated with the reef facies and it seems reasonable to conclude that the reef environment stimulated sponge evolution.

At the beginning of Skinner Ranch time *Catenispongia* and *Stratispongia* appear in the region without known antecedent forms. The same is true of *Guadalupia,* which appears in the mid-Skinner Ranch, and of *Virgola,* which appears at the beginning of the Cathedral Mountain. Thus, Skinner Ranch time appears to have been a period of immigration of new forms. It is possible that geographical changes, possibly changes in sea connections or perhaps the opening of a connection with Tethys—which is the focal area for late Paleozoic calcisponge distribution (Finks, 1969, p. 16 and fig. 12)—permitted these incursions.

By the end of Skinner Ranch time two interesting sets of events had taken place. One is the extinction of the old, and hitherto abundant, silicisponge genera *Heliospongia* and *Stereodictyum.* The other is the abrupt radiation of the newly arrived calcisponge *Guadalupia* and of the indigenous calcisponge *Stylopegma.* These faunal changes have taken place within the reef and shallow water facies. The contemporaneous basin facies retains a rather conservative silicisponge fauna (see Finks, 1960). It is not unreasonable to see a connection between these events.

The extinction of *Heliospongia* and *Stereodictyum* must have opened up niches (*voluminous-branching* and *low-encrusting* space-occupancy, respectively) which became available to the calcisponges (*Stylopegma* for the one and *Guadalupia* for the other) and may have thus stimulated their evolution. Whether the extinction was caused by environmental change, competition from the calcisponges, or both, is difficult to decide. One clue, however, is the fact that both *Heliospongia* and *Stereodictyum* are abundant in the Taylor Ranch Member of the Hess Formation (the *vokesi-dunbari* acme-association) along with the beginnings of the *Guadalupia* and *Stylopegma* radiations (the newly evolved *Guadalupia auricula* and *Stylopegma annulata*). This indicates that the calcisponges did not diversify solely because of the extinction of the two silicisponges, and suggests that they were becoming competitors of the silicisponges in the shelf environment. It also indicates that whatever eventually caused the extinction of the silicisponges had not had an effect on their numbers even this shortly before their final disappearance.

The coincidence of these developments with the putative opening of new seaway connections suggests that if such a geographic change took place it could have triggered a chain of events beginning with immigration and leading both to the extinction of old forms and to the endemic evolution of new ones. Climatic change, rather than seaway change, could also have brought about the same sequence of events, including the initial immigration.

Subsequent evolutionary development among the sponges seems to have proceeded at a more leisurely pace, as did the decline and ultimate extinction of the Pennsylvanian holdovers *Girtyocoelia* and *Fissispongia* (see Figure 3).

If we look at the opposite limiting case, so to speak, and assume that all evolution took place *outside* the area, then the beginning of Cathedral Ranch time will be a time of maximum invasion of new forms. It seems likely, however, that much endemic evolution did take place because of the intergrading nature of many species, the existence of consistent trends, and the existence of a much greater variety of *Guadalupia* and *Stylopegma* than is known anywhere else in the world.

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Permian Gonioloboceratidae (Ammonoidea)

ABSTRACT

The ammonoid *Gonioloboceras discoidale* Böse, 1920, generally has been regarded as an Upper Pennsylvanian fossil. Restudy of this species indicates that it differs from similar Upper Pennsylvanian forms and that it occurs in Lower Permian strata at the type locality near Tularosa, New Mexico. Record of this same ammonoid from Oklahoma in beds firmly established as Lower Permian verifies the assignment. The genus *Mescalites* is proposed for Permian Gonioloboceratidae, with *G. discoidale* as the type species. Distinctive features include a secondary lobe on the flank of the ventral saddle, and a thick dorsolateral shell deposit in the mature body chamber.

Fifty years ago there was considerable uncertainty in the gross age assignments for some Late Paleozoic strata in southwestern United States. Fossils were difficult to find in Permo-Carboniferous sections, such as the red beds in the shelf area of New Mexico. Emil Böse, who had studied the Abo Sandstone and associated formations, then (1920) noted the discovery of some ammonoids from a shale bed near Tularosa. This fauna was thought to provide a correlation with comparable fossils in Texas. The cephalopods were later studied in more detail by A. K. Miller (1932), but the consensus remained that "lower Abo" faunas could be assigned with certainty to the Upper Pennsylvanian. The key fossil was *Gonioloboceras discoidale* Böse, specifically related to forms common in the Cisco Group of north-central Texas. The gonioloboceratids have since been studied in comprehensive fashion by Plummer and Scott (1937), Elias (1938, 1962) and Miller and Downs (1950). All these workers made significant contributions to understanding of the group, but a difficulty involving the age of *G. discoidale* remained. Faunal and stratigraphic studies indicated that a lower marine portion of the Abo Formation, in its original sense, is separated by an unconformity from strata above and below. The fusulinids in this portion of the section were determined to be Wolfcampian in age (Thompson, 1954; Otte, 1959) and either Bursum Formation or Laborcita Formation was applied to the strata in question. Thus, it was apparent that an index Pennsylvanian ammonoid was being recorded in the Permian. Cephalopod workers discounted the age assignment or speculated that some structural complexity might explain the incongruity. In 1957, Miller and Furnish (in Moore, 1957) recorded the genus *Gonioloboceras* from the Permian of Oklahoma; however, Elias (1962) still placed the New Mexico locality in the Pennsylvanian and regarded *G. discoidale* as conspecific with the Cisco representatives of north-central Texas.

In discussing systemic boundaries, there is a constant problem of semantics even with agreement on correlation; however, for the last 30 years it has been customary for almost all workers to employ the same boundary definition between Pennsylvanian and Permian (e.g., Dunbar and Skinner, 1937). Perhaps the best area in which the stratigraphic sequence is firmly established on a physical basis lies in the cyclic sediments of the midcontinent, from Nebraska to Texas. Thompson (1954) recorded about a dozen fusulinid horizons within the Wolfcampian Series in Kansas and Texas. Recognition of this basal Permian boundary in western Texas and New Mexico is based upon identical or similar species as those in the midcontinent.

In the light of such a controversial example as the basal Permian Gonioloboceratidae, some statement of

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principle is in order. The confrontation of an extended range for supposedly time-sensitive fossils, such as *Gonioloboceras,* has now become commonplace, and scarcely deserving of special consideration. A few similar extensions into younger strata have been found by comprehensive collecting of Late Paleozoic ammonoids. As a corollary, "early" occurrences have come to be expected in faunas with elaborate representation involving several families. Provincialism, limited geographical occurrence, gives an added dimension to anomalous fossil records. The local distribution problem can usually be solved by reference to various taxa or by arrangement in a phylogenetic series. On the basis of theory, early occurrence before culmination is to be expected, but the "horizon of extinction" becomes more of a vagary. In practice, few of these problems are difficult to solve as far as Late Paleozoic ammonoids are concerned. Most of the "links" in an evolving series have been recognized and these lineages have been traced as a continuum through more than one geologic system. There are very few spontaneous variants which escaped this chain. In addition, the highest observed stratigraphic occurrence of a taxon has been demonstrated in a multitude of examples to have chronologic significance in a worldwide sense. Ammonoid studies seem to be approaching a state where most of these data can be fitted systematically into a pattern. *Gonioloboceras* proves to be no exception; a sequence can be traced from Middle Pennsylvanian into the Permian.

Several developments have now clarified the nature of the ammonoid fauna at Tularosa, New Mexico.

1. Fossils were known to be sufficiently abundant at the locality that a collecting effort would almost certainly reveal additional ammonoid taxa. However, by far the most abundant forms associated with *Gonioloboceras* are species of *Eoasianites,* a genus with little stratigraphic significance. Nevertheless, rare specimens of *Properrinites, Almites, Crimites,* and *Artinskia* have now been found; these can be identified with distinctive basal Permian species. Comparable representatives of all these genera are known from the type Wolfcamp, and a few scattered specimens have been found in the midcontinent. With the exception of the perrinitids and goniolobоceratids, all of these Lower Permian ammonoids can be duplicated in Asselian rocks of the Southern Urals. Ancestry of the taxa found in the Bursum Formation is known in the Upper Pennsylvanian, but in no case are the Pennsylvanian and Permian forms congeneric. Thus, a secure basal Permian age assignment can be made on the Tularosa ammonoid faunal assemblage alone.

2. In the midcontinent sequence of northern Oklahoma a variety of cephalopods was discovered in the Red Eagle Limestone by G. A. Cooper, A. L. Bowsher, and W. T. Allen. This stratigraphic unit is well established in the fusulinid faunal sequence and occurs in the lower Council Grove Group. Most of the ammonoids from the Red Eagle are *Eoasianites* specifically comparable to those from Tularosa and elsewhere, but nondistinctive. One specimen represents the family Gonioloboceratidae and substantiates a Permian tie with the Bursum Formation of New Mexico.

3. Direct comparision of shell features in the Upper Pennsylvanian representatives of *Gonioloboceras* with similar Permian shells indicates that consistent differences exist between them. The addition of a lobe element, plus a change in the form of the ventral surface of the shell, means an extension of the phylogenetic lineage to younger forms. That is, the Pennsylvanian whorls are only slightly flattened ventrally, instead of furrowed, and the new lobe exists only as a small septal flexure, in the earlier species. As might be expected, small shells (15–20 mm in diameter) of the Permian forms possess characteristics present in the Pennsylvanian species at full size (60–70 mm in diameter).

Several persons have contributed important materials for study. Particularly we wish to thank G. A. Cooper for his interest and for providing specimens from the United States National Museum (USNM) collections (catalog numbers are given under systematics). R. H. Flower allowed one of us (W.M.F.) to examine large collections from Tularosa at the New Mexico Institute of Mining and Technology. Research funds for fieldwork and laboratory expense were secured from the National Science Foundation (GB-5530). The University of Iowa and Texas Technological College provided facilities, and graduate students from both of these institutions aided in field collecting. Unpublished dissertations of Floyd W. Beghtel (1962) and Richard W. Moyle (1963) in the University of Iowa Library give information on related faunas, and both treat the Tularosa ammonoids briefly.

Family GONIOLOBOCERATIDAE Spath, 1934

Diagnosis.—The gonioloboceratids are characterized by an involute discoidal conch and by closely spaced high-relief simple sutures. Growth lines are biconvex, with a prominent ventrolateral salient and median lateral sinus. The mature conch which normally attained a moderately large size, 100-mm diameter, was nearly smooth and fragile. No complete conch has been reported, but related forms have a body chamber about a volution in length with only moderate changes in the peristome. The innermost whorls are evolute and ribbed; narrowly double-keeled *Gonioglyphioceras* and furrowed *Mescalites,* new genus, show modifications in the ventral surface of mature whorls. The goniatitic, eight-lobed suture is characterized by a subangular lateral saddle and an exceptionally broad ventral lobe. The prominent median secondary ventral saddle is attenuated in type *Gonioloboceras* of the Upper Pennsylvanian, and the Lower Permian *Mescalites* modified this feature by addition of a distinct sutural element close to the venter. The siphuncle in this family is relatively small and on the ventral shell margin; it has a specialized type of prochoanitic goniatitic structure in the mature conch.

Occurrence.—The gonioloboceratids should be regarded as exclusively Pennsylvanian and Lower Permian. *Gonioloboceras* Hyatt, 1900, of the Middle and Upper Pennsylvanian occurs widely in the midcontinent region of North America, but other reported occurrences are in question. *Gonioglyphioceras* Plummer and Scott, 1937, is found characteristically in late Middle Pennsylvanian strata of the same general area in Oklahoma, (?) Texas, Illinois, and Ohio. *Mescalites,* new genus, is known only from the basal Permian of New Mexico and Oklahoma.

In some Pennsylvanian strata small specimens of *Gonioloboceras* or *Gonioglyphioceras* occur in remarkable abundance. Literally hundreds of well-preserved immature limonitic shells less than 10 mm in diameter have been found at single localities. It is a curious fact that in such places the larger whorls are relatively rare. The gonioloboceratids usually occur in shales, so they characterize a low-energy zone of deposition. These sites are on shelf areas, indicating relatively shallow normal marine water. The ammonoids of this family were probably good swimmers, but are found associated in most localities with nodose loosely coiled nautilids that must have been less active; inner whorls representing young forms of the nautilids are almost nonexistent. Probably there is little inference to be drawn except that the gonioloboceratids were a group in which all growth stages coexisted in a population. There is some indication that these stages can be grouped into "hatches" or generations, with a preponderance of the smallest.

Remarks.—The only practical interpretation of the Gonioloboceratidae is to include a group of closely similar forms from the Pennsylvanian and basal Permian. The later representatives form a single evolving lineage. There was some instability within the Middle Pennsylvanian, and the Lower Pennsylvanian ancestry of the family is not clear. *Wiedeyoceras* Miller, 1932, of the Lower and Middle Pennsylvanian is a somewhat generalized goniatite that resembles growth stages of the gonioloboceratids closely and may constitute the important link with more globular ancestral types. *Wewokites* Furnish and Beghtel, 1961, is even more closely similar in some respects. Still, there are Mississippian genera, such as *Eogonioloboceras* Librovitch, 1957, and *Arcanoceras* Ruzhencev, 1965, occurring in strata of late Chesterian [lower Namurian] age, that are normally classified with the Gonioloboceratidae. The strongly asymmetric prongs of the ventral lobe and narrow secondary ventral saddle indicate that these Mississippian forms are more closely allied with the Girtyoceratidae. Some of the "Middle Carboniferous"discoidal goniatites need to be examined more closely before their true relationships can be established. For example, the figured specimen of "*Gonioloboceras* sp." (Miller and Owen, 1944) from the uppermost Mississippian Rhoda Creek Shale of southern Oklahoma is now known to represent the genus *Eumorphoceras,* and the two additional specimens are crushed examples of the associated *Cravenoceras friscoense* (Miller and Owen).

There may be a number of recognizable species ot *Gonioloboceras* from the midcontinent Upper Pennsylvanian, but at present there is no sound basis for differentiation of all those that have been proposed. Several have been placed in synonymy with *G. goniolobum* by Miller and Downs (1950). Forms stratigraphically older than the type occur in the Missourian Stage and have been named *G. parrishi* (Miller and Gurley), *G. welleri* Smith [in part, from Illinois], *G. gracellenae* Miller and Cline, *G. bridgeportense* Plummer and Scott, and *G. schmidti* Elias. Use of septal spacing as a primary taxonomic criterion (Elias, 1962, pp. 32–34) has not been verified in the present study. A general observation is that length of camerae in ammonoids is one of the more variable features that can scarcely be evaluated without a considerable number of well-preserved fully mature conchs for examination. In taxonomy, greater emphasis can be placed upon sutural outlines, particularly the ventral portion in gonioloboceratids; however, most diagrammatic illustrations are too inexact for detailed comparison. *Gonioloboceras eliasi* Miller and Owen, from Middle Pennsylvanian beds in Missouri, has primitive sutural characteristics which serve to distinguish it.

Mescalites Furnish and Glenister, new genus

Diagnosis.—The genus *Mescalites* is exemplified by its type, the only known species. The conch attained a moderately large size for Late Paleozoic ammonoids; that is, the phragmocone was about 75 mm in diameter at maturity. No complete mature conchs have been observed in this form, or in any other member of the family. The conch is thinly discoidal in cross section (width/diameter ratio about 30 percent) with converging flanks. The ventral surface is nearly flat, but has a distinct concavity or furrow in larger whorls. The umbilicus is small (umbilicus-diameter ratio less than 10 percent) as observed on internal molds. If shell is preserved, however, the umbilical opening is covered by a callous which developed at maturity (Plate 1: figure 1). Secretion of this umbilical plug preceded the leading edge of the peristome. The thick deposit greatly strengthened the umbilical area; it extends onto the dorsal surface and perhaps halfway across the interior wall of the external whorl. Such a feature is analogous to the umbilical plug in *Nautilus pompilius* Linné. There is also a resemblance to the "helicolateral" deposits of the Pennsylvanian ammonoid *Clistoceras* (Nassichuk, 1967); however, *Mescalites* differs in restriction of the deposit to the mature body chamber.

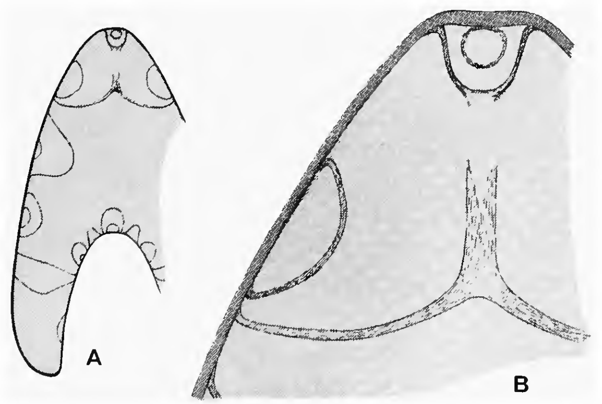

Figure 1.—A, Diagramatic cross section (× 1) of *Mescalites discoidalis* (Böse, 1920) based on a topotype (SUI 33021) from the basal Permian (Asselian Stage) middle Bursum Formation near Tularosa, Otero County, New Mexico. Figure B represents the enlarged (× 6) ventral portion of the diagram in A. The specimen which served as the basis for these drawings is somewhat fragmented, but it appears to be only slightly distorted. Flattening of the ventral surface is representative for this stage of growth.

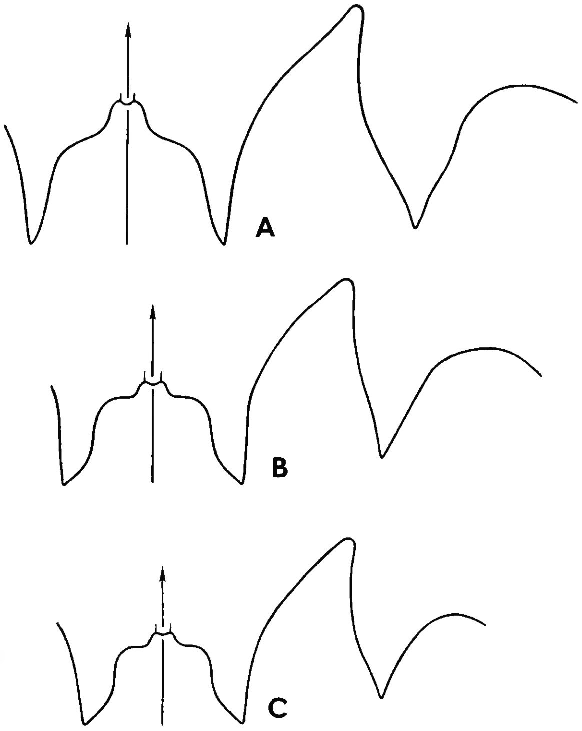

Figure 2.—Diagrammatic illustration of sutures in *Gonioloboceras* and *Mescalites*: A, *Gonioloboceras goniolobum* (Meek, 1877), based on the holotype (USNM 156437) from some unknown horizon and locality, probably the Upper Pennsylvanian of New Mexico (× 2). Suture at a conch diameter of 65 mm. Same specimen as shown in figures 5 and 6 of Plate 2. B, *Mescalites discoidalis* (Böse, 1920), based on a hypotype (USNM 165845, collected by G. A. Cooper) from the basal Permian (Asselian Stage) Red Eagle Limestone in a quarry just northeast of Burbank, Osage County, Oklahoma, at a diameter of 22 mm (× 4). In this immature growth stage, the suture is comparable to larger *Gonioloboceras* of the Upper Pennyslvanian. Same specimen as shown in figures 9 and 10 of Plate 2. C, *Mescalites discoidalis* (Böse, 1920), based on a topotype (USNM 165846, collected by A. L. Bowsher and W. T. Allen) from the basal Permian (Asselian Stage) middle Bursum Formation near Tularosa, Otero County, New Mexico, at a diameter of 22 mm (× 4); introduced for comparison with figure B.

The conch surface is nearly smooth, although growth lines are visible. As the whorls approached maturity, marginal outlines were accentuated and were characterized by a prominently biconvex form. There was a ventrolateral lappet and a deep rounded ventral sinus. Some specimens retain the dorsal pustulose "runzelschicht." The external wall of the test is relatively delicate and only about 0.3 mm in thickness near the periphery at a diameter of 75 mm.

Sutures in *Mescalites* (Figures 2, 3) are similar to those of other members of the family in gross aspect. The lobes are angular, and the first lateral saddle is attenuate and narrowly rounded. Camerae are relatively short, so that there are as many as 30 sutures in the ultimate volution of the phragmocone. Apparent crowding is accentuated by high relief of the suture pattern. The genus is characterized, in part, by possessing a secondary ventral element added to the basic goniatitid suture. This small lobe flanks the siphuncle closely and developed during ontogeny on the median ventral saddle. In this respect, then, the suture is analogous to representatives of the Neodimorphoceratidae. Both produced a flexure in the septum and a ventral furrow in the test in order to protect the vital marginal siphuncle. A corollary exists in the fragile nature of the thin shell on the venter. Such a "response" can be observed in various ammonoid lineages; the homeomorphs *Neodimorphoceras* and *Mescalites* appear to have been in separate ancestral stocks even during the Lower Pennsylvanian.

During early ontogeny, the conch form and suture of *Mescalites* differed spectacularly from mature characteristics. These stages were well illustrated for the type species by Miller (1932) who referred them to the genus *Wiedeyoceras*. The whorls at 5 to 6 mm diameter are relatively evolute (umbilicus/diameter ratio about 35 percent); they also bear umbilical ribs and transverse constrictions. The suture at this stage has a deep narrow ventral element and a shallow rounded lateral lobe. There is scarcely a single morphologic resemblance between the mature and juvenile conchs.

Type-species.—*Gonioloboceras discoidale* Böse, 1920.

Discussion.—The type of *Mescalites* has already served in part as the basis for proposals of two genera, both supposedly gonioloboceratids with a ventral furrow. Miller's (1932) *Gurleyoceras* is now regarded as a subjective synonym of *Gonioloboceras* Hyatt. Smith's (1903, pl. 21, fig. 3; Stanford University Collection 5898) larger figured paratype of the type-species of *Gurleyoceras, Gonioloboceras welleri,* was illustrated by Elias (1938, pl. 19: figs. 1a, b) to possess a rounded

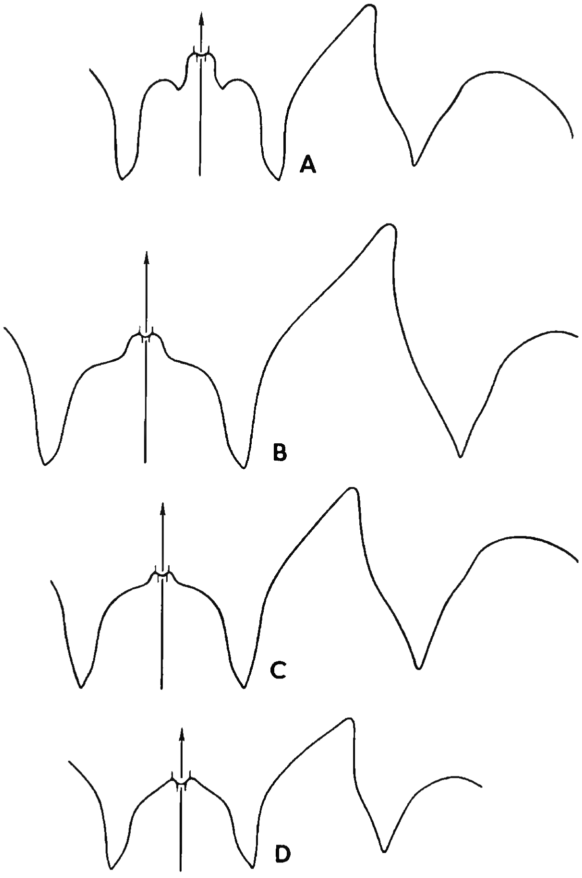

Figure 3.—Diagrammatic illustrations (× 2) of sutures in *Mescalites* and *Gonioloboceras.* This series is arranged in stratigraphic sequence, and the drawings have been prepared to show a trace of the siphuncle apicad of the true suture. a, *Mescalites discoidalis* (Böse, 1920), based on a topotype (SUI 8876B) from the basal Permian (Asselian Stage) middle Bursum Formation near Tularosa, Otero County, New Mexico; at a conch diameter of 50 mm. b, *Gonioloboceras goniolobum* (Meek, 1877), based on a hypotype (SUI 8884C) from the Upper Pennsylvanian (Virgilian Stage) Finis Shale in the Graham Formation about three miles east of Jacksboro, Jack County, Texas; diameter, 75 mm. c, *Gonioloboceras parrishi* (Miller and Gurley, 1896)?, based on a hypotype (SUI 33033) from the Upper Pennsylvania (Missourian Stage) Chanute Shale in the Ochelata Group west of Skiatook, Osage County, Oklahoma; diameter 60 mm. d, *Gonioloboceras eliasi* Miller and Owen, 1939, based on a paratype (SUI 13528) from the Middle Pennsylvanian (Desmoinesian Stage) lower Cabaniss Group just above the Tebo Coal in Vansant Pit, Henry County, Missouri; diameter 50 mm; the umbilical portion of the suture is restored.

venter. Plummer and Scott (1937, pp. 332, 336, 337) had previously concluded that Smith's cross-section (1903, pl. 21, fig. 4) was erroneous and that it was probably based upon a nonseptate *Neodimorphoceras* found in association within the Graham Formation. It should be noted that Elias' designation of a lectotype for *G. welleri* is invalid, for Smith (1903, p. 126) had originally specified a holotype (Stanford University Collection 5616).

Plummer and Scott's proposed *Gonioglyphioceras* (type: *Gonioloboceras welleri* var. *gracile* Girty, 1911) is valid for some Middle Pennsylvanian representatives of the family, because they differ in possessing a rounded lateral lobe of the suture and narrow bicarinate ventral margin of the conch (Plate 2: figures 1–3). *Gonioglyphioceras* is a characteristic fossil of the Desmoinesian (late Middle Pennsylvanian) in which *G. gracile* (Girty, 1911), *G. hathawayanum* (McChesney, 1860), and *G.* species (Miller and Sturgeon, 1946) occur. Slightly higher in the section *G. collinsvillense* (Miller and Owen, 1937) has been found in the basal Missourian Stage of the Upper Pennsylvanian. In spite of this similarity in conch form, no direct connection with the Permian furrowed *Mescalites* is visualized. It should be emphasized, however, that all gonioloboceratids are closely related; some occur together and immature stages are nearly indistinguishable.

Mescalites discoidalis (Böse)

FIGURES 1, 2b, c, 3a; PLATE 1: FIGURES 1–6; PLATE 2: FIGURES 9, 10.

Gonioloboceras discoidale Böse, 1920, pp. 52–54.
Gonioloboceras? sp. Böse, 1920, p. 58.
Milleroceras minusculum Miller, 1932, pp. 73–76, pl. 12, figs. 8–11.
Gurleyoceras discoidale (Böse).—Miller, 1932, pp. 77–79, pl. 12, figs. 14–16.
Wiedeyoceras nodomarginatum Miller, 1932, pp. 80–82, pl. 13, figs. 6–8.
Wiedeyoceras lineolatum Miller, 1932, pp. 82–83, pl. 13, figs. 3–5.
Gonioglyphioceras discoidale (Böse).—Plummer and Scott, 1937, p. 337.
Gonioloboceras goniolobum (Meek).—Elias, 1958 (part), p. 91; 1962 (part), p. 30.—Miller and Downs, 1950 (part), p. 197.
Gonioloboceras, sp. Miller and Furnish (in Moore, 1957), p. 60.

MATERIAL.—With the exception of one specimen from Oklahoma, all known representatives of *M. discoidalis* have been secured from a single locality near Tularosa, New Mexico. Only about 25 of these are sufficiently well preserved and large enough to show the distinctive mature characters. All were secured from calcareous concentrations in a dark shale matrix; smaller specimens and a few larger weathered conchs are limonitized, but most of the fragmented outer whorls preserve the external shell.

Originally, Böse examined about 40 specimens of this species from Tularosa. Ten, regarded by him as immature *Gonioloboceras?* species were described as representatives of *Wiedeyoceras* by Miller (1932) and the 20 smaller syntypes of *M. discoidalis* were designated as types of *Milleroceras minusculum* Miller. Only a single representative of the remaining 10 syntypes has been illustrated, so it must be designated as lectotype (Yale Peabody Museum 13084). This type has a shell diameter of about 25 mm, but there are portions of another half-volution of phragmocone attached.

PLATE 1.—All specimens are from basal Permian (Asselian Stage) middle Bursum Formation near Tularosa, Otero County, New Mexico. Figures 1–6.—*Mescalites discoidalis* (Böse, 1920). 1, Lateral view (× 2.7) of a fragmentary topotype (SUI 33019) that preserves the umbilical area in a mature conch. Growth lines and dorsal "runzelschicht" are covered by a shell deposit within the body chamber, and the umbilicus is closed. The broken adoral margin appears as a thick structure comprising the original thin wall together with a thicker layer secreted within the body chamber. 2, 3, Lateral and ventral views (× 1.5) of a topotype (SUI 33024), a nonseptate fragment displaying lappets in the growth lines, a ventral furrow, and a pair of ventrolateral ridges characteristic of the mature whorl. 4–6, Views (× 1.5) of topotype (SUI 33020, collected by C. C. Branson); umbilicus is open at this stage, but the scar around lower half of the umbilical shoulder represents initial part of the shell deposit, which has closed the opening in the specimen represented in figure 1.

Figures 7, 8.—*Eoasianites subtilicostatus* (Böse, 1920). View (× 1.7) of topotype (SUI 33027, collected by John Emery Adams) showing the extreme modifications of the fully mature body chamber. The pronounced umbilical groove was first developed about a volution and a quarter apicad of the ultimate peristome. Six species had been recognized for immature gastrioccrins from this locality by Miller in 1932, and there are a variety of other names erected for similar Asselian forms elsewhere. It now appears that most of these taxa should be placed in synonymy; in general, such a population contains only two fairly distinct types and these probably represent a dimorphic pair differing mainly in conch proportions.

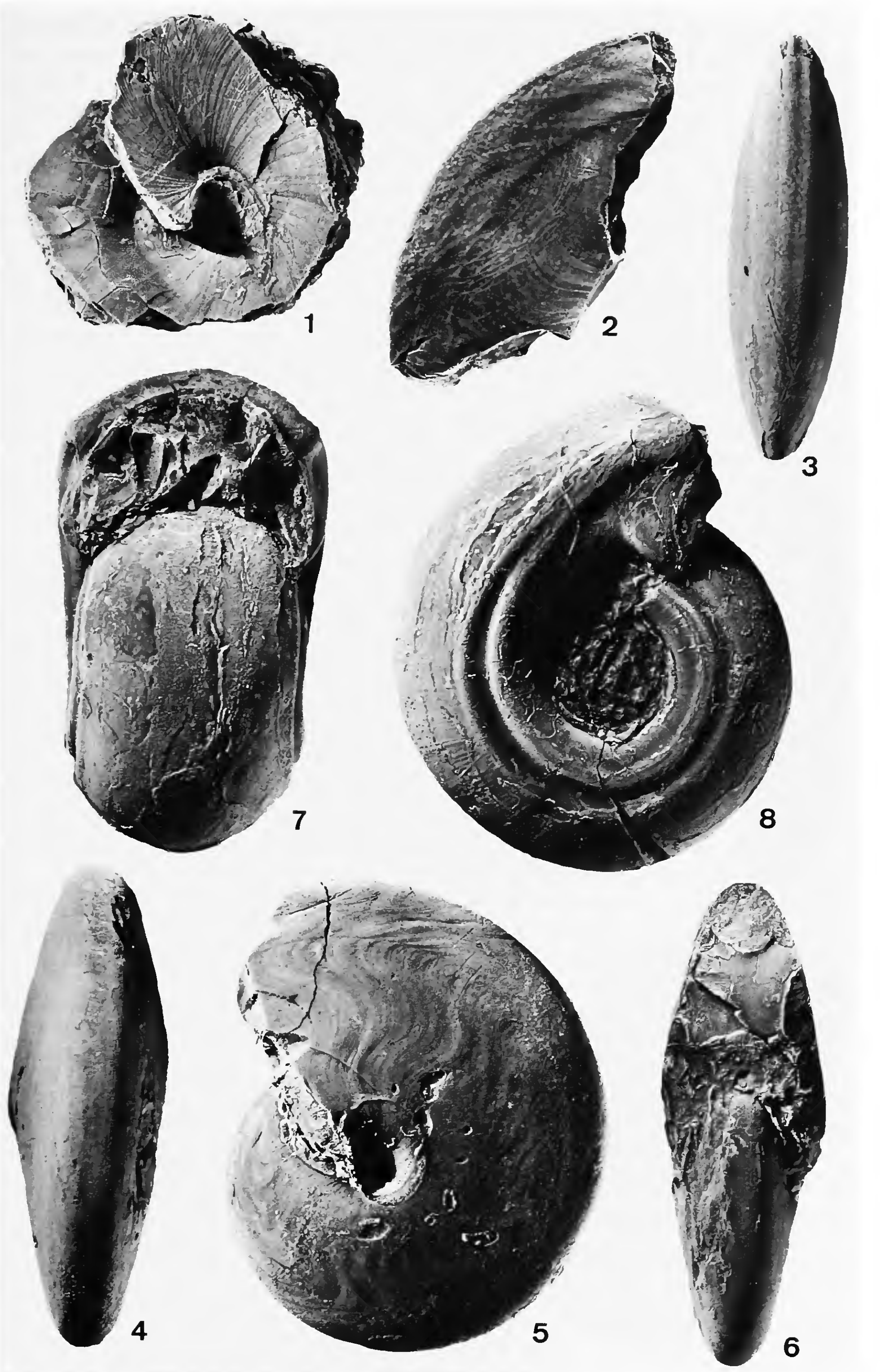

PLATE 1

Miller (1932) illustrated the earlier growth stages adequately, under different taxonomic designations, and also described the aspect of larger whorls. Our newer collections indicate that the species attained a septate diameter of at least 75 mm and an estimated ultimate diameter, therefore, of about 140 mm. In this material, most of the larger conchs are fragmented whereas the more common ones, less than 10 mm, are preserved as entire whorls.

A collection of Tularosa cephalopods studied by Böse (1920) and by Miller (1932) had been secured by C. L. Baker and N. F. Drake; all these specimens were purchased by Charles Schuchert from Böse's estate and are reposited at Yale University. About the same time, I. A. Keyte visited the locality and found a larger number of ammonoids that eventually reached the hands of J. B. Owen; Owen's entire collection is now at the University of Iowa. Other specimens from Tularosa were donated for study by J. E. Adams and by C. C. Branson. Loaned collections belonging to the United States National Museum were assembled by W. T. Allen and A. L. Bowsher. More recently, staff and graduate students from the University of Iowa and from Texas Technological College have added larger collections. There is also a large collection, secured by R. H. Flower, at the New Mexico Institute of Mining and Technology. Altogether, the number of additional specimens of *M. discoidalis* is more than five times the original collection from Tularosa.

The single Oklahoma specimen representing *M. discoidalis* does nor add appreciably to our knowledge of the species. It is a reasonably well-preserved internal mold of half a volution 25 mm in diameter, still partially imbedded in a dark argillaceous carbonate matrix. The external suture and conch form appear to be similar to those in the New Mexico collection. Sutural development stage is slightly more advanced than in the lectotype of *M. discoidalis,* a shell of comparable dimension. Such a small difference is not regarded as significant, for there is some variation in the specimens from Tularosa. Also, there can be some difference in the size attained by these shells at maturity; if the Oklahoma form had a smaller ultimate size, it would be reflected in the sutures at this stage.

Discussion.—A considerable amount of the uncertainty regarding relationships of *M. discoidalis* has been associated with the true nature of *Goniolobocera*s *goniolobum* (Meek, 1877). The type of that species is a large well-preserved shell from some unknown locality supposedly in New Mexico. Elias (1962) discussed the various aspects of its history, including a record of rediscovery of this important specimen in the British Museum (cat. C38093). This type had been recognized by L. F. Spath in an otherwise nondescript group of fossils purchased by the Museum from Gregory Bottley and Company in 1935 as the "V. Robson Collection." Although original labels had been lost (it carried an attached number 4130), there can be little doubt of its authenticity. The specimen has been graciously returned to the United States National Museum by M. K. Howarth; it bears the number USNM 156437. It would have been logical to assume that Meek's specimen might have come from Tularosa, as Elias suggested, for the similar-appearing ammonoids there have been regarded as conspecific with *G. goniolobum*. Also, there are but few other known ammonoid localities in the state near this stratigraphic

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Plate 2.—Figures 1–3.—*Gonioglyphioceras gracile* (Girty, 1911). 1, View (× 1) of large hypotype (SUI 13810A) from the Middle Pennsylvanian (Desmoinesian Stage) lower Wewoka Formation near Lovelady School, east of Ada, Pontotoc County, Oklahoma; from the J. B. Owen Collection. 2, 3, Views (× 1.5) of moderate-size hypotype (SUI 8811) from the Middle Pennsylvanian (Desmoinesian Stage) upper Wetumka Formation about two miles west of the same Wewoka locality. This specimen (donated by Helen Tappan and A. R. Loeblich, Jr.) illustrates the change in conch form from a slightly flattened ventral area to a narrowly furrowed conch.

Figure 4.—*Eoasianites subtilicostatus* (Böse, 1920). View (× 4) of a cluster of immature conchs (SUI 33025) from the type-locality in the lowermost Permian (Asselian Stage) middle Bursum Formation near Tularosa, Otero County, New Mexico. Four of the specimens illustrated had achieved only a single whorl with one septum, the proseptum; therefore, these conchs may have represented a larval stage at the time of "hatch."

Figures 5–8.—*Goniolobocera*s *goniolobum* (Meek, 1877). 5, 6, Views (× 1) of the holotype (USNM 156437), from an unknown horizon and locality, probably the Upper Pennsylvanian of New Mexico. The ultimate septum occurs at a conch diameter of about 80 mm, and the entire shell would have had a size of about 150 mm. Both views demonstrate that the suture is markedly asymmetric in the last half-volution of the conch. Figure 2a is based on this specimen. 7, 8, Views (× 1) of a hypotype (SUI 8884B) from the Upper Pennsylvanian (Virgilian Stage) Finis Shale Member of the Graham Formation at a locality about three miles east of Jacksboro, Jack County, Texas. Both this specimen and the holotype possess a slightly flattened venter at maturity.

Figures 9, 10.—*Mescalites discoidalis* (Böse, 1920). Views (× 2) of a hypotype (USNM 165845) from the lowermost Permian (Asselian Stage) Red Eagle Limestone in a quarry just northeast of Burbank, Osage County, Oklahoma; collected by G. A. Cooper. Figure 2b is based on this specimen.

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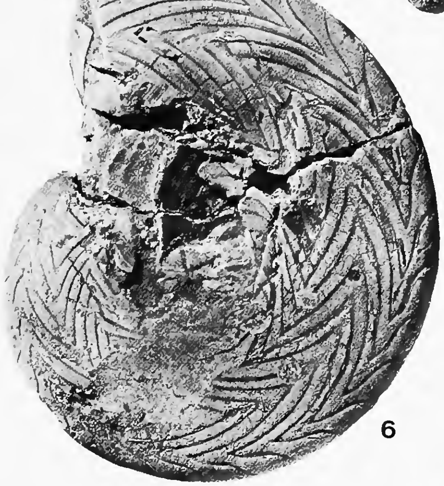

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PLATE 2

level. Our studies of the Tularosa species first described by Böse (1920) indicate that his *Gonioloboceras discoidale* is sufficiently distinct from the type of the genus to be regarded as a separate generic category, *Mescalites,* new genus. There is also an appreciable difference in the age of the two forms, Upper Pennsylvanian and Lower Permian, and the preservation is not closely similar in conchs of comparable dimension. Meek's type was originally deposited in the General Land-Office, Washington, D.C., and had presumably been found by a nonprofessional. The specimen also appears to have been handled or carried for a considerable time; Elias thought that it might have been exposed to fire. A hundred years ago New Mexico was a frontier; the possibility should be considered that such a large spectacular fossil had been picked up and carried some distance from its original site. Hundreds of *G. goniolobum* have been found loose on the surface at various localities in north-central Texas from shale members of the Upper Pennsylvanian Graham Formation. Size and preservation, as well as morphological details, are the same as in the holotype. Fossiliferous strata of comparable age to the Graham do occur in western Texas and elsewhere in New Mexico. Well-preserved Pennsylvanian cephalopods have been found less than 100 miles from Tularosa; although no *G. goniolobum* are known, the possibility of this occurrence exists. Exact circumstances will always remain in doubt, but *G. goniolobum* is exclusively an Upper Pennsylvanian fossil, as we now visualize the species.

OCCURRENCE.—The type-locality for *M. discoidalis* is at the eastern edge of the town of Tularosa, Otero County, New Mexico (center SW¼, Sec 21, T 14 S, R 10 E). All specimens have been secured from clay (shale) pits on the Marr Ranch about a quarter of a mile south of U.S. Highway 70 (the Mescalero Road, from which name the generic proposal was derived). There are shale exposures near the base of the escarpment for a considerable distance north and south of Tularosa Canyon, but a concentration of cephalopods has been found only at the one locality. These beds have been identified with several stratigraphic terms; Bursum Formation seems to be the most appropriate (Keroher and others, 1966). Laborcita Formation of Otte (1959), however, is generally an equivalent and its type area is in the immediate vicinity of Tularosa. The fossiliferous shales occur near the middle of the formation, but subjacent beds are apparently below the surface along the escarpment east of Tularosa. Associated strata include impure carbonates and conglomeratic sandstones. Thompson (1954) indicated that the Bursum in this general part of central New Mexico is lower Wolfcampian in age and about 500 feet thick; it rests unconformably on the Bruton (Holder) Formation of Virgilian (Upper Pennsylvanian) age. In his outline of the biostratigraphy, Thompson (1954, pp. 17, 18, figs. 4–6) recorded the occurrence of the fusulinid genera *Triticites, Schwagerina,* and *Dunbarinella* in these beds. At the Tularosa ammonoid locality tens of feet of dark marine shales contain only calcareous nodules and nodular beds of carbonate in which no fusulinids were observed. Otte (1959) has a detailed discussion of the age of the Laborcita Formation [Bursum], based upon specialists' identification of the various fossils. The ammonoids being considered are from his locality M–1, which lies immediately beneath a conglomeratic sandstone, his marker bed 32. A basal coarse clastic in the overlying nonmarine Abo Formation was believed by Thompson (1954, fig. 5) to be a probable equivalent of the Powwow Conglomerate of the Hueco Mountains farther to the south.

In describing the fossil cephalopods at Tularosa, Miller (1932) observed that gastropods also occur in the collection; he had not visited the locality. Actually, other molluscan groups and brachiopods are much more common than ammonoids. A variety of well-preserved gastropods occurs in profusion (Bowsher, in Otte, 1959, pp. 101–102); there are pelecypods and scaphopods as well. Orthoconic cephalopods, *Pseudorthoceras,* are common. Large nautilicones are referable to *Stenopoceras, Metacoceras,* and *Tainoceras;* the last seems to include the immature type of *Endolobus schucherti* Miller, 1932. As far as is known, none of these nautiloid cephalopods has a restricted range in the Pennsylvanian and Permian Systems. By far the most common ammonoid species at Tularosa is a gastriocerin of the *Eoasianites* gens. Böse's *Gastrioceras subtilicostatum* (1920) and five other species proposed by Miller (1932) were based upon about 40 immature shells, less than 10 mm in diameter. There are now about 500 comparable specimens for examination, plus a few as large as 60 mm with mature apertural modifications (Plate 1: figures 7, 8). Collectively, these gastriocerins show greater variation than those originally described. So many names have been proposed for such specimens that no meaningful specific assignments can be made; a variety of closely similar forms has been found to occur throughout the Pennsylvanian. It is noteworthy that identical maturely modified shells are known from the basal Permian and Upper Pennsylvanian of the Southern Urals (e.g., Ruzhencev, 1962, figs. 11c,d). Others are known from strata of the same age in Oklahoma and north-central Texas. In a practical sense, such complete mature shells are so rare in this group of ammonoids that it is impossible to assess taxonomy based upon peristomal features.

Intensive search has produced a few ammonoids of definite Permian aspect from the Bursum Formation at Tularosa. One small specimen found by Keyte was identified by Miller (1932, p. 93) as *Shumardites,* new species, a logical assignment at that time. It now appears to be most closely related to *Properrinites bakeri* (Plummer and Scott, 1937), an index for the lower Wolfcamp Group. Another fragmentary ammonoid represents the ventral portion of *Artinskia lilianae* Miller and Youngquist, 1947; the type of that species was secured in the Camp Creek Shale Member of the basal Permian Pueblo Formation near the Colorado River in McCulloch County, Texas. Conspecific forms have been secured from the base of the Neal Ranch Formation in the Wolfcamp Hills, Brewster County (Furnish and Glenister, manuscript). An immature ammonoid in the Tularosa fauna represents still another Permian form in the family Adrianitidae. This species seems to resemble *Crimites glomulus* Ruzhencev, a form described from strata of Wolfcampian age in the Southern Urals; similar undescribed ammonoids have been found in the type Wolfcamp. Additionally, two specimens of *Almites* cf. *A. sellardsi* (Plummer and Scott) have been found at Tularosa. This species is widespread in the Lower Permian of Texas.

The single specimen representing *M. discoidalis* from Osage County, Oklahoma, was found in a loose block within the large Red Eagle Limestone quarry about one half mile east of the small town of Burbank, 75 miles northwest of Tulsa. Ammonoids occur with a variety of other fossils in the eastern part of the quarry (SE¼ Sec. 25, T 26 N, R 5 E). A dark shaly zone, possibly equivalent to the Bennett Shale, below the upper limestone ledge contains large well-preserved brachiopods and nautiloids. About 25 specimens of *Eoasianites* species have been examined from this locality; most are less than 10 mm in diameter, but large mature forms occur and are comparable to the Tularosa goniatites. The Red Eagle Limestone falls within the lower Council Grove Group near the base of the Kansas-Oklahoma Permian. Limestones in the Red Eagle carry abundant fusulinids of the genera *Triticites, Schwagerina,* and *Dunbarinella* (Thompson, 1954, fig. 2). Ammonoids generally are extremely rare in this part of the midcontinent section, in comparison with other fossils.

TYPES.—The lectotype and unfigured paratypes of *Mescalites discoidalis* (Böse) are deposited in Yale Peabody Museum under catalog number 13084. Smaller specimens from the Baker-Drake collection there now referred to this species are numbered 13081, 13082, 13083, 13085, and 13086. Topotypes collected by I. A. Keyte about 50 years ago are at the University of Iowa (SUI 13807, 13851). Others numbered SUI 8876 were secured by C. C. Branson in 1946. Additional material found within the past few years is numbered SUI 33018–33021, 33023, 33024, and 33026. United States National Museum collections of *M. discoidalis* from Tularosa (locality 03284 and USNM Accession 191737) were secured by A. L. Bowsher and W. T. Allen in 1951. A hypotype of this species from near Burbank, Oklahoma, is also in the United States National Museum collections (USNM Accession 199311) and was collected by G. A. Cooper in 1953.

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Richard E. Grant

Taxonomy and Autecology of Two Arctic Permian Rhynchonellid Brachiopods

ABSTRACT

Septacamera Stepanov, formerly classed with the Stenoscismatacea, is removed to the Tetracameridae. *Septacamera* lived attached by a pedicle and evolved an *Uncinulus*-like shell with elaborate protective mechanisms. New species are *S. stupenda, S. pybensis, S. opitula;* none has been found outside of the Permian nor farther south than latitude 44°N. *Camerisma* Grant, with new subgenus *Callaiapsida,* remains in the Stenoscismatacea. *Camerisma* (*Callaiapsida*) lived free on the sea floor, probably almost completely buried, and obtained feeding currents through an ingenious pair of peripheral pipes. A set of flanges and flaps made it possible for the shell to gape only at the crest of the fold, while remaining effectively closed around most of the commissure. The subgenus has not been found farther south than 55°N; it ranges from the middle part of the Pennsylvanian into the early part of the Late Permian. *Camerisma* (*Callaiapsida*) *kekuensis,* a new species from southeastern Alaska, is the type species.

A short paper in honor of G. A. Cooper is not an easy matter. The volume that contains it is not designed as a solemn memorial to an ancient hero, but as a jubilee for a scientist vigorously at work, for whom a *Festschrift* is merely a punctuation mark in a continuing tale. As a close associate, collaborator, field partner, and daily luncher with the honoree for the past dozen years, I appreciate the standards that have been set. "Coop" himself is not given to short works; the 15- to 20-year project is more his style. He is, however, a firm believer in sound taxonomy, with revision where necessary to clarify relationships among fossils that have been described. This seems a fine opportunity, therefore, to tie up some loose ends and to add comments about brachiopods that were the subject of a larger work (Grant, 1965).

The Stenoscismatacea are a small group of Rhynchonellida, comprising eleven genera as put forth in the *Treatise on Invertebrate Paleontology* (Grant, in Moore, 1965). But now it is necessary to exclude one genus, to admit an error in classification, and to reinstate *Septacamera* Stepanov as a member in good standing of the family Tetracameridae where the Russians have placed it for the past ten years (Rzhonsnitskaja, 1958; Likharev, 1960). The justification, of course, is that "new" material has come to hand (some of which has been in collections of the United States Geological Survey since 1905, most since 1918, but has remained in unstudied collections from Alaska). The morphology of *Septacamera* now can be elucidated beyond the shadow of doubt, although the classification based on those morphological features remains an interpretation subject to revision, as are all questions of taxonomy.

The second genus treated in this short tribute to G. A. Cooper is *Camerisma* Grant, which remains among the Stenoscismatacea. Similarly, "new" material from Alaska (some actually collected as recently as 1968, some as early as 1904) has revealed morphologic de-

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tails of adaptive features unique among brachiopods. *Camerisma* developed a system of grooves, flaps, and flanges around the commissure that enabled the shell to gape at the extreme anterior while remaining effectively closed around 80 percent of the commissure. Nevertheless, feeding currents could enter and exit the same as in more conventional rhynchonellid brachiopods. This elaborate mechanism is interpreted as an adaptation for survival under nearly complete burial in an infaunal or semi-infaunal habitat.

I thank Donald A. Dean, United States National Museum (USNM) and Osborne B. Nye, Jr., University of Cincinnati, for advice and help in techniques of making serial sections and acetate peels; Haruo E. Mochizuki for photographic prints, Frances C. Smith for graphs, and Roberta Wigder for drawings and reconstructions, all United States Geological Survey (USGS). I was accompanied in southeast Alaska, June 1968, by F. G. Stehli, Case Western Reserve University, Cleveland, Ohio. I also thank J. T. Dutro, Jr., and Ellis L. Yochelson, United States Geological Survey, for reviewing the manuscript.

Order RHYNCHONELLIDA Kuhn, 1949

Superfamily RHYNCHONELLACEA Gray, 1848

Family TETRACAMERIDAE Likharev (in Rzhonsnitskaja), 1958

Diagnosis.—Outline and profile wedge shaped; lateral and anterior margins flattened; commissure uniplicate; costae simple, beginning at or near beaks, sharply flexed at anterior, meeting and interlocking at anterior valve edges. Ventral interior with large low spondylium braced by short lateral buttress plates; dorsal interior with divided hinge plate; septalium supported by median septum; septum continuing anteriorly beyond septalium.

Nomenclature.—The family name Tetracameridae in an abstract by Rzhonsnitskaja (1956, p. 126), but was attributed to Likharev in 1955. The full article by Rzhonsnitskaja (1958) contains the same abstract with the attribution to Likharev, 1955, but the text (p. 115) attributes the family to Likharev in 1956. No published work by Likharev in 1955 or 1956 contains this usage, and McLaren (in Moore, 1965, p. 588) attributed the Tetracameridae to Likharev in Rzhonsnitskaja, 1956. The fact that Likharev (in Sarycheva, 1960, p. 249) presented Tetracameridae as a new family in the *Osnovi Paleontologii,* suggests that Rzhonsnitskaja saw this manuscript in 1955 and credited Likharev for the family grouping. According to Article 51c of the International Code of Zoological Nomenclature, the name must be attributed to Likharev because Rzhonsnitskaja indicated that it was his grouping. The abstract of 1956, however, gave no indication of the constitution of the family group or how it differs from other such groups, and therefore the name is unavailable under Article 13a of the Code. The date of the family name must be that of the full article by Rzhonsnitskaja in 1958, where the taxon is explained and its constituent genera listed. Tetracameridae continues to be attributed to Likharev, however, as indicated by Rzhonsnitskaja.

Discussion.—As originally constituted by Rzhonsnitskaja in the two abstracts (1956, p. 126; 1958, p. 108) , the Tetracamerinae was a subfamily of Rhynchotetraidae in the superfamily Stenoscismatacea. As revised in the text of the article (Rzhonsnitskaja, 1958, p. 115), it is a family in the Rhynchonellacea. This latter usage is followed in the *Osnovi Paleontologii* by Likharev (1960) and in the *Treatise on Invertebrate Paleontology* by McLaren (in Moore, 1965), and is accepted here.

The error in assigning *Septacamera* to the Stenoscismatacea lay in interpretation of internal structures of the dorsal valve. Stepanov (1937, p. 149) wrote, "There is a camarophorium in the dorsal valve." Examination of Tschernyschev's (1902) figure 28 suggests a normal stenoscismatcean interior, except that the anterior part of the camarophorium seems to be broken off. The only published cross section (Likharev, 1960, p. 250, fig. 290) shows no diagnostic detail.

Silicified specimens of *Septacamera stupenda,* new species (described below), from the Permian of southeastern Alaska show the internal structures unambiguously. Initial reaction to the first etched specimen, with its short septalium rather than long camarophorium, was that the interiors were incompletely silicified. All specimens emerged from the acid, however, showing similar structures, and close study revealed many differences from the Stenoscismatacea in the structures of both valves.

It could be argued that specimens of a distinct species from Alaska cannot settle questions of the morphology and taxonomic position of a genus based on species from the Ural Mountains. Fortunately, a topotype specimen of *S. kutorgae,* identified as such by its author, Tschernyschev, is available in the collections of the United States National Museum. The specimen is about half of a nearly empty shell, broken longitudinally to expose inner structures (Plate 1: figure 23). A small encrustation of calcite obscures the cardinalia to some extent so that, in absence of the insight provided by the silicified Alaska specimens, they could not be interpreted. Now that the camarophorium is known to be absent from the genus, the interior features of this topotype specimen and specimens of the genus from the Assistance Formation of Devon Island, Canada, can be assessed correctly. Moreover, the longitudinal sections illustrated by Tschernyschev (1902, figs. 26–30) now make sense.

Genus *Septacamera* Stepanov, 1937

Septacamera Stepanov, 1937, p. 146, 149.—Rzhonsnitskaja, 1958, p. 115.—Grant, 1965, p. 156; in Moore, 1965, p. 632.

Septocamera Stepanov.—Likharev, 1960, p. 249 [variant spelling].

TYPE-SPECIES.—*Camarophoria kutorgae* Tschernyschev, 1902, p. 90, 500, fig. 28, pl. 22, figs. 16, 17 [original designation by Stepanov, 1937].

ADDITIONAL SPECIES. — *Camarophoria isorhyncha* Tschernyschev (1902, p. 89, 499, pl. 44, figs. 6a–d), *Pentamerus plicatus* Kutorga (1884, p. 89, pl. 9, figs. 3a–c), *Camarophoria plicata* (Kutorga) (holotype redescribed and illustrated by Tschernyschev, 1902, p. 92, 502, pl. 21, figs. 1a–d), *Stenoscisma* cf. *S. plicata* (Kutorga) of Cooper (1957, p. 54, pl. 10, figs. 32–35), also illustrated by Grant (1965, p. 159, pl. 4, figs. 3–3a), *Stenoscisma plicata* (Kutorga) of Harker and Thorsteinsson (1960, p. 62, pl. 18, figs. 1–4) described below as *Septacamera opitula,* new species.

Stepanov (1937, p. 149) assigned *Rhynchonella hofmanni* Krotov, and *Rhynchonella krotovi* Tschernyschev, both as described and illustrated by Tschernyschev (1902, p. 60, 477), to *Septacamera.* These are small rhynchonellids that bear little resemblance to other species of *Septacamera.* In the absence of documentation to contradict Tschernyschev's (1902) description of normal rhynchonellid dental plates and median septum, these two species should not be assigned to *Septacamera.*

DIAGNOSIS.—Shell large, wedge shaped with flattened or gently convex anterior surface; commissure uniplicate; costae strong, numerous, simple, beginning at beaks; interlocking *Uncinulus*-like at anterior; valve edges slightly flanged, with moderate overlap along posterolateral commissure; ventral beak strongly curved, but remaining high enough for open pedicle foramen (or foramen may make elongate slot through beak); deltidial plates small, disjunct, essentially internal. Ventral interior with large spondylium containing muscle marks, formed by dental plates, elevated on low median septum, braced by small lateral buttress plates. Dorsal interior with strong divided hinge plate, distally forming inner edges of hinge sockets, produced anteriorly to form crural bases; cardinal process absent; septalium deep, formed by two plates from underside of hinge plate, joining at sides of median septum; septum moderately high at septalium, extending forward as low bisector of muscle area; muscle marks on floor of valve.

DISCUSSION.—The features enumerated above show clearly that *Septacamera* is not a representative of the Stenoscismatacea. Possibly it belongs in a separate rhynchonellacean family, but comparison of sections of *S. stupenda* from Alaska (Figure 2) with sections of *Rotaia subtrigona* (Meek and Worthen) by Weller (1914, p. 219) certainly suggests a relationship to that Mississippian species. Differences between *Septacamera* and *Rotaia* are obvious; the hinge plate of *Rotaia* is constructed somewhat differently, the median septum does not bisect the septalium, and the lateral buttress plates seem to extend farther forward than in *Septacamera.* The general arrangement of internal features is similar in the two genera, however, and the striking external similarity of *S. kutorgae* and *R. subtrigona,* also seems to require uniting them in a family despite the wide disparity in their stratigraphic positions.

Most authors employed the specific names *plicata* and *kutorgae* for species now considered to belong to *Septacamera.* This usage apparently meant to indicate that brachiopods of the *Septacamera* group were being identified (most under the name *Camarophoria* or *Stenoscisma*), without regard for specific characters of *S. kutorgae* or *S. plicata.* Therefore, it has become necessary to establish some new species of *Septacamera,* and to emphasize their differences from one another and from *S. kutorgae* and *S. plicata.*

RANGE.—No authenticated occurrences of *Septacamera* in other than Permian rocks have been reported. The range of the genus seems to be confined, moreover, to the early half of the Permian, extending from the Sakmarian of Svalbard through the Artinskian (Leonard in the United States) of Arctic North America and the Ural Mountains, although it would not be surprising to find it ranging somewhat higher. Citation of a species in Oregon from rocks equivalent in age to the lower part of the Word Formation (Cooper, 1957, p. 2) now requires emendment in light of the Leonard age of the former First Limestone Member of the Word (now termed the Road Canyon Formation by Cooper and Grant, 1966, p. 6).

If the familial grouping of Mississippian *Rotaia* and Permian *Septacamera* is correct, species linking them can be expected to be found in Pennsylvanian rocks. None is known at present, however; *Septacamera* is confined to the Lower Permian.

The earliest examples are from the Upper Wordiekammen Limestone and Cyathophyllum Limestone of Svalbard where Gobbett (1963, p. 124, pl. 16, figs. 1–3) identified as *Camarotoechia? sp.* a specimen that has the external characteristics of *Septacamera*. Its interior is unknown, so identification remains tentative. *Camarotoechia,* however, is primarily a Devonian genus never identified certainly in the Permian, whereas *Septacamera* is common in Permian faunas of the Arctic.

Species from the Ural Mountains that now are assigned to *Septacamera* were reported by Tschernyschev (1902) from the *Omphalotrochus* level to the *"Schwagerina"* horizon. In modern terminology this means essentially a Wolfcamp or Sakmarian age for *S. isorhyncha* (M'Coy), *S. kutorgae* (Tschernyschev), and *S. plicata* (Kutorga).

An unidentified species of *Septacamera* has been found in the Halleck Formation in the Keku Islets of southeastern Alaska. This formation has been dated as of probable Leonard age by Dutro (in Muffler, 1967); presence of a species of *Septacamera* helps to substantiate this determination, although it does not preclude an older Permian age. The Pybus Formation (Muffler, 1967) directly above the Halleck Formation on the Keku Islets and Kuiu Island contains the best suite of *Septacamera* yet discovered. The age of this formation has not been determined precisely yet, but it probably spans the upper part of the Leonard Series of the southwestern United States, including the Road Canyon Formation (formerly First Limestone Member of the Word Formation) which now is placed in the Leonard (Cooper and Grant, 1966).

Septacamera has been found in the Assistance Formation of Grinnell Peninsula, Devon Island, in the Canadian Arctic Archipelago. This formation is considered equivalent in age to part of the Artinsk plus part of the "Svalbardian" (essentially the Leonard as now constituted) by Harker and Thorsteinsson (1960, fig. 4) although Nassichuk et al. (1965, p. 10) correlate it exclusively with the Road Canyon Formation at the very top of the Leonard Series. Oregon specimens mentioned above (Cooper, 1957) also now would be correlated to this interval, so the youngest known species of *Septacamera* remain Leonard in age.

LIVING HABITS OF SEPTACAMERA.—Salient morphologic features indicative of life habits are the pedicle foramen, the strongly uniplicate commissure with unciniliform interlocking costae, strong geniculation that produces a flattened anterior surface, overlap of the valve edges along the posterior slopes, large and deeply impressed muscle areas, and the thickened posterior parts of both valves, especially of the ventral valve.

The ventral beak is curved so tightly that the dorsal beak is essentially internal, but the spondylium is wide and deep enough to provide ample space for a pedicle and pedicle muscles. That the pedicle adjustor muscles were powerful is attested by the four raised bosses in the posterior part of the spondylium of some specimens (Plate 1: figures 16, 17, 20). The foramen and adjustor marks imply that the shell was attached, and probably that it could be raised, lowered, rotated, and tilted by its pedicle as living pediculate forms have been observed to do (Figure 1).

The divided and thickened hinge plate, plus the septalium and the thickened part of the median septum within it, served as the functional equivalent of a cardinal process. The inner surface of the septalium is smooth, like the inside of the spondylium and the muscle area on the floor of the dorsal valve, in contrast to the slightly roughened interior surfaces of the valves, suggesting strongly that the entire inner surface of the septalium served as the locus of attachment for the diductor muscles. The thickened and rounded inner edges of the slot through the hinge plate, and the thickening of the median septum, corroborate the interpretation that the muscles passed between the halves of the hinge plate and attached within the septalium.

The lateral buttress plates of the spondylium helped to absorb stress directed posteriorly to the sides of the spondylium, such as would have been imposed by short and powerful diductors. The more directly dorsoventral stress imposed by the adductors was exerted in the plane of the median septum, its direction

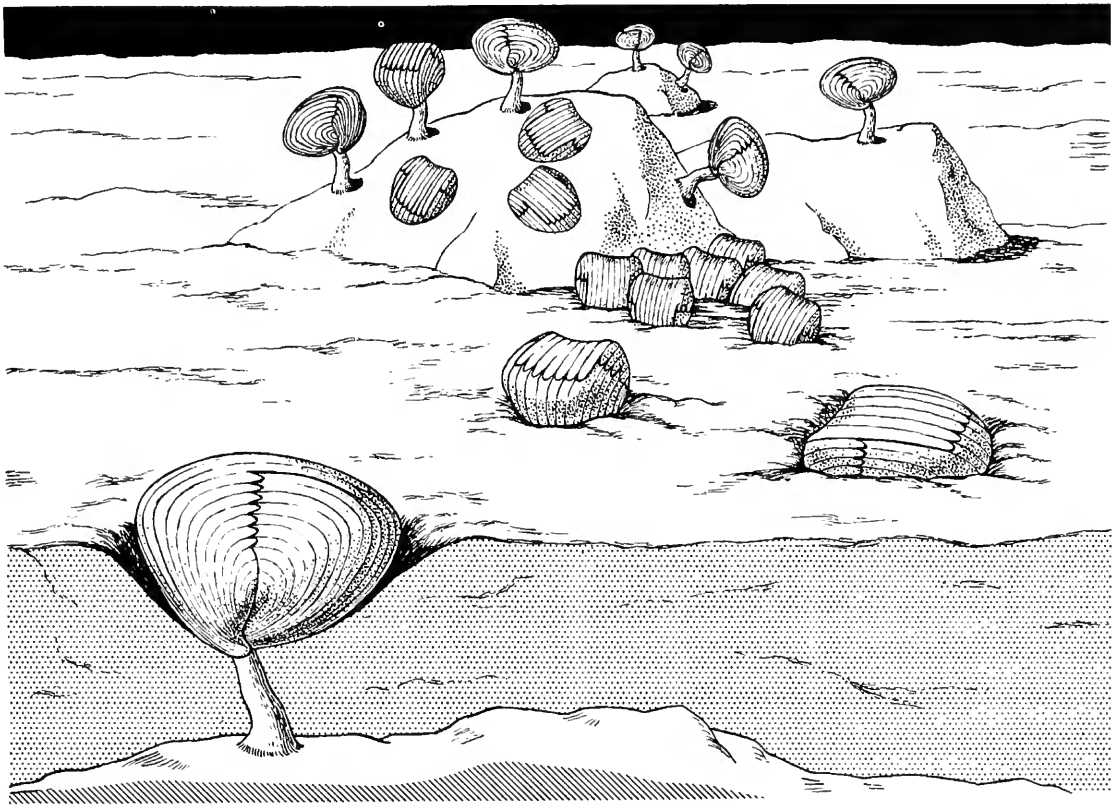

FIGURE 1.—Reconstructed habitat of *Septacamera,* depicted by stylized *Septacamera stupenda.* Shells represented as having attached to hard substrate (or hard objects originally on surface of substrate), but nevertheless able to survive under progressive burial by sediment.

of maximum strength. Stress on either the dorsal or ventral median septum was transferred to the valve itself along the internal crest of a costa (externally, a trough between costae).

The form and function of serrate commissures and of extended costae that interlock across the commissure (Plate 2: figures 13, 22, 23) have been analyzed in detail by Schmidt (1937), Rudwick (1964), and Westbroek (1967). The inescapable conclusion is that their primary function was to protect the visceral cavity from entrance of possibly harmful, or at least indigestible, particles or organisms. The mechanism was twofold: by simple screening and by providing a warning device that caused the shell to snap shut. The screening mechanism was effected through the serrated commissure that allowed the shell to gape while presenting only a narrow slit through which particles could pass. The effective opening would be greatest at the crests of the costae, but in unculiniform shells such as *Septacamera* the costae are extended at the crests, barring the opening and reducing greatly the size of particle that could enter there (Rudwick, 1964, p. 154; Westbroek, 1967, fig. 48). Such spines can interlock without breaking only if they are short or if the anterior edges of the valves meet nearly in a plane (Rudwick, 1964, p. 155) as in the strongly geniculate *Septacamera.* The same narrowness of slit provided warning by bringing the sensitive mantle edges near to one another so that a very small particle could be detected and the valve closed against the incursion (Rudwick, 1964).

Flanged and overlapping posterolateral valve edges (Plate 1: figure 17; Plate 2: figure 23) occur in many brachiopods and are especially well-developed in the nonpediculate, free-living genera of Stenoscismatacea (Grant, 1965a). The valve edges of *Septacamera* do not overlap as strongly, nor for as great a distance forward, as in most Stenoscismatacea. The edges are not tapered to form broad overlapping flanges, but instead are more like beveled edges with short overlap. Nevertheless, the effect in *Septacamera* was to provide a seal at the posterior, so that the shell could gape at the anterior but remain closed for some distance anterior to the hinge axis.

Whatever the cause for the posterior filling of secondary shell (Plate 1: figure 20) in so many diverse groups of brachiopods, it had the effect of weighting the posterior part of the shell. Normally this filling is greater in the ventral than in the dorsal valve, in groups as widely separated taxonomically as spiriferids, stenoscismataceans, and *Septacamera*. The broad hinged spiriferids are visualized as having lived on the substrate, perhaps supported by the wide hinge extensions, perhaps attached directly to fine sediment or to shells or pebbles within the sediment by means of a splayed pedicle, much as some species of the clam *Arca* attach to the sea floor by the byssus.

Life in the substrate would account for the combination of features in *Septacamera* (Figure 1). The genus obviously was pediculate, and it can be inferred that it was attached to the substrate in some manner by the pedicle. The posterior part of some specimens is greatly thickened, and all shells are heaviest at the posterior end, a condition similar to that seen in free-living forms. Furthermore, the posterior edges are flanged to remain sealed against sediment, as in free-living forms. These features suggest that *Septacamera* attached with the beak down, possibly to hard substrate, but also possibly anchoring to hard objects within soft substrate. Sediment could have built up around the attached shell without harm to the animal. The immediate surroundings could have been kept excavated by raising, lowering, and twisting of the shell on the pedicle, and if a sudden influx of sediment buried the shell the exceptionally powerfully seated diductor muscles could have separated the valves against the confining pressure. The posterior part of the shell remained closed under all circumstances, and the sides and anterior parts were barred against all but the finest particles by the serrated valve margins and the interlocking marginal spines.

Attachment with the beak lowermost would place the flattened anterior surface nearly parallel to the substrate. The very strong uniplication of the anterior commissure assured separation of incurrents from excurrents.

The Halleck Formation in southeastern Alaska contains beds of conglomerate that could have provided numerous anchors for *Septacamera*. The overlying Pybus Formation, in which *Septacamera* is especially abundant, is mainly biogenic limestone that also contains many particles large enough to anchor *Septacamera* in the manners suggested.

Septacamera stupenda, new species

FIGURES 2–4; PLATE 1: FIGURES 1–20; PLATE 2: FIGURES 22–29

DESCRIPTION.—Shell large for genus; outline rounded subtrigonal; profile exaggeratedly wedge shaped with strongly inflated dorsal valve, strongly geniculated to form flatly convex anterior surface as high as shell length in adults; commissure strongly uniplicate, area of overlap at posterior short; costae simple, beginning at beaks, fine and numerous for genus, numbering 5–12, normally 8 or 9 in sulcus, and 10–14, normally about 12 on each side; margins strongly serrated by extended ends of costae, forming mutually interlocking spine system as in uncinulids.

Ventral valve flatly convex behind geniculation, sharply geniculated at flanks, gently geniculated through sulcus; beak following general curvature of valve, pressed tightly against dorsal beak; foramen slot shaped, cutting forward through tip of beak to provide pedicle opening despite tight fit of beaks; sulcus shallowly depressed for most of shell length, but slightly convex along anterior geniculated surface.

Dorsal valve moderately convex for most of shell length; fold raised prominently only just behind geniculation, slightly convex on anterior surface; geniculation sharp at fold, more gently rounded on flanks.

Ventral interior with very long, boat-shaped spondylium, extending beyond point of geniculation in some

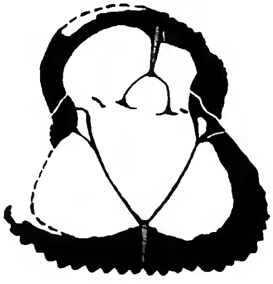

FIGURE 2.—*Septacamera stupenda*. USNM 163657, from the Pybus Formation, Kuiu Island, Alaska, USGS loc. 2450; transverse section near anterior end of septalium, showing lateral buttress plates of spondylium; presented for comparison with sections of *Rotaia* (Weller, 1914, p. 219, fig. 17; Likharev, 1960, p. 250, fig. 289; McLaren, in Moore 1965, p. 587, fig. 3d–k).

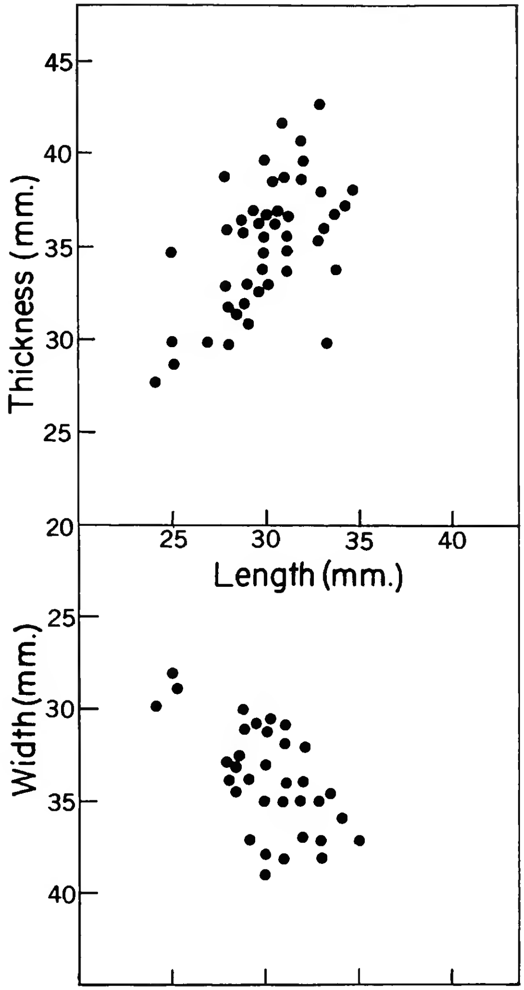

FIGURE 3.—*Septacamera stupenda* from the Pybus Formation, Kuiu Island, Alaska, USGS locs. 2450, 2451, 2452. Scatter diagram of shell width and thickness plotted against length. Length measured parallel to commissure, thickness measured perpendicular to commissure (thus not necessarily equal to maximum height of shell).

specimens and thus dorsally curved at anterior end; lateral buttress plates short; median septum low, height slightly increasing anteriorly, buried in secondary shell in many specimens; muscle marks weak, but visible in spondylium; pedicle adjustor muscles forming four low bosses on posterior sides near beak. Dorsal interior with thick divided hinge plate, thickened along mesial edges of division and laterally flattened at anterior edges to form crural bases; septalium large, bisected by median septum from floor of valve, inner walls smooth and septum thickened for muscle attachment; median septum thin anterior to septalium, height decreasing anteriorly, bisecting muscle area; hinge sockets deep, elongate, convergent toward beak, apparently smooth; muscle area flabellate, deeply impressed at thickened posterior of valve, individual muscle marks not clearly differentiated.

HOLOTYPE.—USNM 163628 (Plate 1: figures 5–8).

COMPARISONS.—*Septacamera stupenda* has all the features that characterize *Septacamera,* but the external features are exaggerated beyond those of any other species of the genus. Especially notable is the extreme thickening of the shell profile by growth after geniculation of the shell (Figure 3). This thickening produces a highly wedge-shaped profile, indeed most adult shells are thicker than they are long. The other feature that makes this species immediately distinguishable is the fineness and great number of the costae, more than in any other known species of *Septacamera* (Figure 4).

OCCURRENCE.—Many of the conclusions regarding the morphology and living habits of the genus *Septacamera* are derived from study of silicified specimens of *S. stupenda* from the Pybus Formation on Kuiu Island, southeastern Alaska. Specimens studied for this report are all from the northeast shore of Halleck Harbor in

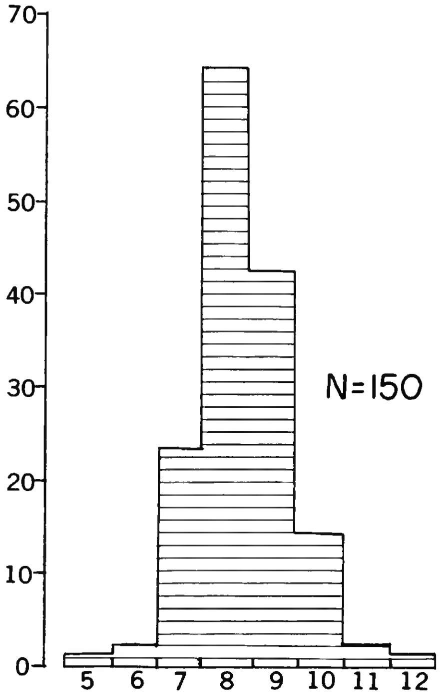

FIGURE 4.—*Septacamera stupenda* from the Pybus Formation, Kuiu Island, Alaska, USGS locs. 2450, 2451, 2452. Histogram showing frequency of costae in sulcus.

Saginaw Bay, from blocks of limestone at the base of the cliff formed by the Pybus Formation. The formation is just less than 500 feet thick along the shore of Halleck Harbor (Muffler, 1967). Measurements by Grant and Stehli in 1968 located fossiliferous beds with *Septacamera* about 150 feet above the base although there is no certainty that specimens in loose blocks were derived from a single bed or narrow interval.

Collections from below the Pybus cliff in Halleck Harbor were made by Wright in 1904 (USGS loc. 2382; see Wright and Wright, 1908), Kindle in 1905 (USGS loc. 2381), Kirk in 1917 (USGS loc. 2385) Waters and Girty in 1918 (USGS locs. 2450, 2451), Muffler in 1963 (USGS locs. 23400, 23401), and Stehli and Grant in 1968.

Septacamera pybensis, new species

FIGURES 5, 6; PLATE 2: FIGURES 1–16

DESCRIPTION.—Shell about average size for genus; outline rounded subtrigonal; profile subglobose to wedge-shape; geniculation rounded, producing flat to gently convex anterior surface; commissure uniplicate, height of fold variable; costae simple, beginning at beaks, crests bluntly angular, numbering 5–7 in sulcus, most frequently 7, numbering about 9 or 10 on each side of ventral valve, ends extended at anterior to interlock, length of extensions decreasing laterally and posteriorly.

Ventral valve flatly convex, gently to sharply geniculated at flanks, normally evenly curved through sulcus, but strongly geniculated (sharply curved, not angulated) in some; beak curved tightly over dorsal beak; foramen open, normally a triangular slot in beak ("epithyrid"). Dorsal valve moderately to strongly inflated, normally rather evenly convex, but strongly geniculate in some specimens, producing exaggerated wedge form.

Ventral interior with small, triangular disjunct deltidial plates; spondylium relatively short, braced by short lateral buttress plates; median septum extending forward well beyond spondylium. Dorsal interior with thick hinge plate, deep dental sockets; septalium short, thick, bisected by median septum that becomes thickened within septalium, remains thin between septalium and valve floor; muscle marks weakly impressed on valve floor, incompletely bisected by septum; crura broad, flat, twisted, curving ventrally.

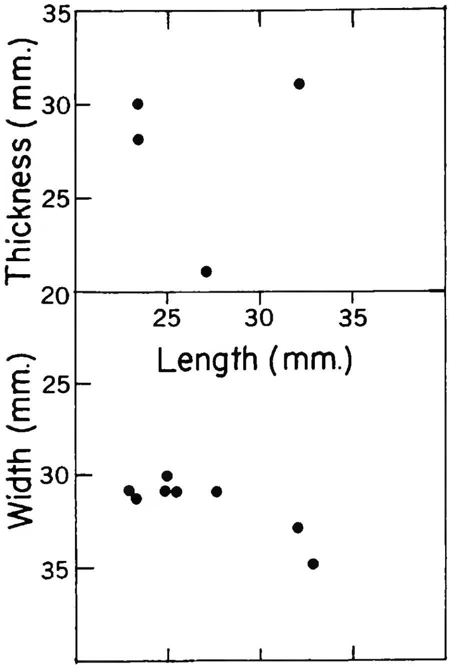

FIGURE 5.—*Septacamera pybensis* from the Pybus Formation, Admiralty Island, Alaska, USGS locs. 2541, 2547, 18345. Scatter diagram of dimensions of the few measurable shells; the numerous fragmentary valves and shells in the collection fall within this size range.

HOLOTYPE.—USNM 163640 (Plate 2: figures 7–13).

COMPARISONS.—*Septacamera pybensis* is characterized externally by its globose shape, moderately inflated dorsal valve, convex anterior surface, and its 5–7 costae in the sulcus (Figure 6) and internally by it proportionately short spondylium. Its closest relative undoubtedly is *S. stupenda* new species, and a few specimens of *S. pybensis* have the highly inflated dorsal valve that characterizes that species. *Septacamera pybensis* of that form is distinguishable from *S. stupenda* by its smaller size and fewer costae. It differs from *S. plicata* (Kutorga), which it resembles in its rotundity and member of costae, by its smaller size, proportionately narrower outline, and especially in its much flatter and more strongly geniculated ventral valve. It differs from *S. kutorgae* (Tschernyschev) in its more trigonal outline, and its lower costae that number 5–7 rather than 2–3 in the sulcus. It is smaller than *S. optilua,* new species, from the Assistance Formation of Grinnell Peninsula on Devon Island, Arctic Canada, and normal specimens of *S. pybensis* are less sharply geniculate and less flattened at the anterior surface. The few grossly inflated specimens of *S. pybensis* recall *S. stupenda* in the form of the fold, with great convexity both longitudinally and transversely; the fold of *S. opitula* is rather flat in anterior view (see Harker and Thorsteinsson, 1960, pl. 18, fig. 1).

OCCURRENCE.—*Septacamera pybensis* is abundant in the Pybus Formation where it occurs in dolomite facies along the shores of Pybus Bay, Admiralty Island, Alaska (Loney, 1964, p. 36). Specimens studied were collected by Wright in 1904 (USGS loc. 2368, the point at south entrance to Pybus Bay), Kindle in 1905 (USGS loc. 2370, in west arm of Pybus Bay; USGS loc. 2371, same as Wright's 2368), Waters and Girty in 1918 (USGS loc. 2541, point at south entrance to Pybus Bay, presumably same as locs. 2368 and 2371; USGS loc. 2547, east side of east arm of Pybus Bay), and Dutro in 1957 (USGS loc. 18345, peninsula on southwest shore of Pybus Bay, see Loney, 1964, pp. 40, 95).

Only two specimens from Kuiu Island (USGS loc. 2450) have the low profile and few costae in the sulcus that characterize *S. pybensis.* Their occurrence with a large population of *S. stupenda* suggests that they are variants of that species, although they could be individuals of *S. pybensis* that migrated beyond the bounds of that species' major habitat. More than 60 specimens of *S. pybensis* are identifiable (57 are preserved well enough to count costae), but few resemble *S. stupenda* in shape, and they are small and have the low number of costae typical of *S. pybensis.*

Unfortunately, the detailed stratigraphy of the Pybus Formation at Pybus Bay on Admiralty Island and Saginaw Bay on nearby Kuiu Island is insufficiently known to determine whether *S. stupenda* and *S. pybensis* are contemporary. Merely on the basis of morphology and what appear to be "trends" in the development of *Septacamera* as a whole, it seems likely that *S. pybensis* is earlier, perhaps ancestral to *S. stupenda.* Evidence is in the resemblance of *S. pybensis* to *S. plicata* of the Sakmarian, and to the unnamed species from the Halleck Formation that underlies the Pybus in southeastern Alaska, as well as resemblance of some specimens to *S. stupenda* that occurs about 150 feet above the base of the Pybus on Kuiu Island. Its seemingly intermediate morphology suggests that *S. pybensis* has an intermediate stratigraphic position. Such reasoning has led paleontologists astray more than once, so this speculation should be considered only as an hypothesis that needs checking in the field.

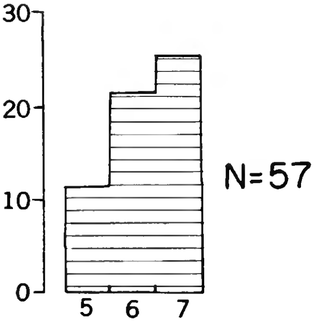

FIGURE. 6.—*Septacamera pybensis* from the Pybus Formation, Admiralty Island, Alaska, USGS locs. 2368, 2371, 2373, 2541, 2547, 18345. Histogram of frequency of costae in sulcus.

The old (1904–1918) collections of *S. pybensis* are not accompanied by stratigraphic data, and the nature of the terrain (the Pybus makes a steep cliff, and fossils are apparent only on weathered surfaces) made it possible to check the position of *S. stupenda* in only a general and "probable" way in 1968.

If *S. stupenda* and *S. pybensis* should prove to be contemporary or nearly so, their taxonomic status might be revised to that of two local subspecies of *S. stupenda.* The two forms are unmistakably different in several features, however, so that any specimen near the mean in either population can be identified at a glance.

Septacamera opitula, new species

PLATE 2: FIGURES 17, 18 (19–21?)

Stenoscisma plicatum Harker and Thorsteinsson, 1960 (not Kutorga), p. 62, pl. 18, figs. 1–4.

DESCRIPTION.—Shell large for genus; outline transversely subpentagonal; profile wedge shaped to semiconvex, with ventral valve rather flat and dorsal valve inflated; geniculation of ventral flanks and crest of fold sharp, producing flattened anterior surface, geniculation of sulcus and dorsal flanks gentle; costae strong, sharp crested, numbering 6 or 7 in sulcus, 5–8 on each flank; margins strongly serrated by interlocking extensions of costae.

Ventral beak curved tightly against dorsal beak; pedicle foramen a wedge-shaped slot in epithyrid position in ventral beak; sulcus wide, depressed about mid length on valve; posterolateral flanks smooth, extended to form flange overlapped by similar dorsal flange. Dorsal valve much more strongly convex, somewhat flattened along crest of fold.

Ventral interior with large and long spondylium, strong hinge teeth. Dorsal valve with thick divided hinge plate; hinge sockets deep; septalium short, elevated on median septum; further details of septum and muscle area not observed.

HOLOTYPE.—GSC 13737; see Harker and Thorsteinsson, 1960, pl. 18, figs. 2–4.

COMPARISONS.—*Septacamera opitula* is characterized by its large size, transverse outline, convex but not grossly inflated profile, and its large and relatively few costae. It is longer and wider, but not proportionately as thick as *S. stupenda,* new species, and has larger and many fewer costae. It is larger in all dimensions than *S. pybensis,* new species, and proportionately wider; its costae are proportionately wider and higher, although the number of costae in the sulcus is about the same as in *S. pybensis.* Among Alaska specimens, the unidentified fragments from the Halleck Formation most nearly resemble the corresponding parts of *S. opitula,* although the Halleck specimens have a flat crest to the fold, and the anterior surface is transversely concave.

Septacamera opitula is similar to *S. plicata* (Tschernyschev) in size, and perhaps also in number of costae (although too few specimens of the Sterlitamak species are known for the range of variation to be established); the ventral valve is not nearly so convex as in *S. plicata.* It is larger and has stronger and more numerous costae on fold and flanks than *S. kutorgae* (Tschernyschev) and bears only a generic resemblance to that and other similar species of Tschernyschev.

OCCURRENCE.—This species has been found in the Assistance Formation on Grinnell Peninsula, Devon Island, in the Canadian Arctic Archipelago. The holotype (GSC 13737) is from Geological Survey of Canada loc. 26406, which is loc. 5 described by Harker and Thorsteinsson (1960, fig. 2) near Belcher Channel. Illustrated topotypes (Plate 2: figures 17, 18) are from USNM loc. 769, Assistance Formation at Belcher Channel, and USNM loc. 770, Lyall River, five miles southwest of Whitmore Point, collected by F. G. Stehli (essentially at GSC loc. 26406).

A few specimens from the Pybus Formation on the little island near the cannery in Saginaw Bay, Kuiu Island (not in Halleck Harbor), USGS loc. 2385, bear strong resemblance to *S. opitula.* One is illustrated (Plate 2: figures 19–21) for comparison. As with the specimens of *S. stupenda* that resemble *S. pybensis,* these may be variants in a large population of *S. stupenda.* The similarity is sufficiently striking, however, to tempt identification of these Pybus specimens with *S. opitula,* and to suggest a possible correlation of the Pybus Formation with the Assistance Formation. Regardless, it seems significant that *S. stupenda* in its typical form is present only at Halleck Harbor, and that a short distance away the genus is represented by *S. pybensis* or *S. opitula?*.

Septacamera sp.

PLATE 1: FIGURE 21

DISCUSSION.—Distinctive fragments from the Halleck Formation that clearly belong to a species of *Septacamera* cannot be identified certainly with any known species, although they most nearly resemble the fragments identified by Yanishevskiy (1935, p. 63, pl. 6, figs. 1–7) as *Camarophoria* aff. *C. kutorgae* Tschernyschev. The best preserved fragments are two slightly distorted and broken dorsal valves that have the fold only slightly raised above the flanks, but very sharply geniculated at the anterior. The anterior surface that is flattened or slightly convex in most species of *Septacamera,* is depressed in these specimens to give the shell an emarginate outline. Ventral valves are fragmentary, but by analogy with other species they can be interpreted as strongly and sharply geniculated at the flanks. Geniculation of the dorsal fold and ventral flanks are comparable in *Septacamera,* so the ventral valve also can be reconstructed as having a moderately sharply bent sulcus, probably sharper than in *S. opitula.* There are 5 or 6 costae in the sulcus similar to the number in *S. pybensis,* but this undetermined Halleck species has a lower dorsal profile and much sharper geniculation of the fold than the Pybus species.

OCCURRENCE.—Two collections contain this species of *Septacamera*: both are from the northeastern part of the northernmost of the Keku Islets in Keku Strait just off Cornwallis Peninsula of Kuiu Island. These are USGS locs. 3685 and 3700 of Waters and Girty, 1918. The location and lithology leave little doubt that they are from the unit now designated the Halleck Formation (Muffler, 1967, p. 22, and pl. 1).

Occurrence of a species of *Septacamera* in the Halleck Formation is recorded as additional evidence for a Permian age for the formation. Although collected in 1918, these specimens were not reported in published lists.

Superfamily STENOSCISMATACEA Oehlert, 1887

Family ATRIBONIIDAE Grant, 1965

Genus *Camerisma* Grant, 1965

Laevicamera Grabau, 1936, p. 87.

Levicamera Sarycheva and Sokolskaja, 1952 [not Grabau, 1934], p. 171.

Camerisma Grant, 1965, p. 63.—Sokolskaja and Grigorieva, 1968, p. 163.

Type-species.—*Camerisma prava* Grant, 1965, p. 66, pl. 8, figs. 1–1b.

Diagnosis.—Shell smooth or very weakly costate; fold high and typically sharply vaulted; ventral beak tightly curved over dorsal umbo, allowing no space for pedicle foramen; shell normally thickened at posterior; posterior flanks broadly flanged, the dorsal flange overlapping the ventral; interior with spondylium, camarophorium, and intercamarophorial plate.

Callaiapsida, new subgenus

Type-species.—*Camerisma* (*Callaiapsida*) *kekuensis*, new species.

Additional species.—*Camarophoria pentameroides* Tschernyschev, 1902, pp. 100, 510, pl. 22, figs. 1a–c; pl. 23, figs. 1–3; Holtedahl, 1911, p. 19, pl. 2, figs. 5–6; Ivanova, 1949, p. 109, fig. 30, pl. 15, figs. 5–9. *Camarophoria* (*Levicamera*) *pentameroides* Tschernyschev of Sarycheva and Sokolskaja, 1952, p. 171, pl. 48, fig. 268. *Camarophoria sella* var. *arctica* Holtedahl, 1924, p. 34, pl. 21, figs. 1–2; Likharev and Einor, 1939, pp. 69, 208, pl. 14, figs. 5a–v; Gobbett, 1963, p. 128, pl. 16, figs. 13–16. *Camarophoria sella* var. *quadrata* Likharev and Einor, 1939, pp. 70, 208, pl. 14, figs 4a–e.

Diagnosis.—Shell large, broadly trigonal with widely flared flanks; fold high, with crest typically sharp (but rounded in some) and sulcus with corresponding median groove; costae absent. Valves flanged with dorsal flange strongly overlapping ventral flange along posterior slopes; ventral flanges becoming indented toward anterior, producing deep peripheral grooves around valve edges, meeting at crest of fold; peripheral grooves covered by thin extension of ventral valve and commissure protected by thin flap of dorsal valve. Interior as in *Camerisma* (*Camerisma*) except that intercamarophorial plate normally is buried in shell that fills space between hinge plate and camarophorium.

Discussion.—Several large species that seem to be confined to the late Pennsylvanian and the Permian form a natural grouping within the generic concept of the more widely ranging *Camerisma.* Species of this group, here designated the subgenus *Callaiapsida,* have the generic characters of *Camarisma,* but all are much larger than the group containing *C. prava* Grant, *C. girtyi* Grant, *C. sagmaria* Grant, *C. sella* (Kutorga)?, *C. sella* (Kutorga, of Tschernyschev, 1902), *C. rotayi* Sokolskaja, and *C. aplicata* Gregorieva, that together comprise the subgenus *C.* (*Camerisma*). The subgenus *Callaiapsida* also has the additional feature of the deep peripheral grooves with their peculiar set of flaps and flanges, which are described and explained below.

Pentamerus sella Kutorga (1844, pl. 9, figs. 4a–d), now assigned to *Camerisma,* appears to belong to the *C.* (*Callaiapsida*) group of species, but the concept of this species seems to be derived from Tschernnyschev's (1902) interpretation of it (e.g., Schellwien, 1900). Tschernyschev (1902, pl. 23, fig. 4) illustrated as *C. sella* a small and slightly asymmetrical species that is more closely related to the subgenus of *Camerisma* that contains *C. prava.*

Occurrence.—Species belonging to *Callaiapsida* are reported from rocks as old as the "middle" Carboniferous. Ivanova (1949) and Sarycheva and Sokolskaja (1952) reported *Camarophoria pentameroides* Tschernyschev from the Podolsk Horizon of the Union of Soviet Socialist Republics, and Gobbett (1963) mentioned specimens referred to *Laevicamera arctica* (Holtedahl) from the middle Carboniferous Scheteligfjellet Beds of Svalbard. The record of the group is continuous into the Permian, with examples from the Gzhelian of the Union of Soviet Socialist Republics reported by Sarycheva and Sokolskaja (1952). Similarly, Gobbett (1963) reported them from the Passage Beds, Lower Wordiekammen Limestone, and the upper Carboniferous to Sakmarian Cyathophyllum Limestone, a span from middle Carboniferous to lower Permian.

Lower Permian species are from the *Schwagerina* Horizon of the Ural Mountains (Tschernyschev, 1902), the Sakmarian of Svalbard (Gobbett, 1963), the Halleck Formation of southeastern Alaska (Muffler, 1967), and unnamed Permian rocks near Skolai Pass in the eastern Alaska Range (Moffit, 1938a). The Alaska species are described below. Species of this subgenus have not been found in the younger (i.e., post-Leonard) rocks in Alaska, but *C. arctica* (Holtedahl) is reported from post-Artinskian (i.e., Paikhoian) rocks of Taimyr (Ustritskiy and Chernyak, 1963). Apparently the genus is absent from the East Greenland Permian (Dunbar, 1955).

Available data suggest that *Camerisma* (*Callaiapsida*) is exclusively boreal in its distribution. No examples are known from rocks south of the 55th parallel, including those from the Ural Mountains. *Camerisma* (*Camerisma*), in contrast, is more widely distributed, occurring in boreal regions such as Alaska as well as in southern China (Grabau, 1936) and the Karawanken Range of northern Yugoslavia (Grant, 1965). Whether regions that now are boreal were boreal in the Permian is a question not yet answered to everyone's satisfaction.

Stehli (1957, 1964) presented convincing data and interpretations suggesting strongly that Permian climatic belts were parallel to the present ones. The restricted high-latitude distribution of species of *C.* (*Callaiapsida*) seems to fit this picture for climatic belts in the Permo-Carboniferous, so it may be concluded that these species lived in northern waters, although not necessarily under Arctic conditions.

FUNCTIONAL MORPHOLOGY.—Ivanova (1949, p. 109), chose *C. pentameroides* Tschernyschev as an example to illustrate the life habits of "*Camarophoria*" (an objective junior synonym of *Stenoscisma;* see Grant, 1965, p. 141). She depicted it lying on the ventral valve, with the thickest part of the umbonal region lowermost and the shell slanting upward at an angle that brings the flanks slightly above the substrate (Ivanova, 1949, fig. 30). Ivanova pointed out that this species must have lived free on the substrate, because the ventral beak is curved tightly over the dorsal beak leaving no space for a pedicle opening. Furthermore, the mutual fit of the beaks is such that as the shell gaped, the end of the dorsal beak would slip partly into the ventral spondylium, preserving a tight seal that would exclude sediment, at the same time allowing not the slightest opening for a pedicle.

This reasonable analysis of the life habits of *C. pentameroides* was accepted by Grant (1965, p. 26) as depicting the general mode of life of all the nonpediculate Stenoscismatacea, with minor variations among the several genera. Ivanova's figure was redrawn by Ager (1967, fig. 1f) to illustrate the living position of "*Camarophoria.*" There is little doubt that *C. pentameroides* and its relatives—species of *Camerisma* (*Callaiapsida*)—lived in a position similar to that shown by Ivanova and Ager. But further study of specimens from Alaska has revealed some unique structural modifications of the shell that adapted it to this mode of life, and suggests that individuals could have survived while buried much deeper in the substrate than heretofore believed.

Ivanova (1949, p. 110) pointed out two features of the shell of *C.* (*Callaiapsida*) *pentameroides* that fitted it for its life on the sea floor. First, the posterior part of the shell, especially of the ventral valve, is greatly thickened, thus placing the center of gravity where it would tend to stabilize the shell in the inferred living position. Second, the edges of the valves are flanged in the area of articulation and the dorsal edge strongly overlaps the ventral edge. The shell could gape at the anterior and by this mechanism remain effectively closed where the posterior part is below the surface of the substrate. The strong overlap of the posterolateral edges of the valves was shown by Grant (1965, pp. 4–6) to be an adaptive feature of many Stenoscismatacea, and its evolutionary history was traced from Devonian through Permian representatives of the superfamily.

One problem that arises in considering *C.* (*Callaiapsida*), which lived partly buried, is the circulation of feeding currents without their being contaminated by sedimentary particles. Ivanova (1949) and Ager (1967) showed only the umbonal part of the ventral valve actually below the surface of the substrate, with the commissure entirely above the surface and the shell tilted upward toward the anterior end. This orientation would have exposed enough of the commissure to allow feeding currents to enter and exit at positions that promote circulation, but would have required the shell to maintain a precarious balance with substrate and sedimentation for its entire lifetime in order to survive.

Camerisma (*Callaiapsida*) solved the problem of maintaining separate entrances and exists for feeding currents, while living buried in the substrate, by evolving a pair of peripheral grooves at the edges of the ventral valve anterior to the overlapping dorsal flanges. The grooves begin, one on each side, where the ventral flange narrows and essentially terminates—a locus normally indicated by a slight flexure in the slope of the shell's outline (Plate 3: figures 3, 6). The groove is formed by a strong curl in the edge of the ventral valve (Figure 7; Plate 3: figures 21, 22) and is covered by a thin flap formed by an additional extension of the valve edge. The dorsal valve, whose posterolateral flange overlaps the ventral one, continues to overlap

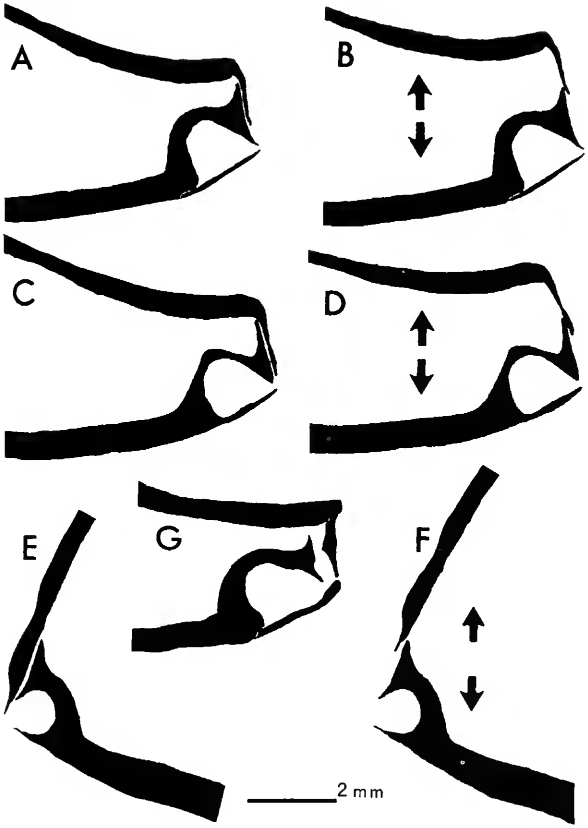

FIGURE 7.—*Camerisma* (*Callaiapsida*) *arctica* (Holtedahl). Sections of peripheral flange and covered groove system for ducting of feeding currents and sealing of commissure; all from specimen USNM 163651 (shown on Plate 3: figures 7–10), from Wrangell Mountains, Alaska, USGS loc. 7109. A, C, G, sections of right side, between 20 and 25 mm from ventral beak; E, section of left side, about 20 mm from beak; B, D, F, positions of flanges as shell gaped, reconstructed by tracing from the actual sections shown in A, C and E. Section G is shown, uninked on Plate 3: figure 21; compare with Plate 3: figure 22, showing similar system in *C.* (*Callaiapsida*) *kekuensis.*

the distal edge of the curl that forms the peripheral groove. Thus, the shell could gape at the anterior while the posterior part remained sealed by the overlapping flanges, and the peripheral groove remained closed by means of its thin cover. The segment of the commissure anterior to the flanges and up to about half the height of the fold also remained effectively sealed by the thin edge of the dorsal valve when the shell gaped wide enough to raise the dorsal valve above the peripheral groove. This mechanism is best explained by the illustrations (Figures 7A–F; Plate 3: figures 21, 22).

These peripheral grooves have not been discussed previously, but they can be seen in illustrations of *C. pentameroides* by Tschernyschev (1902, pl. 23, figs. 1b–d, 2d) and Sarycheva and Sokolskaja (1952, pl. 48, fig. 268) and of *C. arctica* by Holtedahl (1911, pl. 21, figs. 1, 2). Many specimens are preserved as steinkerns that do not show these structures clearly, but the cited illustrations confirm their widespread presence and provide evidence that they are consistent features of the subgenus.

About halfway from the turn of the flanks to the crest of the fold each lateral peripheral groove terminates in a shallow notch that provided an opening to the seawater. (Plate 3: figures 1, 5). This notch is essentially parallel to the midline of the shell, and opens toward the posterior, thus turning the course of each groove through a sharp angle. The line of juncture of the valves then continues on its slightly posteriorly directed course, bringing it well inside a broad flap of the dorsal valve. The ventral valve, from this point on each side of the fold to the crest, forms another set of shallow grooves that appear to meet at the crest. Instead of being covered by a flap of the ventral valve, however, these short segments are covered by extensions of the dorsal valve, so that they opened when the valve gaped (Plate 3: figures 1, 3).

The net effect of this elaborate flap and groove system was to keep the shell very tightly sealed everywhere when the shell was closed, and to keep it just as effectively sealed everywhere except at the top half of the fold when the shell opened. If the circulation was similar to that in some modern rhynchonellid brachiopods, namely with incurrents lateral and the excurrents median (Rudwick, 1962), the water would have flowed in through the notches in the sides of the folds, then through the essentially cylindrical pipes formed by the lateral grooves with their thin covers, and entered the visceral chamber just anterior to the broad posterolateral flanges. Excurrents would have flowed directly out near the crest of the fold, through the opening provided when the thin dorsal flap lifted off the shallowly grooved edge of the ventral valve. This shallow recessing of the ventral valve edge seems more likely to have provided a slight tongue-and-groove effect for tight sealing of the closed shell, rather than a channel for currents entering or leaving the gaping shell.

According to Ager (1967, p. 163), the question of the direction of flow of feeding currents in fossil brachiopods cannot be considered settled. If incurrents were median in *C.* (*Callaiapsida*), waste and outward-flowing water would have left the shell through the pipes provided by the lateral grooves, and then would have been projected downward toward the substrate by the notches on the fold.

Circulation could have been maintained entirely by ciliary action of the lophophore. Expelling water through the fold would suck it in through the lateral pipe system, or conversely, bringing it in through the open fold would force it out through the pipes. The pipes themselves, however, had to have been lined by epithelium which could have been ciliated. Active cilia within the pipes would have contributed to maintenance of flow through the system, but nothing that was observed in the shells offers solid evidence for or against this speculation.

The gape of average-size adults could not have been wider than about 2 mm in order for the flange and peripheral groove system to have functioned in excluding sediment. This narrow gape would have kept the dorsal flap over the opening on the fold in such a position as to continue to provide protection while the shell was open. A gape of 3 or 4 mm seems likely for the very large specimens that attained a shell width near 60 mm.

McCammon (1968, p. 193) cites evidence that living brachiopods can survive on dissolved nutrients alone, without ingesting particles of any kind. At least this is true of species that now live in cold waters containing high concentrations of dissolved nutrients. If this boreal form *C.* (*Callaiapsida*) lived on dissolved nutrients alone, the peripheral grooves would have been sufficient to carry the inflowing nutrient-bearing currents as through a pipeline.

This brachiopod was admirably adapted for living free on the sea floor, able to withstand the effects of a rain of sediment or of oscillating currents that caused the shell to settle into the substrate. The probably ideal position of the shell was with the deepest part of the ventral valve lowermost, buried to the level of the edge of the fold (Figure 8A). Thus, the dorsal flap over the

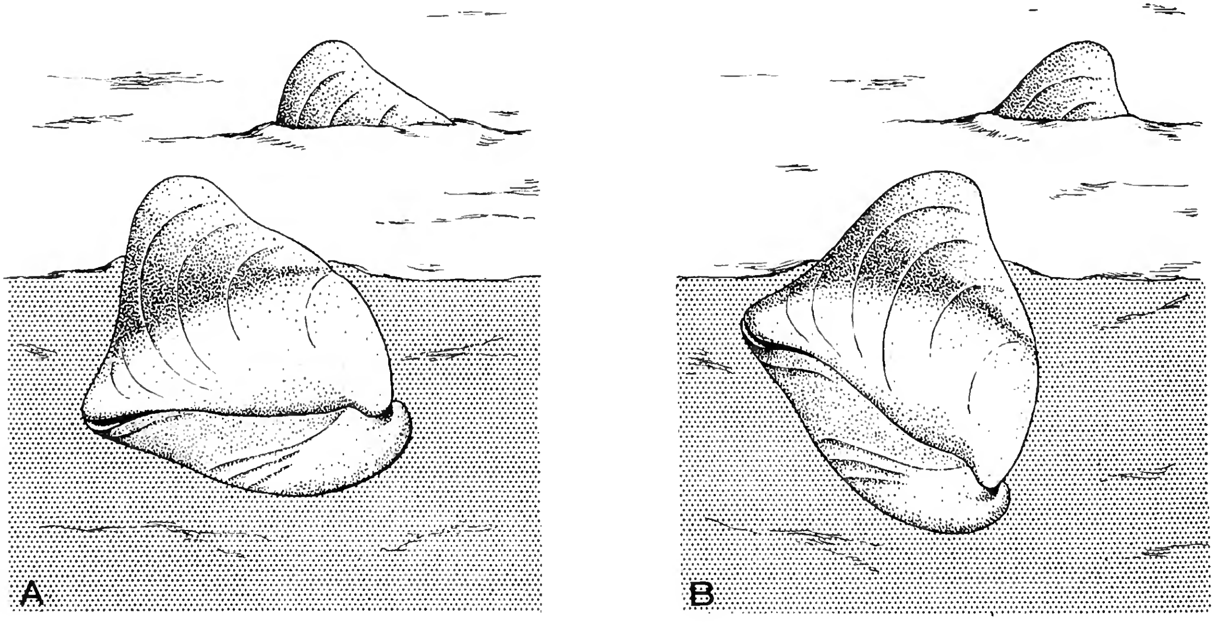

FIGURE 8.—*Camerisma* (*Callaiapsida*). Possible living positions under nearly complete burial. The covered grooves and overlapping flanges around the commissure enabled the shell to admit and expel water currents while excluding sediment.The system would work best to the depth of burial depicted, but probably could have functioned with the shell completely buried as long as sediment remained uncompacted. A, Shell lying on ventral valve in position similar to that illustrated by Ivanova (1949, fig. 30) and Ager (1967, fig. 1f); B, shell buried with ventral beak lowermost, current system remaining protected in this position by extended valve edges.

gape at the fold would have been in a position to protect it from falling sediment, and the openings to the two lateral groove-flap systems would have faced downward. Thin sections show, however, that the posterior part of the dorsal valve is thickened also, but not quite to the thickness of the ventral valve. This posterior weight, and the heavy beak of the ventral valve curled around the posterior end of the shell, could have caused the shell to settle into the substrate wedgelike, beak lowermost, the flared fold and anterolateral flanks providing stability and a slowdown in shell settling by their displacement effect on the surrounding sediment (Figure 8B). The complicated valve edges and protected water-current system undoubtedly could have allowed the animal to function while completely buried in sediment that was loose or only mildly compacted, as deeply as nutrient-bearing water could penetrate. The narrow gape, pipes for lateral currents, and the roofed opening at the fold crest, all worked to allow the animal to bring in and expel water while excluding unwanted sediment. Such an adaptation would have enabled this group of brachiopods to survive as a constituent of the infauna.

ENCLOSING ROCK.—The largest collection of *Camerisma* (*Callaiapsida*) is from the Halleck Formation of southeastern Alaska (Muffler, 1967). The specimens are from Kuiu Island and the northernmost of the Keku Islets just off the northeast point of Kuiu. The dominant rock type of the Halleck Formation on Kuiu Island is described by Muffler (1967, p. 22) as, "dark gray very calcareous siltstone that grades into silty limestone." The formation contains several other rock types at Halleck Harbor, but the specimens of *C.* (*Callaiapsida*) *kekuensis* (new species described below) from there were collected from dark gray argillaceous limestone of nearly uniform grain size near 0.02-mm diameter, containing quartz, biogenic calcite, dark rock fragments, pyrite, micrite, sparite cement, and about 50 percent clay. On a wave-cut terrace on the northernmost of the Keku Islets, the Halleck Formation contains many beds of conglomerate in dark argillaceous matrix, but specimens of *C. kekuensis* from there were found in a matrix of dark gray calcareous mudstone.

Specimens identified as *C.* (*Callaiapsida*) *arctica* (Holtedahl) from the lower Permian near Skolai Pass, Alaska Range, are in black argillaceous limestone with authigenic pyrite. The section there also contains basalts and tuffs, as well as massive limestones (Moffit, 1938a). The same species was reported by Holtedahl (1911, p. 34) from Novaya Zemlya in "beds of a grey limestone, finely crystalline and not unlike the *mosquensis*-limestone, yet of a less compact and homogeneous character." Ivanova (1949, p. 109) reported *C. pentameroides* from the Upper Carboniferous of the Moscow Basin "exclusively in argillaceous facies." Tschernyschev (1902, pp. 15, 448) reported this species from white and light gray limestone, without further lithic description.

Species of *C.* (*Callaiapsida*) seem to have inhabited muddy sea bottoms in northern waters; those in Alaska, at least, lived near areas of volcanic activity. The mudstones and shales that enclose these brachiopods are calcareous, and massive limestones occur above or below them, suggesting that, although the latitude was high, conditions were not Arctic. The interbedded conglomerates suggest intermittent turbidite activity, possibly in conjunction with volcanism, and the jumbled occurrence of many shells in these beds indicates that they are not in the exact place they inhabited. Some shells, especially those of *C.* (*Callaiapsida*) and other Stenoscismatacea remain articulated although somewhat crushed; others are single valves, especially ventral valves. It may be inferred that they lived upslope from where they now are found, but probably in the same kind of sediment.

Camerisma (Callaiapsida) arctica (Holtedahl)

FIGURES 7, 9; PLATE 3: FIGURES 1–10, 18–21

Camarophoria pentameroides Holtedahl, 1911 [not Tschernyschev, 1902], p. 19, pl. 2, figs. 5, 6.

Camarophoria sella var. *arctica* Holtedahl, 1924, p. 34, pl. 21, figs. 1, 2.—Likharev and Einor, 1939, pp. 69, 208, pl. 14, figs. 5a,b.

?*Laevicamera* cf. *L. arctica* (Holtedahl) Gobbett, 1963, p. 128, pl. 16, figs. 13–16.

Levicamera pentameroides (Tschernyschev) Ustritskiy, in Ustritskiy and Chernyak, 1963, p. 100, pl. 27, fig. 14, pl. 28, figs. 3, 4.

DESCRIPTION.—Shell large, attaining length near 50 mm, width near 60 mm, average length about 30 mm; outline wedgelike in all views; commissure strongly uniplicate with sharp fold producing median crest on brachial valve, median groove in sulcus, producing effect of narrow Gothic arch, crest normally deflected slightly left or right; sulcus wrapped strongly around anterior, thus turning commissure through about 90°, with strongest curvature at widely flared flanks; ornament very weak, consisting of radial shell fibers crossed by light concentric growth lines, producing faintly reticulated effect.

Ventral valve moderately strongly convex in umbonal region; beak strongly curved over dorsal umbo, without pedicle foramen; broad flanges on each side anterior to hinge teeth (strongly overlapped by corresponding flanges on dorsal valve), giving way anteriorly to deep peripheral groove; very thin flap of shell covering peripheral groove; shallow notch on each side of fold (about midway between lateral flank and fold crest) where peripheral groove crosses commissure; groove then follows edge of sulcus in slight reflexion toward posterior at crest.

Dorsal valve very strongly convex, swollen in umbonal region, profile nearly straight along sharp crest of fold; flanks sloping very steeply from crest of fold.

Interior of ventral valve thickened at posterior; spondylium large, thick-walled, sessile near beak or partly buried by secondary shell thickening, supported farther forward by low median septum duplex. Interior of dorsal valve less thickened; hinge plate short; cardinal process large, bulbous; crura beginning as ridges along sides of hinge plate, extending forward as slender apophyses; camarophorium buried in thickened apex of beak, extending forward as deep, nearly semicircular spoon supported by increasingly high and slender median septum duplex; intercamarophorial plate present in posterior of camarophorium, obscured in observed sections by shelly filling between hinge plate and camarophorium.

COMPARISONS.—*Camerisma* (*Callaiapsida*) *arctica* is characterized by its large size, proportionately wide outline, sharp fold that projects about the same distance forward from the beak as do the two anterolateral flanks, and its moderately convex ventral valve. It attains the same large size as *C.* (*Callaiapsida*) *kekuensis*, but its average size seems to be somewhat smaller. The sharp crest of the fold begins farther back than in *C. kekuensis*, but farther forward than in the species identified as *C. pentameroides* (Tschernyschev) by Sarycheva and Sokolskaja (1952, pl. 48, fig. 268). The sharp crest of the fold and the lesser convexity of both valves distinguish it from *C. pentameroides* (Tschernyschev, 1902, p. 100, pls. 22, 23). *Callaiapsida arctica* differs from *C. quadrata* (Likharev and Einor, 1939, p. 70, pl. 14: figs. 4a–e) in its higher fold that does not extend as far forward, and the sharp crest begins farther back.

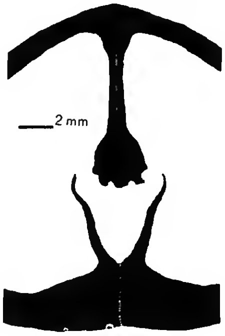

FIGURE 9.—*Camerisma* (*Callaiapsida*) *arctica* (Holtedahl). Section about 8 mm anterior to beak, showing thickened camarophorium; USNM 163656, from Wrangell Mountains, Alaska, USGS loc. 7109. Same sections are shown, uninked, on Plate 3: figure 18.

PLATE 1.—[All figures natural size]. Figures 1–20.—*Septacamera stupenda,* new species, from the Pybus Formation in Halleck Harbor, Saginaw Bay, Kuiu Island, Alaska. 1–4, Specimen of average size and shape; ventral, posterior, side, and anterior views (USGS loc. 2452; USNM 163627). 5–8, Large specimen with grossly thickened dorsal valve, pedicle foramen typical; ventral, anterior, side, and posterior views (USGS loc. 2452; USNM 163628, holotype). 9–12, Large specimen; ventral, side, posterior, and anterior views (USGS loc. 2451; USNM 163629). 13–14, Small specimen with typically inflated dorsal valve, dorsal and side views (USGS loc. 2450; USNM 163630). 15–16, Silicified specimen etched in acid, posterior view showing pedicle foramen, and interior showing septalium and spondylium imbedded in shelly thickening; pedicle adjustor muscle attachments visible (USGS loc. 2452; USNM 163631). 17, Interior of broken silicified specimen lacking secondary thickening, showing septalium, crura, and spondylium (USGS loc. 2452; USNM 163632). 18, Interior of dorsal valve, posterior mesial part showing hinge plate, sockets, crural bases, septalium, septum, and adductor muscle area (USGS loc. 2451; USNM 163633). 19, Same part of a different shell showing similar features as in figure 18, but with slight differences in the hinge plate and somewhat more of the crura (USGS loc. 2452; USNM 163634). 20, Interior of ventral valve with attached fragment of dorsal cardinalia, showing hinge plate and distinct eminences in posterior part of spondylium (USGS loc. 2450, USNM 163635).

Figure 21.—*Septacamera,* species undetermined, from Halleck Formation on northernmost Keku Islet, USGS locality 3700. Anterior part of dorsal valve showing concave anterior margin; USNM 163636.

Figures 22, 23.—*Septacamera kutorgae* (Tschernyschev). Side and interior views of hollow calcareous specimen; USNM 163637. Locality is unknown, but the specimen was identified by Tschernyschev and agrees with his illustrations (Tschernyschev, 1902), so it can be considered an authentic example of the species, probably a topotype.


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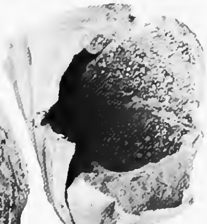
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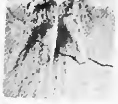
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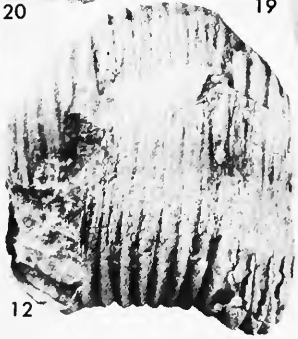
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PLATE 1

OCCURRENCE.—One nearly complete and well-preserved specimen and two fragments that show essential details of the peripheral grooves were collected from Permian rocks near Skolai Pass, Alaska Range, Alaska, by A. Knopf (USGS loc. 7109 grn: see Moffit, 1938a, p. 36). These rocks have not received a formal stratigraphic name but were considered by Girty (in Moffit, 1938a) to be Artinskian in age. Their detailed correlation with the Halleck Formation of the southeastern islands of Alaska, which has been assigned a probable Leonard age (in Muffler, 1967), is uncertain and awaits further study.

The species was described originally from Lower Permian rocks of Novaya Zemlya (Holtedahl, 1924) and subsequently confirmed in that region by Likharev and Einor, (1939). More recently it has been recognized in rocks of Taimyr that are considered Upper Permian (Paikhoian Stage) in age (Ustritskiy and Chernyak, 1963). If identification of the Alaska specimens with *C. arctica* is correct, it suggests an age for the rocks near Skolai Pass somewhat younger than the Halleck Formation, perhaps correlative with the Pybus Formation that overlies the Halleck in southeastern Alaska.

Camerisma (Callaiapsida) kekuensis new species

FIGURE 10; PLATE 3: FIGURES 11–17, 22

DESCRIPTION.—Shell large, typically about 35 mm in length, 40 mm in width, maximum lenth and width 50 mm and 60 mm respectively (Table 1); outline diamond shaped; profile wedge shaped; commissure strongly uniplicate with fold rounded for much of length, crest becoming sharp at anterior crest deflected slightly right or left; median groove in sulcus correspondingly shallow except at anterior end; sulcus curving around anterior, but not for full 90°, thus projecting somewhat anteriorly at crest of fold; curvature of commissure rather gentle at anterolateral flanks; growth lines distinct but weak.

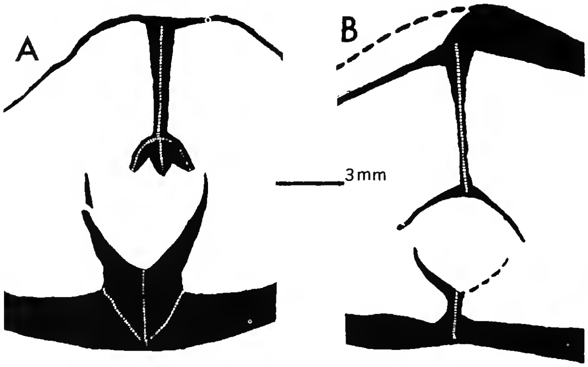

FIGURE 10.—*Camerisma* (*Callaiapsida*) *kekuensis,* new species. Sections of two specimens from Halleck Formation, Kuiu Island, Alaska, USGS loc. 3683: A, section 10 mm anterior to ventral beak, confirming presence of intercamarophorial plate, USNM 163658; B, section of fragmentary specimen, about 12 mm anterior to ventral beak, USNM 163659.

PLATE 2.—[Figure 13, X 2; figure 29, X 1.5; all other views natural size]. Figures 1–16.—*Septacamera pybensis,* new species, from the Pybus Formation, Pybus Bay, Admiralty Island, Alaska. 1–4, Unusually wedge-shaped specimen, slightly compressed, ventral, side, posterior, and anterior views (USGS loc. 18345; USNM 163638). 5, Ventral valve, interior showing spondylium and lateral buttress plates (USGS loc. 2547; USNM 163688). 6, Dorsal valve, interior showing half of hinge plate, septalium, median septum, and muscle area (USGS loc. 2547; USNM 163639). 7–13, Silicified shell, partly broken showing interior, ventral, posterior, dorsal, side oblique showing spondylium and crus, anterior, and side views at natural size; 13, interior view of interlocking anterior marginal spines (USGS loc. 2547; USNM 163640, holotype). 14–16, Decorticated shell showing low number of costae in sulcus and typically low and rounded profile (USGS loc. 2541; USNM 163641).

Figures 17, 18.—*Septacamera opitula,* new species. Specimen USNM 163642, from Assistance Formation, Grinnell Peninsula, Devon Island, Arctic Archipelago, Canada, USNM loc. 769770; essentially at Geological Survey of Canada loc. 26406. 17, Ventral valve, ventral view; USNM 163642. 18, Dorsal interior, partly excavated, showing hinge plate and attached fragment of ventral spondylium; USNM 163644.

Figures 19–21.—*Septacamera opitula?* from Pybus Formation, on island near cannery in Saginaw Bay (numbered 70 on map in Muffler, 1967), Kuiu Island, Alaska. Ventral, side, and anterior views (USGS loc. 2385; USNM 163645).

Figures 22–29.—*Septacamera stupenda,* new species, from the Pybus Formation, Halleck Harbor, Saginaw Bay, Kuiu Island, Alaska. 22, 23, Posterior half of silicified shell, etched, showing interior features; septalium, hinge plate, septum and muscle area of dorsal valve, spondylium with lateral buttress plates in ventral valve, and short lateral marginal spines interlocking (USGS loc. 2451; USNM 163646). 24, 25, Fragment of posterior parts of both valves, with unusually well preserved crura and septalium and good view of hinge teeth and socket (USGS loc. 2451; USNM 163647). 26, 27, Silicified posterior part of thickened shell, with septalium and spondylium imbedded, muscle area deeply impressed in dorsal valve (USGS loc. 2450; USNM 163648). 28, Interior of posterior part of silicified shell showing septalium, hinge plate, and spondylium (USGS loc. 2450; USNM 163649). 29, Interior view of posterior part of dorsal valve (shown on Plate 1: figure 18) showing hinge plate, septalium, and posterior end of muscle area (USGS loc. 2451; USNM 163633).

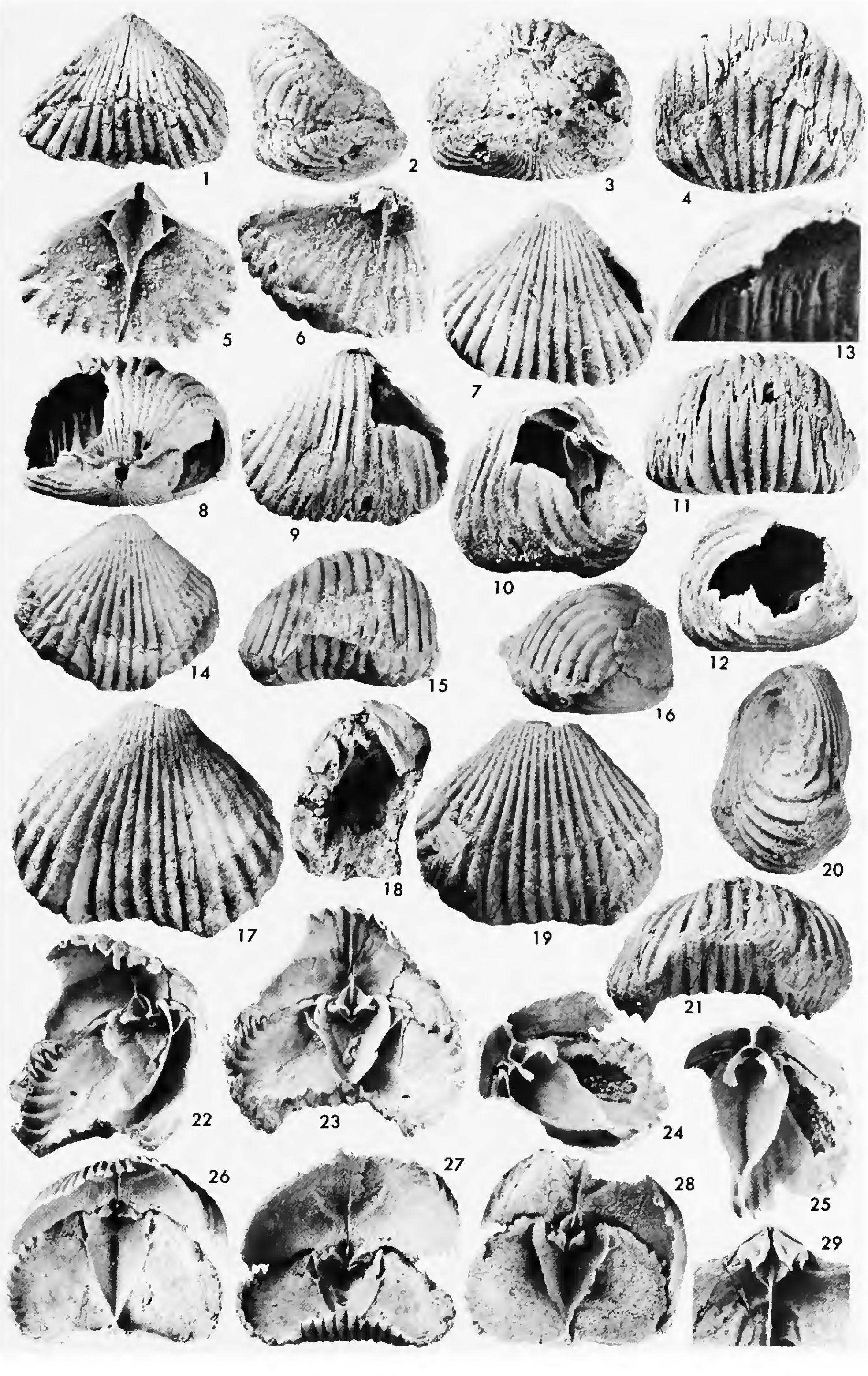

PLATE 2

TABLE 1.—*Measurements in millimeters of* Camerisma (Callaiapsida) kekuensis.

Locality	*Length*	*Width*	*Thickness*
5452	35	38	—
5452	36	38	—
5452	39	36	—
10276	36	44	—
3701	34	45	—
68AFs18	47	55	50

Ventral valve flatly convex in umbonal region; beak fairly straight, but yet pressed against dorsal umbo without room for pedicle foramen; broad posterolateral flanges overlapped by dorsal flanges, leading into relatively shallow peripheral groove; sides of fold notched shallowly where peripheral groove crosses. Dorsal valve swollen in umbonal region, flatly convex along crest of fold, strongly convex transversely.

Interior of ventral valve moderately thickened; spondylium large, wide, with thick walls, buried in thickened shell at posterior, supported on low spondylium duplex toward anterior; pallial lines slender, dichotomous, typically stenoscismatacean. Interior of dorsal valve with bulbous cardinal process; camarophorium thick at posterior end near hinge plate (Figure 10) becoming high and more delicate, curving strongly toward spondylium; intercamarophorial plate thick, normally buried in secondary shell filling between hinge plate and camarophorium.

HOLOTYPE.—USNM 163655 (Plate 3: figures 15–17).

COMPARISONS.—*Camerisma* (*Callaiapsida*) *kekuensis* is characterized by its large size, comparatively flat ventral valve, fold that becomes sharp along the crest farther forward than in *C. arctica* (Holtedahl), and its fold and sulcus that project forward, rather than wrapping around the anterior to become perpendicular to the commissure as in *C. arctica*. In this respect it resembles *C. quadrata* (Likharev and Einor, 1939, p. 70, pl. 14, figs. 4a–e), although the forward projection is stronger in that species, the ventral valve very strongly convex, and the proportionate width narrower. Its sharp-crested fold differentiates it from *C. pentameroides* (Tschernyschev, 1902, pp. 100, 510, pl. 22, fig. 1; pl. 23, figs. 1–3) as do its less-swollen ventral valve and the less strongly convex profile of its ventral valve. The fold of *C. kekuensis* continues nearly straight forward from the umbonal region, where in *C. pentameroides* it curves strongly ventrally, producing a more globular profile for the entire shell. In the Carboniferous species identified as *C. pentameroides* by Sarycheva and Sokolskaja (1952, p. 172, pl. 48: fig. 268) the sharp crest of the fold begins nearly at the dorsal beak, the fold becomes very sharp and narrow toward the front, and the ventral valve is thick and convex throughout its length. This species is clearly different from *C. pentameroides* of Tschernyschev, as well as from the other Alaska species.

OCCURRENCE.—This species is named for its occurrence in the Halleck Formation of the Keku Islets of

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PLATE 3.—[All figures natural size except where indicated.]
Figures 1–10.—*Camerisma* (*Callaiapsida*) *arctica* (Holtedahl) from Permian near Skolai Pass, Wrangell Mountains, Alaska (USGS locality 7109). 1–6, Well-preserved shell (USNM 163650). 1, dorsal view showing shallow groove on fold, covered by flap of dorsal valve (arrow points to notch where peripheral groove opens); 2, oblique view showing peripheral groove on flank; 3, side view showing peripheral groove still partly covered by flap of ventral valve; 4, ventral view with groove visible on left; 5, anterior view showing peripheral groove terminating at notch marked by arrow, also remains of notch on broken side; 6, posterior view. 7–10, Posterior half of broken and slightly compressed shell (USNM 163651) which was cut and polished to show relationships of shell sections inked on figure 7 and shell margins shown on Plate 3: figure 21.

Figures 11–17.—*Camerisma* (*Callaiapsida*) *kekuensis,* new species, from the Halleck Formation, Kuiu Island and Keku Islets, Alaska. 11–12, Ventral valve showing peripheral grooves and fold, ventral and anterior views (USGS loc. 10276; USNM 163652). 13, Section (×1.75) about 10 mm anterior to ventral beak, showing thickened spondylium and camarophorium (USGS loc. 3683; USNM 163653). 14, Rubber mold of shell (×2) broken longitudinally, showing relation of spondylium to long and curved camarophorium, dorsal septum missing (USGS loc. 3683; USNM 163654, for comparison with Tschernyschev's, 1902, pl. 23, fig. 3). 15–17, Large specimen, almost entirely decorticated, from Halleck Formation on northernmost Keku Islet, showing form of shell, high fold, remnants of peripheral grooves, ends of septalium and spondylium, dorsal, anterior, and side views (USGS loc. 68AFs18; USNM 163655, holotype).

Figures 18–21.—*Camerisma* (*Callaiapsida*) *arctica,* from USGS loc. 7109. 18–20, Sections of posterior part of broken shell, 9 mm, 11 mm, and 13 mm from ventral beak; USNM 163656. 21, Section (×6) of right margin of shell shown in Figure 7G and in figures 7–10 on this plate.

Figure 22.—*Camerisma* (*Callaiapsida*) *kekuensis.* Section (× 7) through lateral margin showing relation of dorsal flap to ventral peripheral groove (USGS loc. 3683; USNM 163653). Same shell as in figure 13 of this plate, but about 22 mm anterior to beak.

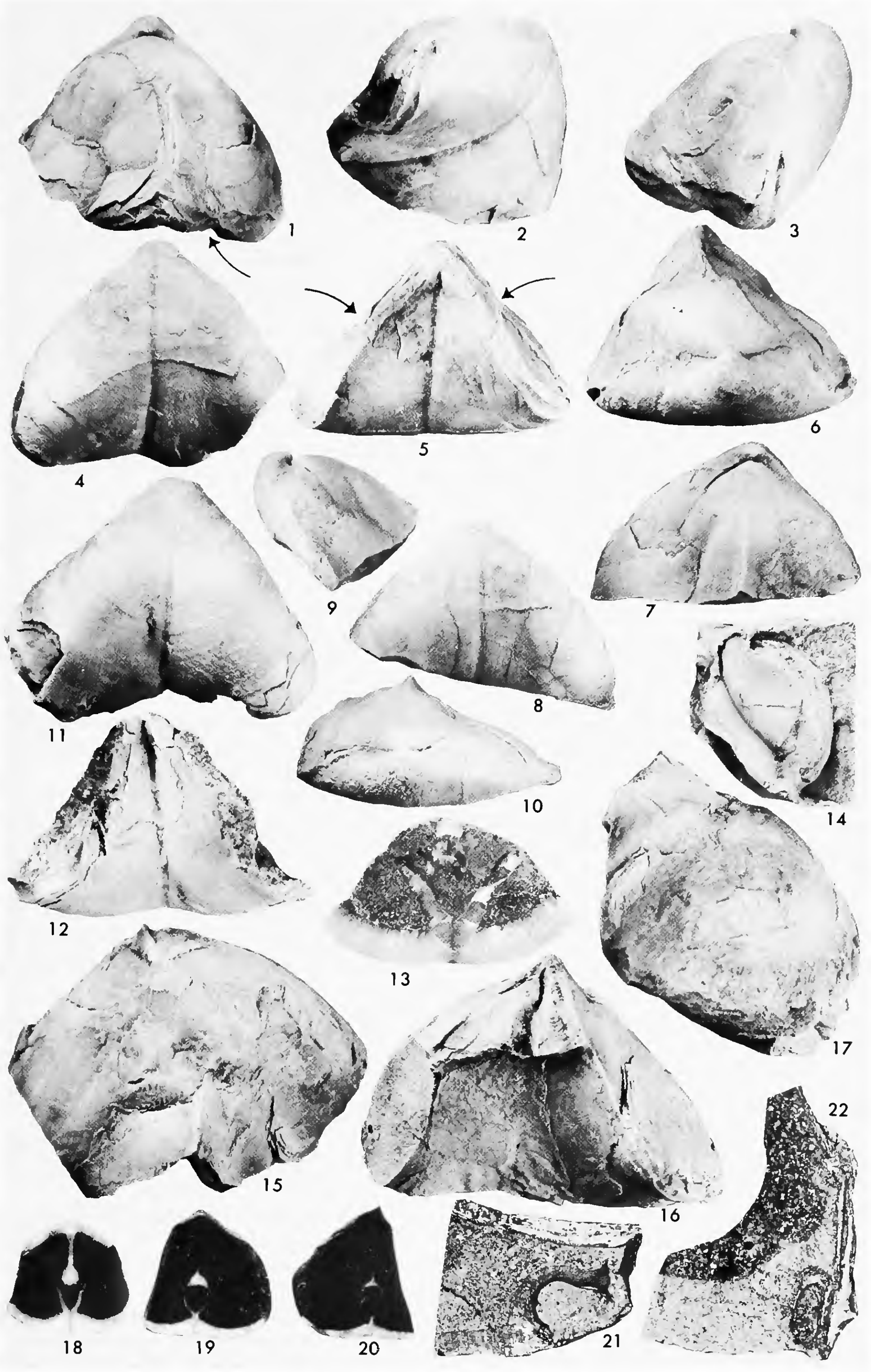

PLATE 3

southeastern Alaska, just off the northeast shore of Kuiu Island where it also is found in the same formation along the tidal flats of Halleck Harbor in Saginaw Bay. The geology of this area was mapped by Muffler and others, and the formation described by Muffler (1967, p. 22). Most of the Kuiu Island, Saginaw Bay, specimens studied here were collected by Buddington in 1924 (USGS loc. 5452), Waters and Girty in 1918 (USGS loc. 3683), Girty in 1918 (USGS loc. 3701), and Williams in 1940 (USGS loc. 10276). Those from the northern Keku Islet were collected by Waters and Girty in 1918 (USGS locs. 3685, 3700), and Stehli and Grant in 1968 (USGS loc. 68A–Fs–18).

The age of the Halleck Formation has been recognized as Permian since the faunas were studied by Girty (as reported in Buddington and Chapin, 1929, pp. 118–126). A probable Leonard age was estimated by Dutro (in Muffler, 1967, p. 23).

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Francis G. Stehli

Tethyan and Boreal Permian Faunas and Their Significance

ABSTRACT

The Tethyan and Boreal faunal provinces of the Permian are shown to be temperature controlled. In terms of brachiopod families, the Boreal fauna consists of cosmopolitan forms and is devoid of endemics. The Tethyan fauna contains in addition to the cosmopolitan families many endemic families. The brachiopod families occurring in the Boreal realm are significantly older and more prosaic than the endemic families of the Tethyan realm, where evolution is evidently more rapid, and more distinctive forms occur. Correlation should be easier within the Tethyan realm than either between it and the Boreal realm or within the Boreal realm, especially during intervals of glacial climate and thus may account for some of the difficulties experienced in intra-Permian correlation.

It has been recognized for many years that Permian faunas seem generally separable into two major, and to a large extent mutually exclusive, assemblages which have been termed *Boreal* and *Tethyan.* The present study evaluates the significance of the Boreal and Tethyan faunas of the Permian in terms of temperature, composition, evolution, and effect upon correlation.

Acknowledgement is made to G. A. Cooper and R. E. Grant for assistance in identification and to P. O. Banks, R. G. Douglas, and W. B. Clapham, Jr. for critical reading and editorial comment.

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General Considerations

Because the fossil record, as presently known, is manifestly imperfect, this study is confined to simple, strongly expressed phenomena which may be expected, under favorable circumstances, to be recognizable and interpretable despite perturbing effects. Preference is given to data which can be expressed in terms susceptible to statistical evaluation. Data relate principally to the northern hemisphere because of the superior expression of marine Permian rocks and the more thorough collecting and study accorded the fossil remains incorporated in them. Marine invertebrates are employed because of their abundance. Emphasis is given to brachiopods because they are the group best known to me and thus most easily and reliably treated.

Faunal Discontinuities

The application of the distinguishing terms, "Boreal" and "Tethyan," to Permian faunas implies the existence of some kind of faunal discontinuity. There is, in fact, an element of exclusivity in the distribution of these two assemblages which, while not complete, results in the dominance of Tethyan faunas in low and intermediate latitudes and of Boreal faunas in high latitudes (Newell, 1955, p. 8). This relationship appears to suggest temperature control. It must be recalled, however, that such a conclusion is supported only if we are justified in assuming that the present earth is a geographically suitable model for Permian time. Since the possibility of continental displacements across latitude is widely asserted, we may not be justified in using such a model. The question of whether the Tethyan-Boreal faunal province boundary is temperature controlled should, if possible, be answered without involving latitude or committing ourselves to a particular configuration of the Permian earth.

A Model

We may begin by considering the causes of faunal discontinuities in the present seas as a model for interpretation of the Permian. Gunter (1957, p. 159) notes that "Temperature is the most important single factor governing the occurrence and behavior of life." This is true since, in a simplistic sense, organisms are physico-chemical machines whose vital reactions are temperature controlled. All ecologists are aware, however, that some faunal discontinuities are not wholly or even primarily temperature controlled, and one problem will be to find a means to distinguish between those which are controlled primarily by temperature and those which are not.

We can use the distribution of present-day organisms as an example. Data on the occurrence of families of modern clams at 39 globally distributed stations accumulated by A. L. McAlester for a study of diversity (Stehli and others, 1967) have been examined by means of a cluster analysis (Bonham-Carter, 1967) which determines the level of association between the sample stations, in this case in terms of their clam family composition. Latitude of the stations is not involved in the analysis, so commitment to any model of the earth is avoided. A dendrogram (Figure 1) portrays the successively lower levels of association (greater differences) among these stations.

When temperature or latitude information is introduced, it becomes apparent that the cluster program has recognized discontinuities in the clam family distribution, the more profound of which can be related to the latitude-controlled planetary temperature gradient. The primary dichotomy (0.25 association level) separates the fauna of the south polar region from that of the remainder of the world.[1] The second dichotomy (0.35) separates the fauna of the north polar region from the warm-water faunas of the world. These lowest branchings probably represent temperature control in its purest form, because branchings at higher associative levels will be determined increasingly by factors other than temperature. To show, however, that the faunal clustering is fundamentally temperature controlled, the value of Jaccard's Coefficient of association for each station relative to one on the equator is plotted against temperature. Figure 2 shows that the relationship to temperature is very clear.

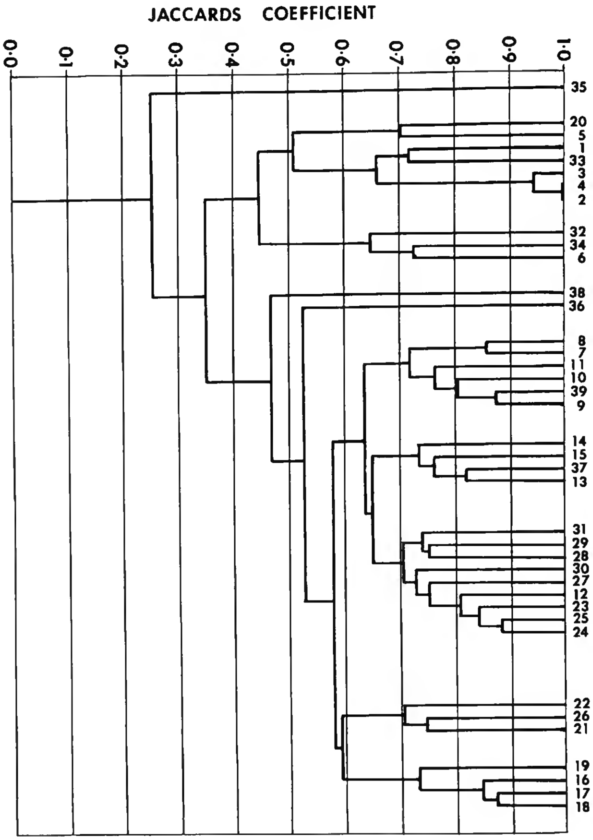

FIGURE 1.—Dendrogram showing levels of association between globally distributed stations in terms of the assemblage of Recent clam families occurring at each as expressed in terms of Jaccard's Coefficient. The stations are as follows: 1, Barents Sea; 2, Kara Sea; 3, Laptev Sea; 4, East Siberian Sea; 5, Chukotka Sea; 6, Orkney Islands; 7, British Isles; 8, Ireland; 9, Portugal; 10, South France; 11, French West Africa; 12, South Africa; 13, Arabian Sea; 14, Japan; 15, Queensland; 16, New South Wales; 17, Victoria; 18, South Australia; 19, New Zealand; 20, Point Barrow; 21, Puget Sound; 22, Monterrey; 23, Baja California; 24, Sinaloa; 25, Panama–Peru; 26, Chile–Argentina; 27, Brazil; 28, Puerto Rico; 29, West Florida; 30, Texas; 31, South Carolina; 32, Eastern Canada; 33, East Greenland; 34, Iceland; 35, Antarctica; 36, Hawaii; 37, Philippines; 38, Mississippi Delta; and 39, Spain: (A map of station locations and the sources of data used may be found in Stehli et al., 1967.)

In the data for present-day clam families we thus find that the single most fundamental discontinuity in

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[1] The south polar clam family fauna is homogeneous around the Antarctic continent; thus, in the interest of economy, it has been entered as a single station.

each hemisphere is that between the cold-water and warm-water fauna. In a less objective way, the basic nature of these discontinuities has long been recognized. For instance, Ekman (1953, p. 186) indicates that the sharpest faunal discontinuity in the oceans is that between temperate and subtropical faunas. Hence, no new information has been added by the present analysis, but an objective technique has been used for recognizing breaks which requires no assumptions about latitude or temperature, yet can be interpreted in terms of both.

The Permian Tethyan-Boreal Discontinuity

Examination of clam family data yields a model which we can use to objectively analyze Permian faunal data for its primary temperature controlled discontinuity—provided that we can get sufficient data of adequate quality. Before attempting to utilize the geologic record, we should consider some of the problems which inevitably become involved if, instead of data like that for the clams derived from an instant in time, we deal with data representing a significant span of time such as the whole Permian Period.

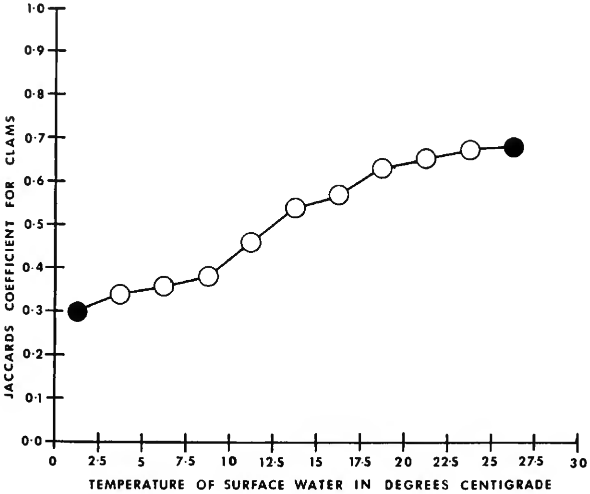

Figure 2.—Jaccard's Coefficient of association for Recent clam family composition, relative to equatorial stations, plotted against surface temperature of each station for the warmest month. Temperature data for August was used in the northern hemisphere and that for February in the southern hemisphere. Data have been averaged for classes of 2.5° C. and plotted as a 3-class running average. Solid points at the end of the curve represent raw data since a 3-class average is, for them, impossible.

In the first place, evolution may cause some problems, for if we are examining the entire Permian, but use organisms that persisted for only a part of the period, their presence in one area and absence in another might be due to different ages of the rocks in the two areas rather than to temperature control. Clearly this is a serious problem, but can be dealt with easily by restricting attention to groups of organisms that persisted through all or almost all of the Permian. This approach involves dealing with high taxonomic categories, and it was for this reason that families of modern clams, rather than genera or species were used in deriving the model.

A second serious problem involves short-term climatic variation. There is evidence to indicate that at least a part of the Permian represents an interval of glacial climate. We know that in the Pleistocene, impressive latitudinal compression of climatic belts occurred during glacial intervals. We know also that despite these marked changes, the earth's climate remained cold in polar regions and warm in equatorial regions throughout the Pleistocene. Thus, although the slope of the latitudinally controlled temperature gradient varies through time, its direction remains constant. The effect of variation in slope is to increase the noise level in the belt between the continually warm region and the continually cold region, for here either cold or warm conditions may be recorded depending on the glacial or interglacial climate at the time of deposition of any particular rock unit. Because the direction of the gradient is constant, however, it will continue to furnish a constant and strong signal in a globally distributed set of data. Thus, if the temperature-related signal is sufficiently strong, we can find the *average* position of a faunal discontinuity regardless of considerable fluctuation in climate.

With the clam family analysis as a model for interpretation, let us attempt a similar analysis of Permian faunal data. The data to be used have been obtained from the literature, from examination of collections, and from information generously provided by colleagues. It pertains to families of articulate brachiopods, as well as a few corals and fusulinids. To achieve a measure of uniformity in taxonomic treatment, the generic assignments of brachiopods were made from specimens or plates by G. A. Cooper, R. E. Grant, or myself, and in some questionable cases, by all three of us. Family assignments for the genera present were then made following the system used in Part H of the

Treatise on Invertebrate Paleontology. The coral data refer to the families Lophophyllidae, Durhaminidae, and Waagenophyllidae. Data for the first family were taken from many sources in the literature and from collections. The studies of Minato and Kato (1965) on the Waagenophyllidae and on the Durhaminidae were used as the primary data source for these two groups, which are treated as a unit. Data for the family Fusulinidae were taken from many sources in the literature while those for the family Verbeekinidae follow the recent study by Gobbett (1967).

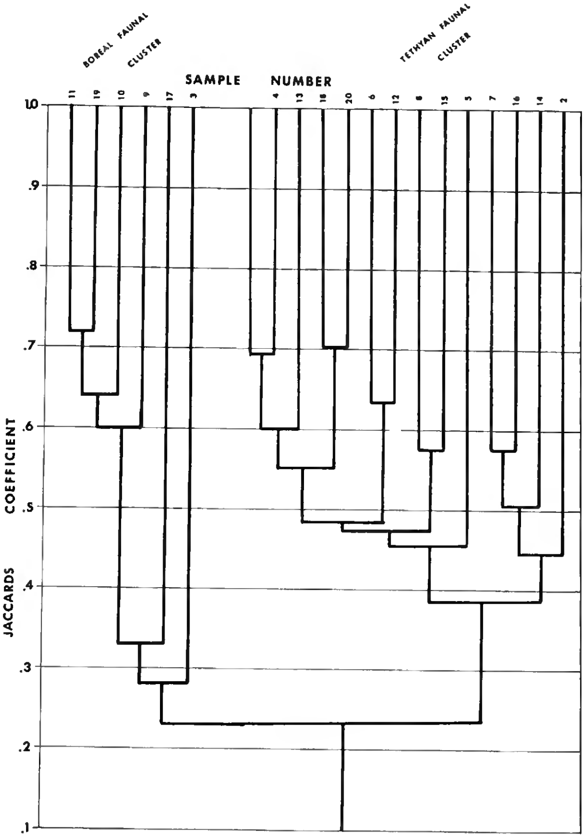

FIGURE 3.—Dendrogram showing levels of association between northern hemisphere stations in terms of the assemblage of Permian families (mainly brachiopods) occurring at each, expressed in terms of Jaccard's Coefficient. The stations cluster in two main groups, one Boreal, the other Tethyan. Stations in the Boreal cluster are: 3, Taimyr; 9, Alaska–Yukon Border; 10, Grinnell Peninsula; 11, Central–East Greenland; 17, Kolyma; and 19, Spitzbergen. Stations in the Tethyan cluster are: 1, Carnic Alps; 2, Japan; 4, Southern Urals; 5, Jisu Honguer; 6, Ussuriland, etc.; 7, Kiangsi; 8, Novaya Zemlya; 12, Central Oregon; 13, Glass Mountains, Texas; 14, Huehuetenango, Guatemala; 15, Kuiu Island and Keku Islets, Alaska; 16, Sicily; 18, Ko Muk, Thailand; and 20, Salt Range, Pakistan.

Data were obtained for 20 reasonably well-known and well-distributed localities in the present northern hemisphere and were subjected to cluster analysis (Figure 3). They separate into two fundamental clusters at the 0.24 level. According to the model, this primary division should represent that between warm-water and cold-water fauna (presumably—but not necessarily—of the northern hemisphere). The primary dichotomy recognized by the cluster program separates the fauna into the long recognized Boreal and Tethyan subdivisions. The noise level in the fossil data is doubtless higher than that in the Recent Model because collection and study are less perfect and because of the time-related problems mentioned earlier. No attempt is made, therefore, to interpret any branches of the Permian dendrogram that occur at higher associative levels. The probability appears strong, on the basis of comparison to the Recent Model, that the Tethyan-Boreal faunal discontinuity is temperature controlled.

It would be desirable to have some independent evidence by means of which to test this conclusion.[2] A study of the same clam family data used in our model has shown a pronounced relationship between the number of clam families present at a sample station and its temperature (Stehli *et al.*, 1967.) This effect is known to be nearly universal in large groups of marine organisms and has been shown to be closely related to both temperature and latitude (Fischer, 1960; Stehli, 1968). As a very simple test, then, let us use this well-known temperature-dependent effect to confirm or deny our conclusion regarding the temperature control of the Tethyan-Boreal faunal discontinuity. We can use the present-day clam family data as a model and determine the average number of families present in typical stations of the warm- and cold-water clusters (Table 1).

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[2] Lowenstam (1964) discusses the few O^{18}/O^{16} paleotemperature determinations for the Permian and shows that they probably are from the high noise region between the warm- and cold-water realms. Globally distributed paleotemperature results for the Permian would be of the greatest interest, but are at present not available and probably never will be. The results given by Lowenstam probably reflect the changes in shallow water between glacial and interglacial intervals, though our knowledge of paleogeography is not yet such as to rule out the possibility that the observed differences were caused by temporary upwellings or some similar phenomena.

TABLE 1.—*Recent clam family data.*

Name of Station	*Number of Recent Clam Families Present*	
NORTH COLD-WATER CLUSTER		
1. Point Barrow, Alaska	16	Average 18
2. East Greenland	20	
3. Laptev Sea, U.S.S.R.	19	
4. Chukotka Sea, U.S.S.R.	17	
SOUTH COLD-WATER CLUSTER		
1. Antarctica	24	Average 24
WARM-WATER CLUSTER		
1. Persian Gulf	52	Average 49
2. Philippines	52	
3. Texas Coast	45	
4. Sinaloa, Mexico	47	
5. South France	50	

TABLE 2.—*Permian brachiopod family data.*

Name of Station	*Number of Permian Brachiopod Families Present*	
"Boreal Cluster"		
1. Grinnell Peninsula, Devon Island	21	Average 21
2. Spitzbergen	19	
3. Central-East Greenland	20	
4. Alaska-Yukon Border	24	
"Tethyan Cluster"		
1. Carnic Alps	29	Average 30
2. Southern Urals	32	
3. Jisu Honguer, Mongolia	27	
4. Glass Mountains, Texas	35	
5. Salt Range, Pakistan	30	

This simple comparison shows a strong difference between the diversity of the warm- and cold-water clusters and shows us a means of testing the conclusion regarding the temperature significance of the Tethyan-Boreal discontinuity. To make a test, the diversity of Permian brachiopods at the family level, as shown in the Boreal and Tethyan clusters, may be considered. Though collecting and study of Permian brachiopod faunas has been vigorous, it certainly has been less precise than that for Recent clams. It follows, therefore, that diversity data for Permian brachiopod families will be less perfect than that for Recent clams. Imperfect collecting, which is certainly the principal source of noise, will have the effect of lowering the apparent level of diversity, because one commonly finds somewhat fewer taxa than were actually present. This difficulty can be minimized if we consider only those stations from each cluster showing the highest diversity, since these will give the closest approximation to the true diversity (Table 2).

Comparison of the family diversity of brachiopods in the Tethyan and Boreal clusters shows that diversity in the Tethyan facies is higher by about 50 percent. This test corroborates the temperature dependence, and we may thus be virtually certain that the faunal boundary is that between the warm- and cold-water faunas.

The Permian data demonstrate that the Tethyan fauna was a warm-water facies and the Boreal fauna a cold-water facies. None of the data involved latitude or commitment to any continental configuration. We are thus free to use this temperature-controlled faunal boundary to select the best fitting model of the Permian earth in terms of latitude.

No extensive test is made in this study, but Figure 4 shows the stations of the Boreal and Tethyan Permian brachiopod clusters and those of the cold-water and warm-water clam family clusters plotted against present-day latitude. Both the Permian and the Recent data show only a minimal degree of overlap between the two groups. In the case of the Recent clams this overlap is seen to be due to ocean currents, particularly the Gulf Stream which accounts for the warm-water fauna of England and Ireland (50°–55° N) and the Labrador Current which accounts for the cold-water fauna of Eastern Canada (45°–50° N). In the Permian data the zone of overlap is farther north, but may again relate to currents. The occurrence of a warm-water station in Novaya Zemlya north of 70° N, for instance, may be due to a warm-water current running north through the Ural Seaway and into the Arctic Ocean during lower Permian time (Ustritskij, 1962). In general it may be said that while data are

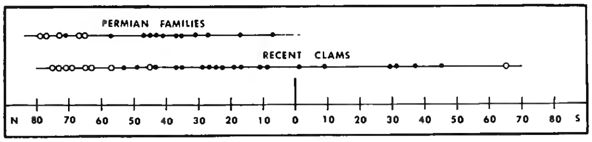

FIGURE 4.—Occurrence of Permian brachiopods, etc., and Recent clams as a function of present-day latitude. Open circles represent stations comprising the cold-water cluster from the dendrograms of Figures 1 and 3, while the solid points are the stations comprising the warm-water clusters in the same dendrograms. Southern Hemisphere data were not used in the Permian analysis.

still limited for the Permian, those which exist fit a present earth-latitude framework about as well as the Recent clam data fit it.

Composition of the Tethyan and Boreal Faunas

The Tethyan fauna, rich in peculiar genera, has received much attention, and it has been widely noted that certain groups seem characteristic of this faunal facies (Newell, 1955; Stehli, 1957; Ustritskij, 1962; Rudwick and Cowen, 1967). The Boreal fauna, having a somewhat more prosaic character, has received less attention. An attempt is made from the data at hand to examine the basic character of both the Tethyan and Boreal brachiopod faunas and to determine at the family level whether the Boreal assemblage contains endemic elements or whether it is distinguished simply by the lack of Tethyan elements.

Definition of Boreal and Tethyan Brachiopod Facies

For the purposes of this investigation, the two Permian faunal facies can be defined in terms of the two primary clusters obtained in the cluster analysis in Figure 3. In this way, it becomes possible to designate various stations as belonging to one faunal association or the other and to examine in some detail the makeup of the brachiopod family fauna characterizing the stations of each cluster.

Figure 5 shows the family composition of the two faunas in terms of the brachiopods and the few other faunal elements employed in the cluster analysis (Fusulinidae, Verbeekinidae, Lophophyllidae, Waagenophyllidae-Durhaminidae). We may assume once more that the stations giving the highest family diversity values for brachiopods are those which have been most thoroughly collected and studied and which therefore provide the most reliable data. The stations of each cluster showing the highest diversity have for this reason been chosen for analysis. There is in this procedure a certain danger because it assumes diversity to be a step function in which two discrete levels of diversity are represented, while in fact diversity is known to be a relatively smooth function of temperature and thus latitude. As an approximation, however, the procedure is justified because the error involved is much smaller than that resulting from poor collecting.

Using what appear to be the most reliable data, it is evident that 19 brachiopod families and one fusuline

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	
																																																							BOREAL CLUSTER
				●	●	●	●	●								●	●	●	●	●	●								●	●	●	●		●	●		●	●	●	●		●	●			●				●			●	24	ALASKA—YUKON
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				●	●	●	●									●	●	●	●	●	●									●	●	●		●			●	●	●	●		●				●								20	CENTRAL EAST GREENLAND
				●	●	●	●									●	●	●	●	●	●									●	●			●			●	●	●	●		●				●							●	19	SPITZBERGEN
																																																							TETHYAN CLUSTER
●	●		●	●		●		●	●				●			●	●	●		●	●	●			●		●	●	●	●		●			●	●		●	●	●		●	●			●	●			●	●	●	●	29	CARNIC ALPS
●	●		●	●	●	●		●	●							●	●	●	●	●	●	●			●			●	●	●	●	●		●	●		●	●	●	●		●	●	●		●	●			●	●		●	32	SOUTHERN URALS
●		●	●	●	●				●				●	●			●	●	●	●	●	●							●	●	●	●		●				●	●	●		●	●			●	●	●		●				27	JISU NONGUER
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●	●		●	●	●	●		●	●					●			●	●	●	●	●							●	●	●	●	●		●	●			●	●			●	●			●					●		●	26	KUIU ISLAND
●		●	●	●	●	●			●			●	●	●			●			●	●	●						●		●		●		●				●		●		●	●			●	●	●		●	●	●	●	25	SICILY
●	●		●	●	●	●	●		●	●				●			●	●	●	●	●	●						●	●	●	●	●		●				●	●	●		●	●			●	●	●		●	●	●	●	30	SALT RANGE

FIGURE 5.—Permian brachiopod and other families occurring in what are believed to be the most reliable stations of the Boreal and Tethyan clusters of Figure 3. The families involved are keyed to the numbers along the top of the figure as follows: 1, Enteletidae; 2, Rhipidomellidae; 3, Isogrammidae; 4, Meekellidae; 5, Schuchertellidae; 6, Orthotetidae; 7, Chonetidae; 8, Strophalosiidae; 9, Teguliferinidae; 10, Aulostegidae; 11, Chonetellidae; 12, Spyridiophoridae; 13, Tschernyschewiidae; 14, Scacchinellidae; 15, Richthofeniadae; 16, Leioproductidae; 17, Overtoniidae; 18, Marginiferidae; 19, Echinoconchidae; 20, Buxtoniidae; 21, Dictyoclostidae; 22, Linoproductidae; 23, Lyttoniidae; 24, Poikilosakidae; 25, Spinolyttoniidae; 26, Uncinulidae; 27, Camarotoechiidae; 28, Rhynchotetraidae; 29, Wellerellidae; 30, Atriboniidae; 31, Stenoscismatidae; 32, Rhynchoporidae; 33, Retziidae; 34, Athyrisinidae; 35, Athyrididae; 36, Ambocoeliidae; 37, Cyrtinidae; 38, Syringothyrididae; 39, Spiriferidae; 40, Brachythyrididae; 41, Spiriferinidae; 42, Reticulariidae; 43, Elythidae; 44, Martiniidae; 45, Mutationellidae; 46, Labaiidae; 47, Dielasmatidae; 48, Notothyrididae; 49, Heterelasminidae; 50, Cryptonellidae; 51, Durhaminidae-Waagenophyllidae; 52, Lophophyllidae; 53, Verbeekinidae; 54, Fusulinidae. Shown in column 55 is the diversity at the family level for brachiopods at each of the stations used in this analysis.

family dominate the Boreal assemblage, occurring at practically all stations. These dominant Boreal families occur in the Tethyan facies as well, and 17 of the 19 brachiopod families continue as dominant elements, as does the family Fusulinidae. On the basis of the data at hand, we find that only the Strophalosiidae and the Syringothyrididae among the brachiopods seem possibly to be more important in Boreal than in Tethyan assemblages. In short, there is a cosmopolitan fauna common to both the Tethyan and Boreal facies and an endemic fauna restricted to and characteristic of the Tethyan facies.

In addition to the dominant forms of the Boreal assemblage, there are 13 families of brachiopods and one of corals (Durhaminidae) which occur sparingly in the stations analyzed or in nearby stations not involved in the cluster analysis. The remaining 18 brachiopod families together with the Lophophyllidae and Verbeekinidae are known only from the Tethyan facies. Many of the families unique to the Tethys are represented by few genera in the Permian or are monotypic or are excessively rare so that their usefulness is impaired. The families which appear to be dominant among those examined and found unique in the Tethyan facies are relatively few. They are: Meekellidae, Richthofinidae, Lyttoniidae, Lophophyllidae, and Verbeekinidae. Presence of these families may be considered diagnostic of the Tethyan facies in the Permian.

In warm-water faunas of the present day, it is found that some groups show greater tolerance to temperature variation than others and consequently have more extensive ranges. This seems also to be true among the Tethyan index families noted above with the Meekellidae, in particular, suggesting by their range less rigorous restriction to warm water. The Verbeekinidae, on the other hand—at least as their distribution is shown by Gobbett (1967)—are very strongly restricted and probably occupied only the warmest water region of the Tethyan facies.

Evolution and the Tethyan and Boreal Discontinuity

In analyzing the brachiopod family distribution in the Boreal and Tethyan facies, it was noted that the primary distinguishing characteristic of the Boreal facies was its complete dependence on cosmopolitan families. Unlike the Tethyan facies, it lacks endemic groups at the family level. It is of interest to inquire somewhat further into this faunal differentiation. A comparison can be made if we consider the relative antiquity of the Boreal (cosmopolitan) and Tethyan (endemic) families. Figure 6 compares the percentage of families in each group as a function of their time of origin prior to the Permian.

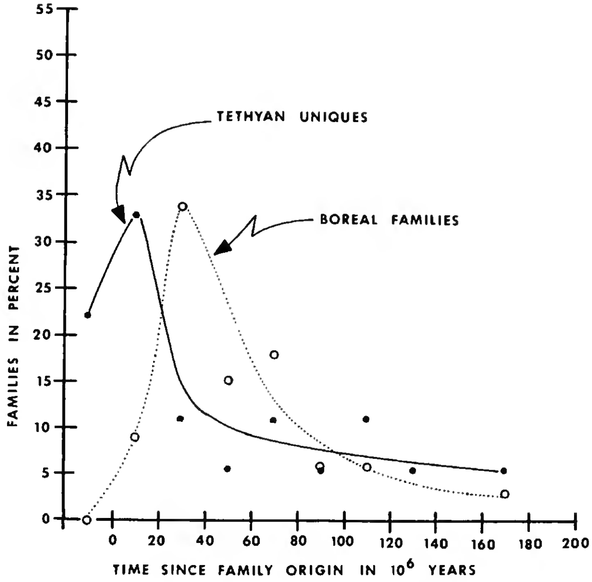

FIGURE 6.—Percentage of brachiopod families that occur in the Boreal facies and of those that are endemic to the Tethyan facies plotted against the number of millions of years since the origin of each family. The time scale is very rough, for it combines the uncertainties of the absolute age scale with those of family ranges given at best in terms of upper, middle, and lower divisions of periods and frequently lacking even that detail. The open circle control points refer to the dotted curve; the solid points to the solid curve. Each point represents an average value for the 20-million year class in which it occurs.

The families of the Boreal (cosmopolitan) assemblage show a pronounced mode in the region about 30×10^6 years. The number of families younger than this is small, and none occur which are first known from Permian rocks. A relatively small percentage are very much older than the model class. The Boreal assemblage thus seems to be composed predominately of well-established middle-aged brachiopod families together with a few successful and more ancient stocks.

The curve representing the endemic Tethyan families shows a pronounced mode in the range of 10×10^6 years and in addition indicates the presence of a large number (22 percent) of families that actually appear first in the Permian itself. Although relatively few forms are materially older than the mode, there is a higher percentage of ancient family stocks present in the Tethyan facies than in the Boreal. In short, the Tethyan fauna shows excesses relative to the Boreal fauna principally in very young groups, but to a lesser extent in very ancient families as well.

The excess in ancient families in the Tethyan fauna can probably be interpreted to mean that successful and stable families were able to persist in the relatively constant warm-water environment almost indefinitely, whereas they were either unable to occupy the Boreal environment or could not persist under its more demanding conditions.

Of far more interest than the excess of ancient families is the excess of very young families in the Tethyan facies. This excess appears to afford clear evidence that evolution proceeds most rapidly in the warm-water region of the world. It appears to be in this region that major new adaptive thresholds are crossed, and it is from this region that their occupants sometimes spread into the cold-water region. It is of considerable interest to deterimne whether this pattern in evolution is a general one or is unique to the Permian brachiopods.

Tethyan and Boreal Faunas and Correlation Problems

Most of the data presented in this study have tended to show that a major temperature-controlled faunal discontinuity separates the Boreal and the Tethyan facies. The Boreal fauna consists of cosmopolitan families which are relatively old. The Tethyan fauna in contrast contains many endemic families which tend to be young. In other words, the Tethyan fauna contains the kind of rapidly evolving, short-lived, and distinctive groups which facilitate correlation, while the Boreal fauna is composed of prosaic, long-lived, and slowly evolving families.

It is quite evident from these considerations that in the Permian, correlation within the Tethyan region should be a relatively simple matter. Correlations within the Boreal realm and between it and the Tethyan realm will tend to be relatively difficult, since in both cases, one must work with those families least favorable for the recognition of short time intervals.

It may be argued that the problem is not serious because, after all, very little correlation is done on the basis of families, which are the units used in this investigation. The problem is serious, however, for families are, after all, abstractions based on the genera and species comprising them, and they reflect the most pronounced properties of these lower ranking groups. It appears probable that north-south correlation will generally prove more difficult than east-west correlation and that biostratigraphy will always be able to produce more refined and useful subdivision of rocks and time in the warm-water regions of the world than in those characterized by cold waters. The problem will undoubtedly be greatest for times such as the Permian and the Present, when, due to the existence of glacial conditions, the earth's planetary temperature gradient is compressed. One might suspect that much of the confusion that has occurred in the recognition and correlation of Upper Permian rocks and fossils is in part a result of this problem.

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The Permian Brachiopod Genus *Terrakea* Booker, 1930

ABSTRACT

The linoproductinid genus *Terrakea* Booker is reviewed. Two lineages are recognized, one with numerous ear spines, one without. The former, represented by *T. pollex* Hill in the early Permian (late Sakmarian, early Artinskian) of eastern Australia and New Zealand developed into the Wordian (Kazanian) *T. brachythaerum,* a very prolific species, or artenkreis including also *solida* Etheridge and Dun and *elongata* Etheridge and Dun. Allies penetrated the northern hemisphere at a slightly early stage, and are represented in Pai Hoi and eastern Siberia, and also in the Canadian Arctic and Yukon as *Terrakea arctica* new species, (basal Word) with specimens from higher Word equivalents, and probably in the Texas Mountains as *Grandaurispina kingorum* Muir-Wood and Cooper, and *G. signata* (Girty). The other lineage, with few ear spines, is first known in basal Wordian beds of New Zealand and eastern Australia as *T. concavum* Waterhouse, and reappears as a new species in Capitanian beds of New Zealand. It is also represented in east Siberia from a fauna not yet described. A poorly known species also occurs in high Permian beds (Ochoan-Djulfian equivalents) in New Zealand, but no specimens are known from the topmost Changsing equivalent of either China or New Zealand. *Terrakea arctica* is described.

Terrakea is a Permian member of the linoproductinid subfamily Linoproductinae Stehli, 1954, closely allied to *Linoproductus* and *Cancrinella,* and distinguished most readily by its posteriorly prolonged spine bases in the pedicle valve, and by its cardinal process, as well as other criteria involving shape, ornament, and internal details.

The genus was proposed by Booker (1930) for *Productus brachythaerus* Sowerby, 1844, as interpreted from a productacean specimen so named and figured by Morris (1845, pl. 14, fig. 4c) from the Illawarra district, near Wollongong, New South Wales (Figure 1). The only specimen extant known to have been examined and described as *brachythaerus* by Sowerby is strophalosiacean (Hill, 1950; Maxwell, 1956), but the International Commission for Zoological Nomenclature in Opinion 486, 1957, suppressed the specific name *brachythaerus* Sowerby, 1844, in favor of *brachythaerus* Morris (1845), making *P. brachythaerus* Morris the type species of *Terrakea* (see Waterhouse, 1964a).

Thanks are due Drs. E. W. Bamber and W. W. Nassichuk, Geological Survey of Canada, for the loan of Arctic and Yukon collections, and Dr. Bruce Runnegar, Department of Geology, University of Queensland, for the loan of a specimen of *Productus solidus.* Dr. G. A. Cooper, Smithsonian Institution, Washington, D.C., kindly provided facilities for examining types of *Grandaurispina.* Dr. Alan McGugan, Department of Geology, University of Alberta, Calgary, showed me specimens from the Ranger Canyon Formation, and Dr. Victor Gamelin showed me Siberian *Terrakea* at the Paleontological Institute, Moscow. The figures were drawn with the help of Mr. M. Jurgeneit, and the photographs were prepared by Mr. D. O'Donovan, both at the Department of Geology, University of Toronto. One photograph was supplied by Mr. S. N. Beatus from the New Zealand Geological Survey, Lower Hutt.

Discussion of Species

All of the species so far ascribed to *Terrakea* come from eastern Australia and New Zealand, where a

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number of forms are extremely useful for detailed correlation. Species are recognized primarily from the distribution of the spines, particularly over the ears, and also the nature of the spine bases and minor internal criteria. Shape is highly variable, particularly for the two best known species *T. brachythaerum* and *T. concavum,* Waterhouse (1964a, figs. 26–30) demonstrating that populations of these species ranged from narrow elongated and highly incurved forms to very transverse sulcate and slightly incurved little inflated specimens. Local populations of *T. pollex* and *elongatum* appear to have more consistence in shape, suggestive of isolated subspecies.

Early marine Permian (lower Sakmarian) beds with the *"Eurydesma"* fauna in the Yarrol Basin of Queensland have not yielded *Terrakea* (Maxwell, 1964), and no occurrences are known for sure from correlative beds of New South Wales and Tasmania, though modern studies on Productida are lacking for these areas. The first species appears in the overlying Cattle Creek and equivalent late Sakmarian or early Artinskian faunas as a typically narrow "thumb"-like species, with a strongly incurved pedicle valve, and numerous ear spines, described as *Terrakea pollex* Hill (1950). Correlative beds of the Telfordian Stage in New Zealand contain a probable subspecies, with identical costellae and spinepattern, but a flatter broader visceral disc and heavily impressed muscle scars, reflecting adaption to a current-swept environment (Waterhouse, 1964a). In both regions the species is often dominant.

The next species to appear is a totally different form, called *Terrakea concavum* Waterhouse, 1964a, with a few ear spines, and body spines inclined from the disc at a high angle. Never more than common, this species characterizes the lower Braxtonian Stage of New Zealand (approximately Road Canyon of the Glass Mountains (Cooper and Grant, 1966) and perhaps Ufimian of the Pre-Urals), and apparently occurs in the upper Grange and basal Malbina beds of Tasmania, and in the Ulladulla beds of New South Wales along the coast south of Wollongong, to judge from visits to these localities with M. R. Banks, University of Tasmania in 1967, and with K. S. W. Campbell, Australian National University, in 1963. First appearance of this plexus with few spines is in the underlying Berriedale Limestone of Tasmania, to judge from collections made by the writer.

The slightly younger Mangarewa Formation, referred to the upper Braxtonian Stage of New Zealand, and equivalent to high (or restricted) Wordian and Kazanian, is characterized by *Terrakea brachythaerum* (Morris) a large extremely abundant form descended from *T. pollex,* with numerous large ear spines and very long spine bases. It occurs also in the correlative Flowers Formation of Nelson, New Zealand, and across the Tasman Sea in the upper Malbina beds of Tasmania and correlative beds at Wollongong, New South Wales, in the Muree and Mulbring Formations of the Hunter Valley, northern New South Wales, and in the Peawaddy (Springsure) and correlative beds of Queensland. The species has been recorded in various Geological Survey reports from older horizons, but while such records are not necessarily unreliable, they have yet to be substantiated. Four other specific names are in use for *Terrakea* of this age. *Terrakea fragile* (Dana 1847, 1849) is based on a suite of specimens much better preserved than the original type, but seems to be identical with it within the limits of preservation (Waterhouse, 1964a). *Terrakea brachythaerum elongatum* (Etheridge and Dun, 1909) is a large elongate *T. brachythaerum,* with a very long trail, suggestive of considerable maturity (Waterhouse, 1964a), and found in New Zealand at least to have inhabited a slightly different environment. *Productus solidus* Etheridge and Dun 1909 from Queensland is based on fragments of very large specimens probably allied to *T. brachythaerum elongatum* (Waterhouse, 1964a). It was treated as valid species by Hill and Woods (1964), but needs detailed study to establish its validity, because specimens loaned me from the University of Queensland by B. Runnegar show ear spines as in *T. brachythaerum.* Small and little inflated *Terrakea* figured by Etheridge and Dun (1909, pl. 43, figs. 6, 9, 11) were referred to a new species *leve* by Booker (1930, p. 70, fig. 1a, pl. 2, figs. 3, 4), but Fletcher and others (1952, p. 12) and Waterhouse (1964a, p. 81) considered *leve* to have been based on immature shells of *brachythaerum.*

Younger species are limited to New Zealand. A widespread limestone (Glendale Limestone, AG 4 limestone) of Capitan age (Puruhauan Stage of New Zealand) contains a new species probably developed from *T. concavum,* with few ear spines, and very short spine bases. Still younger beds of the New Zealand Waiitian Stage (Djulfian of Armenia, Wuchiaping of China) contain rare elongate and incurved *Terrakea,*

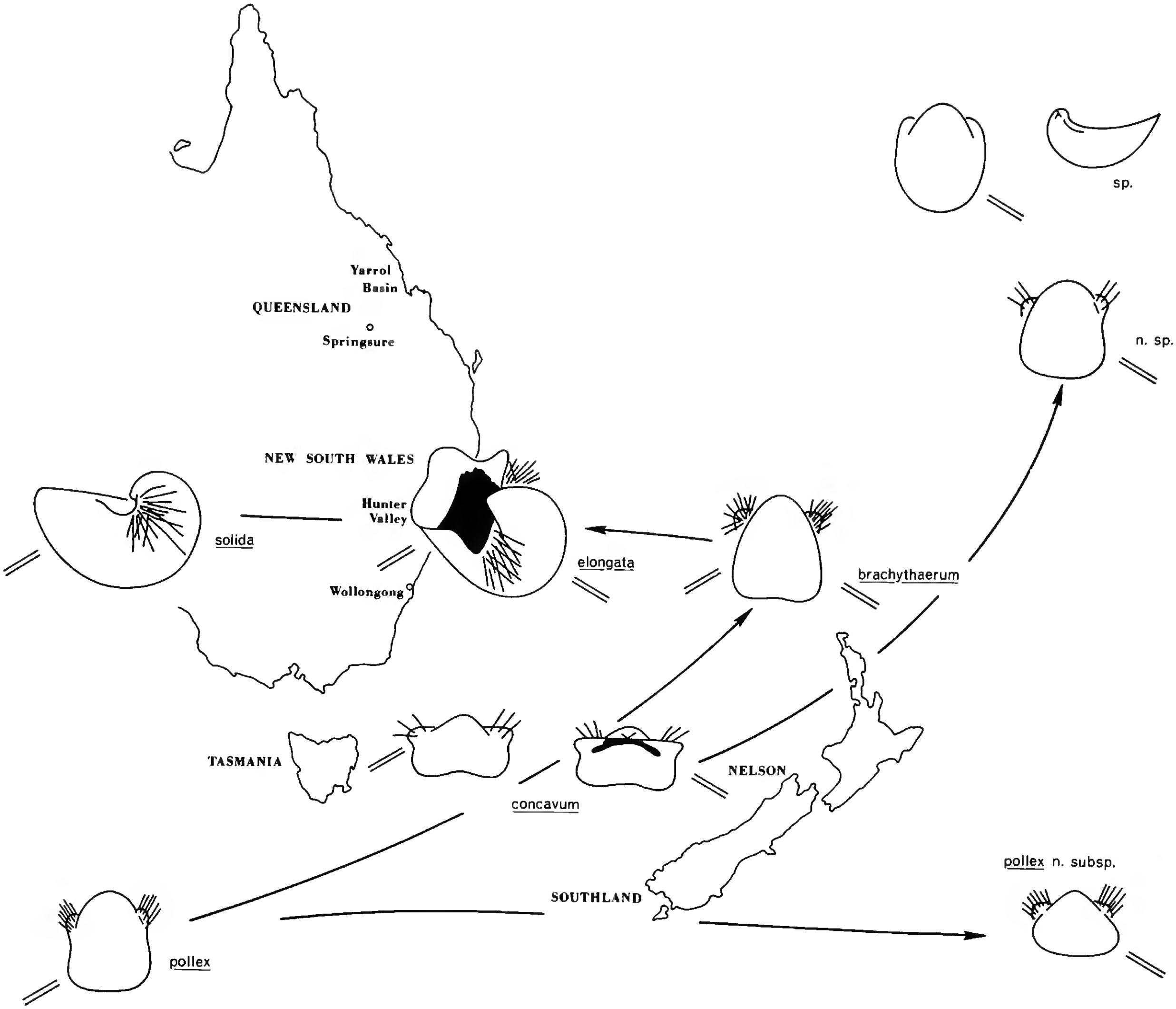

FIGURE 1.—Sequence and distribution of *Terrakea* in Australia and New Zealand. Species are arranged vertically in order of appearance (*T. pollex* coming in first) and horizontally according to geographic distribution. Those on the left are restricted to Australia; those on the right are restricted to New Zealand; and those in the middle are present in both countries (indicated by double side lines). Two lineages are suggested by the density of ear spines. The density is not known for the youngest species.

with the spine pattern poorly known (Waterhouse, 1967a).

No species of *Terrakea* has been found in the approximately correlative fauna of a tillite horizon found below the Cygnet Coal Measures at the top of the Permian succession in Tasmania. Nor has the genus been recorded in topmost Permian beds of New Zealand (Waterhouse, 1967a), ascribed to the Makarewan Stage, and equivalent to the Changsing fauna of south China, and to part of the so-called basic Triassic of Djulfa, Armenia, and Azerbaidzhan.

Distribution Beyond Australia and New Zealand

ARCTIC.—As stated by Waterhouse (1969), Victor Gamelin of the Geological Institute at Magadin has discovered two species of *Terrakea* in the Upper Permian deposits of eastern Siberia. I have examined these specimens at the Paleontological Institute, Moscow, and fully agree with Gamelin's identifications. The specimens figured from the upper Talatin Suite and reported from the Vorkutsk Suite of Pai Hoi by Solomina (1960, pl. 8, figs. 8–12) as *Cancrinella koninckiana* also look somewhat like *Terrakea.* Permian faunas of Siberia are so similar to those of Canada that it is therefore of no surprise to discover *Terrakea* near the base of the Upper Permian in the Richardson Mountains of the Yukon, and in the Arctic Archipelago on Melville Island. They have been found by the writer in collections submitted for examination by the Geological Survey of Canada. A single species occurs in the Assistance Formation of Melville Island, and approximately correlative beds in the Richardson Mountains, and is here described as a new species, *Terrakea arctica.* Specimens are also known in slightly younger beds (Plate 2: figure 15) in glauconitic sandstone above the Assistance (Formation B of Nassichuk, 1965), and in the correlative Ranger Canyon Chert of British Columbia (McGugan et al., 1965; Logan and McGugan, 1968) to judge from collections seen at the Department of Geology, University of Alberta, Calgary, and kindly shown to me by A. McGugan. *Terrakea,* therefore, appears to be one of those genera with disjunct distribution noted by Waterhouse (1967c, 1969) as characterizing the Arctic realm of Siberia and Canada (at present latitudes of 65° to 70°), and the East Australasian realm of eastern Australia and New Zealand (at present latitudes of 20° to 45°). See Figure 2.

OCCURRENCE IN TEXAS.—As hinted in Waterhouse (1969), it is by no means certain that *Terrakea* does have a more or less bipolar distribution, because specimens from the Glass Mountains of Texas closely approach *Terrakea* in many respects. Specimens were referred by Muir-Wood and Cooper (1960, p. 305) to a new genus *Grandaurispina,* with type species *G. kingorum* Muir-Wood and Cooper (1960, pl. 121, figs. 1–13) from the Word Limestone Number 3—see also *Avonia signata* non Girty of King (1931, pl. 20, figs. 16, 17—not 18–24) and the Cherry Canyon Formation of the Guadalupe Mountains. They also referred *Productus signatus* Girty (1909, p. 263, pl. 22, figs. 4a, b) from the Cherry Canyon Formation to *Grandaurispina.* Initially placed in the Linoproductinae Stehli 1954, *Grandaurispina* was transferred to the Overtoniidae by Muir-Wood (in Moore, 1965, p. 341). Examination of the type-species at the Smithsonian Institution suggests that the genus is linoproductinid, with typical ornament and cardinalia. In some specimens the costellae are rather faint, and the nature of the spine bases varies within single specimens, from a rather aprupt emergence of the spine from the costella which may be wider than the spine, to swollen bases suggestive of the Overtoniidae. Frequently the spine bases are prolonged posteriorly for 4 or 5 millimeters into the shell (e.g., USNM 149994, loc. 706e) exactly as in *Terrakea.* The cardinal process is like that of *Terrakea* figured by Waterhouse (1964a) and the septum is very long, and doubled posteriorly, and the marginal ridge well developed in the brachial valve. Juvenile pedicle valves are deeply pited internally in the type species, and grooves appear later in ontogeny just as in *Terrakea.* Dimples occur over the dorsal exterior as in *Terrakea.*

One apparent difference lies in the cluster of spines over the inner ears of the pedicle valve in *Grandaurispina kingorum,* each spine typically about twice as thick as the body spines, in a band between the posterior and lateral margins, though less sturdy and numerous in some individuals. Because of the different preservation of Australian and New Zealand material, workers may not have realised that a similar cluster of sturdy spines on the inner ears is typical of *Terrakea brachythaerum* (Morris), as described by Waterhouse (1964a, p. 76) for New Zealand material and in the Australian material (Etheridge and Dun, 1909, pl. 42, fig. 8; Waterhouse, 1964a, p. 79). It seems probable that the two are congeneric, though no doubt *Grandaurispina* could be treated as a subgenus. It clearly occupied a very different niche and geographic realm.

Paleogeographic Distribution

Assuming that *Grandaurispina* is closely allied, we then have a crudely circum-Pacific distribution for *Terrakea,* a most unusual one as far as the Permian is concerned, for no other similar brachiopod distribution comes to mind. Its apparent absence from even western Australia, apart from Timor, Himalyas, Salt Range, China, and Japan suggests that the genus, though highly tolerant in terms of latitude and therefore presumably of temperature, was restricted by other factors from attaining world-wide colonization. From present knowledge, one might speculate that the genus arose in the early Permian (Artinskian, or perhaps upper Sakmarian) in eastern Australia (from *Cancrinel-*

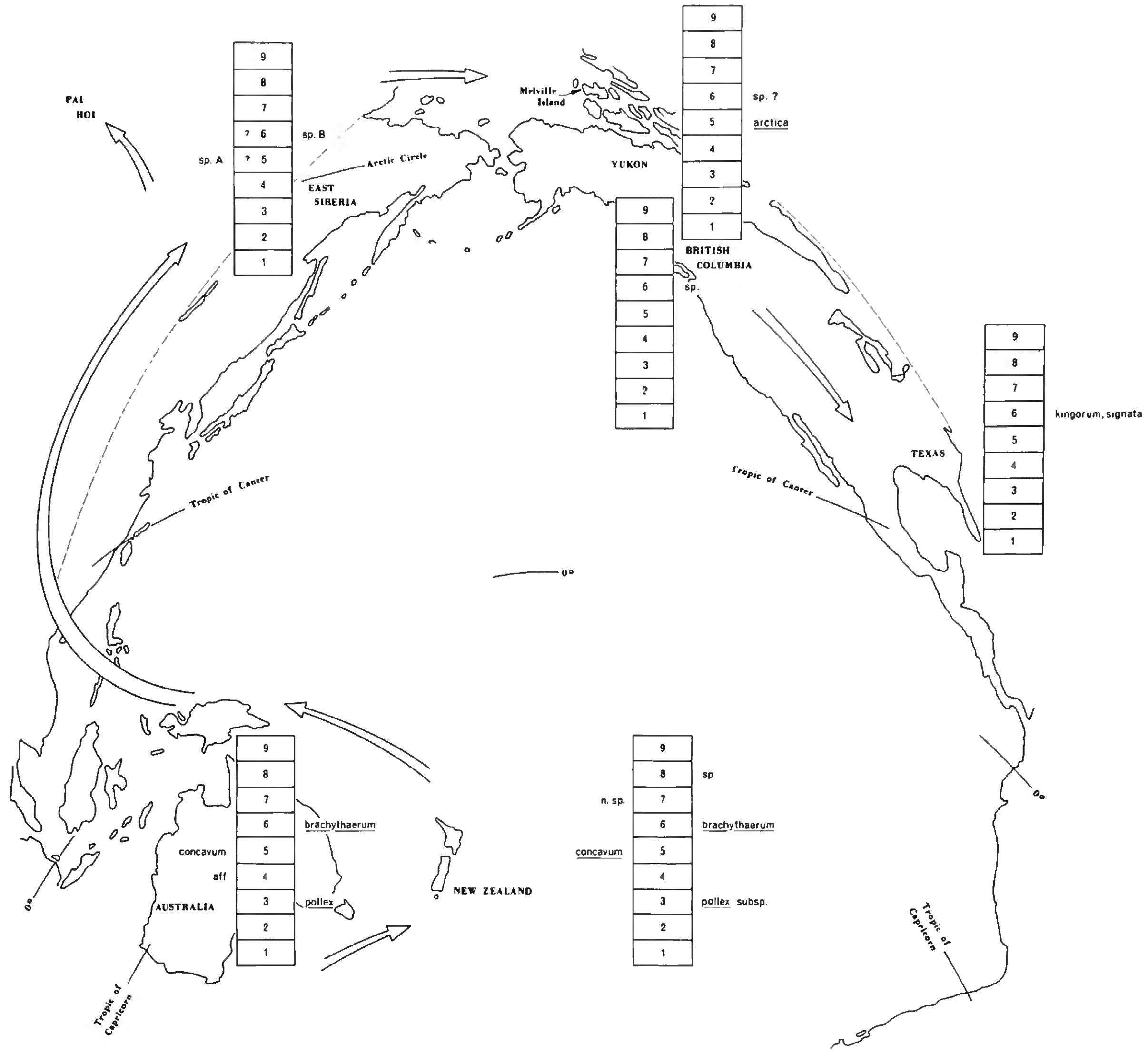

FIGURE 2.—Sequence and distribution of *Terrakea* throughout the globe. Species with few ear spines to left; with many, to right. Arrows indicate possible migration route. The ages indicated in column (1–9 stages) are not known for eastern Siberia. Extension of the arrow from British Columbia into Texas is tentative, in view of uncertainty on the validity of *Grandaurispina* and its relationship to *Terrakea*. Some evidence suggests that this genus was present in the Leonardian Stage.

la?) and rapidly spread to New Zealand. Free interchange of species between these regions persisted throughout most of the period in two lineages, one with densely spinose ears, the other without such spinose ears. At some time near the close of the Lower Permian, or beginning of the Upper Permian, both lineages penetrated east Siberia (presumably along the Tethys from New Zealand through Indonesia though no trace remains), and the spiny lineage continued into the Canadian Arctic, and on into central-southern United States, where rapid speciation probably occurred. Such a reconstruction is hardly well-supported by the fossil record, and further discoveries are bound to show a more complicated pattern. Nevertheless, the distributional history accords well with our present knowledge of Permian climates. The

TABLE 1.—_Occurrences of_ Terrakea* _and Intercorrelation_

Stage	_Russian Platform_	_New Zealand_	_Tasmania_	_Queensland_	_New South Wales_
9		Makarewan	Cygnet		Newcastle
8	Tatarian	*Waiitian	Ferntree	?Blackwater	
7		*Puruhauan		Black Alley	Tomago
6	Kazanian	*Upper Braxtonian	*Malbina D–E	*Peawaddy	*Mulbring *Muree
5	?Ufimian	*Lower Braxtonian	*Malbina A	Ingelara	*Branxton
4	Baigendzinian	Mangapirian	*Berriedale	Albebaran	Greta
3	?Aktastinian Sakmarian	*Telfordian	Nassau Golden Valley	*Cattle Creek	*Farley
2	Asselian	_Mourlonia_ beds	Quamby	Reids Dome	Allandale
1	?Asselian or pre-Asselian	_Atomodesma_			Lochinvar

Stage	_Verchoyansk Siberia_	_Arctic Islands_	_Richardson Mountains_	_British Columbia_	_Texas_
9					Ochoan
8					
7	Hivach		?_Atomodesma_		Capitan
6	Gijigin Omolon	*Formation B	*_Licharewia_	*Ranger Canyon	*Word
5	Djigdalin	*Assistance Formation	*_Lissochonetes_		*Road Canyon
4	Djeltin Munugudjak	Belcher Channel	_Yakovlevia-Liosotella_		*Cathedral Mountain
3	Yasachnin		_Yakutoproductus-Tornquista_		Skinner Ranch
2	Irbichansk		_Attenuatella-Yakovlevia-Tomiopsis_	Ross Creek	Wolfcamp
1	Burgali		_Orthotichia_	Telford Johnson Canyon	

likelihood that _Terrakea_ arose in eastern Australia suggests that it was at first adapted to dwelling in waters severely cooled by ice of the great early Permian glaciation, centered south of Australia, and the fossil record throughout the remainder of the Permian in Australia and New Zealand suggests that the genus preferred cool rather than warm waters. As Waterhouse (1964b, 1967b; in Brown et al., 1967, pp. 211–214) and Banks (1968) have shown, there were three major glacial intervals each followed by a recovery period, then a lengthy warm interval in the Permian of Australia and New Zealand. _Terrakea_ is particularly prolific in the rocks formed during the recovery intervals when the ice, though shrinking, still exerted a considerable cooling effect (e.g., Stages 3 and 6 in Table 1). Specimens are fewer during the warm and to lesser extent the cold episodes. The time that _Terrakea_ appears to have successfully colonized the parts of the northern hemisphere appears to coincide with the cold episode in the middle Permian (Stage 5), when much of the world suffered cooling, though of course not as severe as in eastern Australia. This major cooling may have allowed _Terrakea,_ hitherto restricted to the south by the warm-water equatorial barrier, to expand its world coverage considerably, penetrating the equator by means of an ephemeral invasion to enter the more favorable, cooler waters of Siberia and Arctic Canada. The genus persisted in this realm during the ensuing "recovery interval" of Stage 6 in Table 1. It is believed that the Wordian of Texas does possess a number of "cool-water," otherwise-Arctic genera, but it is nevertheless surprising that _Terrakea_ flourished in the low latitudes of Texas. Perhaps the genus at this stage changed or improved its ecological tolerance, unless I am mistaken in suggesting that *Grandaurispina* is allied to *Terrakea.*

The possible occurrence of *Terrakea* in the Talatin Suite of Pai Hoi may not accord with the preceding reconstruction, because the Talatin faunas are regarded as Baigendzinian (Licharev, 1966). But the Talatin faunas described by Solomina (1960) come from two levels, the lower appearing to be Artinskian, the upper in my view being younger, with forms such as *Stepanoviella (Linoproductus* ex grupo *cora), Megousia (Linoproductus kulikii), Cancrinella janischewskiana,* and other forms suggestive of Stage 5 or 6 in the Canadian and other Siberian sequences.

Habitat

The two lineages in *Terrakea* reflect adaptation to slightly different niches. *Terrakea brachythaerum* and its close allies, including *pollex, arctica* and presumably *kingorum,* posseessed large and numerous ear spines, that functioned somewhat like the lateral halteroid spines of *Marginifera* described by Grant (1968) for steadying the shell, while the body spines curve freely and evenly away from the disc, suggesting growth into water rather than sediment (Grant, 1968). New Zealand and Australian members of this lineage are generally found in sandy sediment, generally arkosic or quartzitic or volcanic graywackes, and even in breccia and conglomerate. It seems highly likely that they dwelt in a sandy or finely graveled seafloor, well winnowed by currents. The sharply geniculated trail in both *pollex* and *brachythaerum* suggests that the brachial valve became partly buried in sediment, so that the trail had to grow, sometimes rapidly, at right angles to the disc in order to maintain contact with the water. A similar habit probably obtained for *T. arctica* from the sandy Assistance Formation of Melville Island. Yet in the Richardson Mountains what appears to be the same species is found in a very limy silt. Shells here are so numerous that the rock was a breccia of shell in a fine matrix. The amount of geniculation is not known for these shells. The habitats of *Grandaurispina* and the Russian *Terrakea* are yet to be described.

Terrakea concavum, with few ear spines, inhabited muddy siltstone, thickly colonized by *Echinalosia* at its type-locality, and also in muddy limestone. Ear spines are scarce from early ontogeny in every known specimen, though the trail varies in geniculation. Since there is no other consistent difference in shape from *brachythaerum,* the shells must have been able to maintain stability without the numerous ear spines, thanks perhaps to quieter bottom conditions, and perhaps a high angle of inclination of the body spines. The younger New Zealand species, not as yet described, is found in a similar calcareous mud in the Glendale Limestone. In the limestone of the Arthurton Group, it is found in a muddy matrix with mats of bryozoa, betokening quiet sedimentation.

Attention should also be drawn to the very sturdy spines along the anterior margin of the mature brachial valve, illustrated by Waterhouse (1964a) for *T.* aff. *pollex* (pl. 10, fig. 5), *T. concavum* (pl. 11, figs. 4, 5) and *T. elongatum* (pl. 15, fig. 15), and less commonly seen in *T. brachythaerum* (Figure 3). A specimen of a new subspecies of *T. pollex* is illustrated (Plate 2: figure 16) to show several rows of the fine spines over the pedicle disc and rows of very coarse spines over the trail. These spines are fully as thick as those over the anterior trail of the pedicle valve, in contrast to the slender posterior brachial spines. Though without adequate material to determine the exact course and length of the spines, I believe that these spines functioned as strainers in the same fashion as the posterior spines, and that their size may have reflected availability of shell material and the fact that, by developing at maturity when the shell was no longer increasing much in length, a long period of time was available

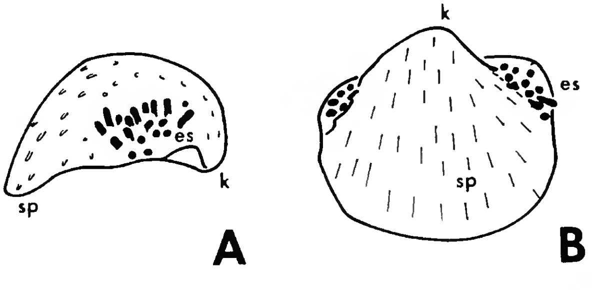

FIGURE 3.—*Terrakea brachythaerum* (Morris). Pedicle valve showing generalized distribution of fine inclined body spines, passing posteriorly into hollow tubules within the shell, and massive erect spines over the inner ears. A, Generalized from BR 158 figured by Waterhouse (1964a, pl. 12, fig. 8); B, from BR 66 figured by Waterhouse (1964a, pl. 13, fig. 12). Both from Mangarewa Formation, Letham Burn, Southland, and kept at the New Zealand Geological Survey, Lower Hutt. All views approximately × 1.5. Abbreviations: es, ear spines; k, umbo; sp, body spines.

for the anterior spines to remain functional. It seems difficult to imagine that these spines had any halteroid function.

Elongated Spine Bases

Spines at the front of the visceral disc, and over the ears, and in juvenile specimens pass straight through the shell. This remains true throughout ontogeny for spines over the brachial valve, and ears of both valves. But as the pedicle valve is thickened internally by layers of calcite over the floor, channels or gutters are left behind each open spine for the tissue that maintained contact with the isolated epithelial lobe growing at the tip of the spine. When the spine ceased to grow, the groove became covered over and sealed off.

Similar open channels are occasionally seen in *Cancrinella* (Campbell, 1953, p. 7), thus providing some evidence for relationships to this genus, as suggested by Waterhouse, 1964a, p. 63). Examples of *Cancrinella* with the grooves are figured by Campbell (1953, pl. 1, figs. 5, 6), Hill and Woods (1964, pl. P 6, fig. 17a) and Waterhouse (1964a, pl. 9, figs. 5, 6).

Genus *Terrakea* Booker 1930

DIAGNOSIS.—Concavoconvex Linoproductinae, usually flattened across the venter, and commonly geniculate. Ears of moderate size, ornament of costellae, rugae inconspicuous or absent, both valves spinose, arranged in quincunx, with many species bearing strong erect spines over the inner ears or adjoining lateral slopes, spines over visceral disc and trail of pedicle valve pass posteriorly into grooves, later enclosed by secondary shell, leaving hollow tubules. Spines of brachial valve erect. Muscle scars productiform, cardinal process usually erect, with high median lobe subdivided by notch, and curving lateral lobes, sometimes with alveolus at base. Septum in brachial valve long, broad immediately in front of process, often subdivided by groove.

TYPE-SPECIES.—*Productus brachythaerus* Morris 1845 non G. B. Sowerby 1844.

Terrakea arctica, new species

PLATE 1: FIGURES 1–15; PLATE 2, FIGURES 1–14, 17

DIAGNOSIS.—Small *Terrakea,* varying in shape from transverse with nonsulcate disc to highly arched with narrow flattened or sulcate disc, small ears, maximum width anteriorly placed, costellae fine, spines numerous over ears, and close set, emerging at high angle from visceral disc of pedicle valve. Cardinal process low with deep median cleft in immature specimen.

DESCRIPTION.—Size small for genus, pedicle valve varying in shape from high elongated vaulted specimens with sulcate of flattened venter and steep sides to transverse specimens with rounded venter, gently inclined sides, and less incurved umbones, especially in specimens from the Assistance Formation at C–464 and C–1872. Specimens from the Richardson Mountains usually have rounder discs and arched venters. Ears small, with slightly acute cardinal extremities maximum width of shell generally near anterior third of length; brachial valve gently concave over venter, curving with strong geniculation into trail which extends nearly half length of shell in mature specimens. Mature specimen apparently sulcate anteriorly, suggestive of "tubiform" trail.

Ornament characteristic. Costellae fine, generally 10–12 in 5 mm anteriorly on pedicle valves, with up to 15 to 5 mm in specimens from C 464 and up to 17 in 5 mm on a brachial valve from C 462.

Spines best preserved on silicified specimens, emerging over visceral disc of pedicle valve at 35° to 45°, with slightly swollen bases, extended posteriorly for 0.5 mm in some instances, arranged roughly in quincunx, in rows nearly 2 mm apart in mature shells, spaced over 2 mm apart along a row, compared with spacing of only 1 mm apart for the first 10 mm or so

PLATE 1.—*Terrakea arctica,* new species. All views are twice natural size. Specimens are from Assistance Formation of Melville Island (see Table 3 for locality details) and are at Geological Survey of Canada, Ottawa. 1, 2, Ventral and dorsal views of internal mold specimen 24487, from C–462, Sabine Bay, Melville Island. 3, Dorsal aspect of external mold specimen 24488 from same locality. 4, External mold of pedicle valve showing costellae and spine bases; specimen 24489, from same locality. 6, 9, 13, Posterior, lateral, and ventral aspects, respectively, of internal mold of pedicle valve 24491 from same locality. 5, Internal mold of pedicle valve 22490 from C 463, Sabine Peninsula, Melville Island. 7, 15, Lateral and ventral views of internal mold of pedicle valve 24492, from same locality. 8, 14, Posterior-ventral and ventral aspects of internal mold of pedicle valve 24493 from C 464, Melville Island. 10, Internal mold of pedicle valve GSC 24484 from C 463, Melville Island. 11, Ventral aspect of internal mold of pedicle valve 24485, from C 464. 12, Internal mold of pedicle valve 24486 from C 1872 from Melville Island.


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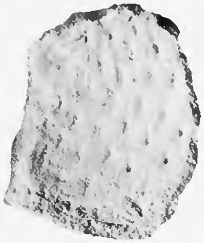
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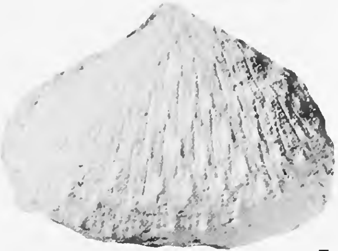
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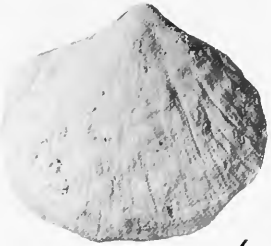
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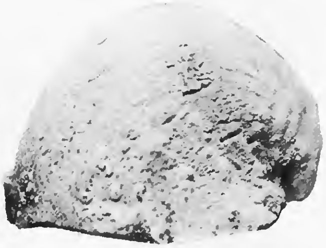
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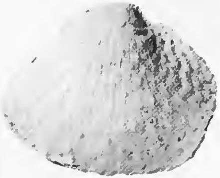
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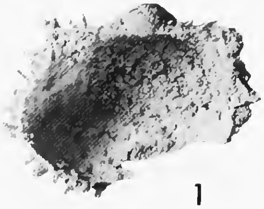
PLATE 1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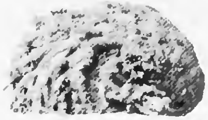
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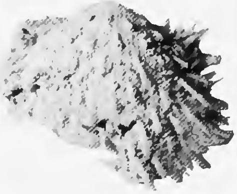
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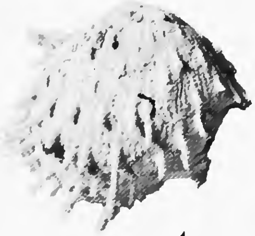
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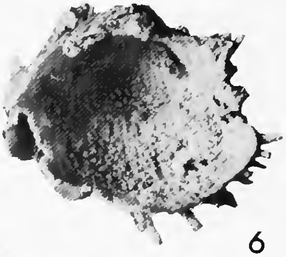
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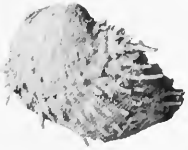
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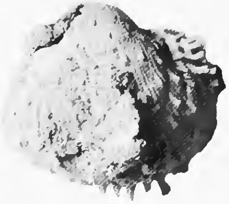
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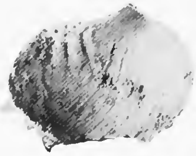
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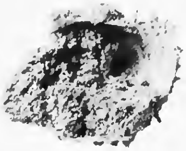
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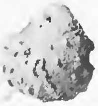
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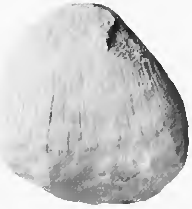
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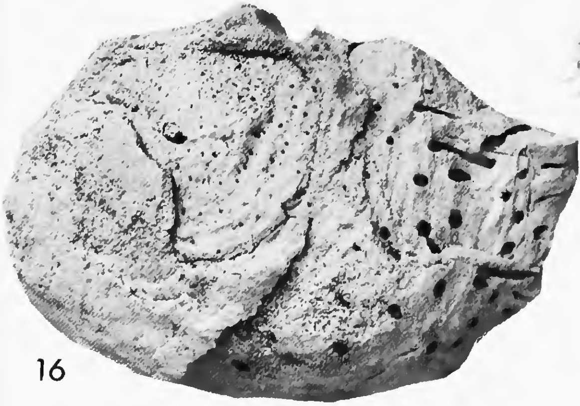
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PLATE 2

of the shell length. The spines curve dorsally forward, and have a diameter as much as 0.7 mm anteriorly. Over the ears the spines increase in diameter to 0.9 mm, and are erect, and closely spaced, 1 mm apart in three of four rows each just over 1 mm apart. There is no obvious row of spines along the hinge, but a few spines may project backward. One specimen from GSC 53850 is unusual in that the body spines (up to 1 mm in diameter) are as thick as ear spines. Spines not seen on the silicified brachial valve, faintly suggested on brachial valve from C 462, 0.5 to 1.5 mm apart anteriorly, and 0.3 mm in diameter. Elongated pits also present, spaced much as spines of pedicle valve. Both valves crossed by low concentric growth wrinkles, defined only near hinge on pedicle valve, and sometimes persisting across anterior disc or trail as very low growth steps; more persistent on brachial valve. Coarseness of matrix, and imperfect silification prevents study of finer growth lamellae seen in New Zealand material (Waterhouse, 1964a pl. 35, fig. 1).

Pedicle valve thin, 0. 2 to 0.4 mm thick, shell penetrated by spine bases, often but not always prolonged posteriorly from the visceral spines for 2 to 9 mm, pedicle muscle scars faintly impressed. Adductors elongated and narrow, slightly dendritic posteriorly, marked by subparallel ridges anteriorly, diductors large, oval, faintly impressed, extending in front of adductors, marked by fine longitudinal grooves and ridges.

Brachial valve best known from C 462. Cardinal process with deep posterior median cleft otherwise not preserved, supported anteriorly by two ridges divided by narrow slit, with low ridge along hinge to each side. Muscle scars divided into outer pair and inner subtriangular pair, marked by ridges, but not strongly dendritic (Figure 4). Median septum arises between anterior part of inner adductors just in front of the posterior slit, and extends well beyond midlength as a very slender low ridge, without a terminal pillar. Brachial ridges poorly defined, anterior floor with sharp pustules and narrow ridges about 1 mm apart. Brachial valve from GSC 53823 has similar high ridge, and double ridge in front of process. Cardinal

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PLATE 2.—All views are twice natural size, except figure 15. See Table 1 for locality details. All specimens except the one shown in figure 16 are at Geological Survey of Canada, Ottawa.

Terrakea arctica, new species: 1–3, holotype; internal, lateral, and ventral views of pedicle valve GSC 24475, from GSC locality 53850, Richardson Mountains, Yukon. 4–6, Ventral, lateral, and internal views, respectively, of pedicle valve 24476, from GSC locality 53850, Richardson Mountains. 7, Ventral exterior of specimen 24477, GSC locality 53823, Richardson Mountains. 8, 13, Ventral exterior of specimen 24478, GSC locality 53823, Richardson Mountains. 9, 10, Ventral and tilted lateral views respectively of specimen 24479, GSC locality 53823, Richardson Mountains. The pedicle umbo has been subsequently removed to reveal internal details of brachial valve. 11, 17, Ventral and internal views of pedicle valve specimen 24480, from GSC 53823, Richardson Mountains. 12, Internal aspect of pedicle valve 24481, from GSC locality 53823, Richardson Mountains. 13, Pedicle valve 24482 from GSC locality 53823, Richardson Mountains.

Terrakea sp.: 15, Ventral aspect of internal mold of pedicle valve 24483 from C-465, Melville Island, Formation B, above Assistance Formation.

Terrakea pollex Hill, new subspecies: 16, External mold of brachial valve showing fine spines (as dark holes) over visceral disc and sturdy spines over trail. Specimen is from Takitimu Group, New Zealand, and is at New Zealand Geological Survey, Lower Hutt.

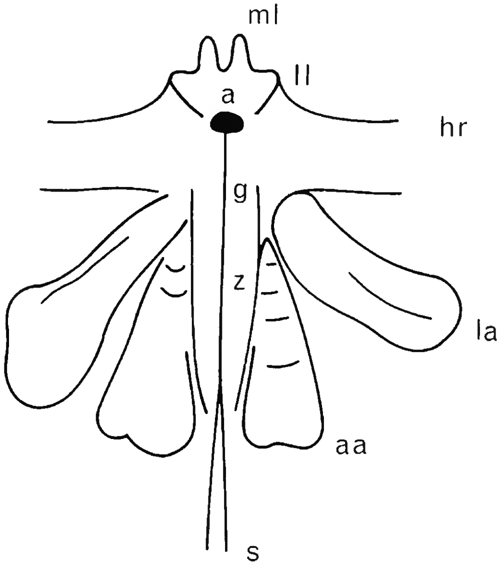

FIGURE 4.—Composite sketch of internal features of brachial valve of *Terrakea arctica,* with cardinal process sketched from specimen 24479 from locality GSC 53823; and remaining details from specimen 24487, locality C-462. × 4 approximately. Abbreviations: a, alveolus; aa, anterior adductor scar; g, posterior ridge; hr, hinge ridge; la, lateral adductor scar; ll, lateral lobe of cardinal process; ml, median lobe of cardinal process; *s*, septum; *z*, median groove between two posterior ridges.

process of two lobes separated by deep alveolus, and each subdivided by shallow cleft (Figure 4).

Measurements (in millimeters) are given in Table 2.

Holotype.—GSC No. 244475, GSC locality 53850, Richardson Mountains, pl. 2: figs. 1–3.

Material.—Specimens from the Richardson Mountains (Table 3) of the northern Yukon are found in silicified limestone, and have been leached out in dilute hydrochloric acid. Mainly pedicle valves have been found, four coming from GSC 53822, 25 from GSC 53823 (one with the brachial valve attached), two from GSC 53834, two from GSC 53848, and about ten from GSC 53859: all fragile, small and more or less broken. From the Arctic Islands specimens are preserved as natural internal and external molds, four pedicle valves coming from NF 64–2–25 (C–463), five from NF 64–2–35 (C–464), one from NF 64–3–19 (C–465), three from C–1872 and a pedicle interior, exterior, a brachial exterior, and an internal mold with valves conjoined from NF 64–2–11 (C–462).

Table 2.—*Dimensions of* Terrakea arctica, *new species.*

Locality	*Width*	*Length*	*Height*	*Umbonal angle*	*Cardinal angle*
			PEDICLE VALVES		
C–462	18.8	17.7	9.1	105°	—
C–463	20.5	19.8	13.8	70°	—
	21.5	+15.7	10.6	110°	120°
	24.2	20.3	14.2	100°	—
C–464	15.3	16.9	9.4	85°	—
	20.5	21.5	12.6	—	—
C–1872	14.0	12.5	6.3	105°	—
	19.2	18.0	8.1	?115°	—
GSC 53823	8.4	8.0	3.0	—	—
	?15.0	12.6	6.5	95°	—
	8.0	7.4	3.2	98°	—
	7.0	5.5	2.3	95°	135°
	10.5	9.1	5.4	98°	100°
	12.5	9.7	5.7	95°	—
	10.4	7.0	3.1	—	140°
	15.4	12.3	5.8	98°	120°
	12.6	11.0	6.5	105°	95°
	17.4	13.5	7.8	93°	80°
GSC 53850	14.0	11.0	4.3	105°	—
	15.5	13.8	8.8	100°	70°
	16.5	?12.0	?8.0	95°	75°
			BRACHIAL VALVES		
C–462	17.0	14.0	7.0	—	75°
	18.8	15.0	6.0	—	—
GSC 53823	12.5	8.0	?3.0	—	—

INTERIOR, PEDICLE VALVE

Locality	*Width*	*Adductor platform*		*Diductor scar*	
		Width	*Length*	*Width*	*Length*
C-463	20.5	3.0	8.0	6.0	8.5

INTERIOR, BRACHIAL VALVE

	Width	*Outer adductors*		*Inner adductors*		*Septum*
		Width	*Length*	*Width*	*Length*	*Length*
C–462	18.8	9.5	3.7	5.8	5.0	9.1

Horizon.—Beds approximately equivalent to the Assistance Formation of Harker and Thorsteinsson, on Melville Island, and in a *"Lissochonetes"* zone of Richardson Mountains (GSC 53848, 53850), and slightly younger beds (GSC 53822, 53823, 53834).

Resemblances.—In the well-defined radial ornament and high angle of emergence of its pedicle spines, this species comes close to *Terrakea concavum* Waterhouse (1964a) from the approximately correlative Letham Formation of New Zealand, also believed to occur in equivalent beds of Tasmania (Grange Mudstone, Malbina A) and southern New South Wales. Though the southern species is generally not geniculate and is ovally transverse without a median sulcus, some specimens, including topotypes, are geniculate, and sulcate. But this species is distinguished by its paucity of spines over the ears of the pedicle valve. A closer ally in this respect is *Terrakea brachythaerum* (Morris) from the Malbina D–E beds of Tasmania, and reported widely from correlative beds of New South Wales (Wollongong) and Hunter River—Muree and Mulbring Formations, and the "Fauna IV" of Queensland, as well as correlative Mangarewa and Flowers Formations of New Zealand. A few Canadian specimens have the identical narrow shape, incurved umbones and flat or sulcate venter often seen in the Australasian species, and the arrangement of spines over the ears is much the same, as well as the geniculate trail. On the other hand, visceral spines emerge at a higher angle in the Canadian form and are much more closely set. Internally the cardinal process differs in being more sessile, with a deeper median cleft, though an alveolus and anterior double ridge are present as in some New Zealand specimens of *T. brachythaerum.* No other species from the southern hemisphere come very close, *T. pollex* Hill generally having an elongated outline with a moderate number of ear spines, but fewer visceral spines, and a younger New Zealand form having few ear-spines.

Grandaurispina kingorum Muir-Wood and Cooper (1960, p. 306, pl. 121, figs. 1–13; also figured as *Avonia signata* non Girty of King, 1931, p. 83, pl. 20, figs. 16, 17?), from Word Limestone Number 3 of the Hess Canyon Quadrangle, has a somewhat similar density of spines over the disc, but its ear spines are much larger, and its cardinal process close to that of Australian and New Zealand *Terrakea.* Closer resemblances to Texan forms might be revealed when the descriptions are published by G. A. Cooper and R. E. Grant.

Table 3.—*Localities with* Terrakea arctica, *new species.*

(A) Northern Richardson Mountains, collected by E. W. Bamber, Geological Survey of Canada, 1962.

Locality number	*Description*
GSC 53822	Three miles north of Horn Lake, Aerial Photograph A 14363–14, 1362 feet below top of measured section (67°47′/136°02′).
GSC 53823	Three miles north of Horn Lake, Aerial Photograph A 14363–14, 1375 feet below top of measured section (67°47′/136°02′).
GSC 53834	Symmetry Mountain, Aerial Photograph A 14361–68, in talus 680 feet above top of Devonian (67°42′/136°15′).
GSC 53848	Same section, 2425 feet above top of Devonian.
GSC 53850	Same section, 2655 feet above top of Devonian.

(B) Melville Island, Assistance Formation, collected by W. W. Nassichuk, 1964.

C 462	Three miles NW of Tingmisut Lake, bearing 335°, Sabine Peninsula NF 64–2–11.
C 463	Four miles NW of center of Tingmisut Lake, Sabine Peninsula, bearing 310°, NF 64–2–25.
C 464	Photo A 16763–171, 16 miles SW of center of Tingmisut Lake, Sabine Peninsula, bearing 235°, NF 64–2–35.
C 1872	Five miles SE of Tingmisut Lake; on the east side of the west arm of Weatherall Bay, Melville Island.
C 465	[*Terrakea* sp.] Photo A 16763, 6 miles west of Tingmisut Lake NF 64–2–27.

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Garner L. Wilde

Phylogeny of *Pseudofusulinella* and Its Bearing on Early Permian Stratigraphy

ABSTRACT

The fusulinid genus *Pseudofusulinella* Thompson is represented in the McCloud Limestone of northern California by 40 species that can be separated into four phylogenetic (phenetic) groups: Group I, Elongate-fusiform species with perched chomata; Group II, Small, rare, very slender-fusiform species with perched chomata; Group III, Intermediate, thickly fusiform species with perched chomata; and Group IV, Large, thickly fusiform species with massive chomata. Recognition of these four groups within Permian (Wolfcampian) rocks of the McCloud Limestone provides a basis for long-range correlation of significant stratigraphic and physical breaks, not only throughout the Pacific Northwest, but with important exposures in Texas and Kansas.

Systematic paleontologists have, until only recently, confined their efforts largely to the description of new genera and species, and to the erection of ontogenetic and phylogenetic schemes for classification purposes. Much of this kind of descriptive paleontology still remains to be done despite the hue and cry from those who feel that too many species have already been named. Even so, criticism is certainly warranted unless every effort is made to apply systematics and phylogenesis to stratigraphic problem solving. It is the purpose of this paper to deal with that objective.

Description of numerous species of the fusulinid genus, *Pseudofusulinella* Thompson (1951) from the McCloud Limestone of northern California by Skinner and Wilde (1965b), provides an excellent starting point for dealing with phylogeny and its applicability to Early Permian stratigraphic problems.

It is generally believed that the Early Permian (Wolfcampian) experienced periods of crustal instability, accompanied by widespread transgressions and regressions of the seas. In many areas around the world unconformities are apparent in Wolfcampian sequences. Because of dense drilling and excellent exposures in surrounding mountainous outcrops, the Greater Permian Basin of western Texas and southeastern New Mexico offers some of the best documented evidence of widespread unconformable relationships in the Wolfcampian.

Coincidental relationships between these physical and faunal breaks have also been observed in the phylogenetic history of 40 species of *Pseudofusulinella*, all of which occur in the McCloud Limestone of the Shasta Lake Region of northern California. Two of the species occur in Leonardian strata.

Recently, Ozawa (1967) has also dealt with the phylogenetic relationships within *Pseudofusulinella*. Ozawa's paper was not yet available to the present writer in early 1968 when some of the material presented here was given in a paper read before the Permian Basin Section of the Society of Economic Paleontologists and Mineralogists in Midland, Texas. In the present study, therefore, Ozawa's contribution is considered.

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Fusulinid Zonation of the McCloud Limestone

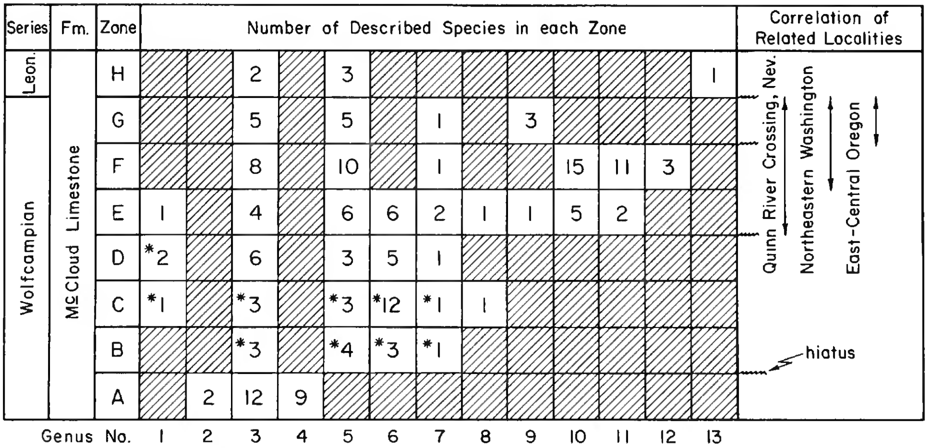
Skinner and Wilde (1965b) divided the McCloud Limestone into eight fusulinid faunal zones with informal letter designations for each zone. Zone A, the oldest, was only tentatively considered to be Permian, Zones B through G were identified as Wolfcampian and Zone H, Leonardian. It is believed now that Zone A is definitely Permian (Wolfcampian) in age. This age assignment also is important to the thesis developed in the present paper. Hoare (1963) has described a fusulinid fauna from the Sunflower Reservoir area of northern Nevada which contains Zone A elements, but which also contains species of *Schwagerina.* This genus is absent in Zone A of the McCloud. Along with *Schwagerina,* Hoare described *Pseudofusulinella symmetrica* Hoare and *Pseudofusulinella nevadensis* Hoare. Both of these species obviously belong to the genus *Thompsonella* Skinner and Wilde, which is common in Zone A. Indeed, later study might prove that identical species occur in the two localities. Species of *Triticites* described by Hoare are not incompatible with those of Zone A of the McCloud.

Interbedded dark brown to black, silty, siliceous limestone and dark gray siltstone and silty shale characteristic of Zone A of the McCloud is in rather sharp contrast to most of the overlying sequences of rocks which are generally light-colored, thick-bedded, and cherty limestones. Accompanying these lithologic differences is a distinct faunal contrast (Figure 1). From Zone A nine species of *Triticites* have been described along with twelve species of *Pseudufusulinella,* two species of the new genus *Thompsonella,* and rare undescribed forms of *Schubertella.* The typical Early Permian genus, *Schwagerina,* has not been seen in Zone A although a few of the species of *Triticites* exhibit *Schwagerina* features. *Triticites* has not been found higher.

In the next higher Zone B only three species of *Pseudofusulinella* are present, accompanied by four species of *Schwagerina,* three species of *Pseudofusulina* (*Rugosofusulina* of earlier authors), and a single species of *Paraschwagerina.* None of the latter three genera have been seen in Zone A. Again, rare specimens of *Schubertella* are present in Zone B, but apparently are different species.

An apparent angular discordance between Zones A and B is seen in at least one large exposure on the western face of Ellery Mountain. It is suggested that this break marks a regionally important unconformity which will be considered in greater detail later.

Zones B and C of the McCloud Limestone are essentially identical lithologically, and six species of fusulinids are common to the two zones. In Zone C, however, the typical Middle Wolfcampian genus, *Pseudoschwagerina,* makes its first appearance. It is repre-



Series	Fm.	Zone	1	2	3	4	5	6	7	8	9	10	11	12	13
Leon.	McCloud Limestone	H			2		3								1
Wolfcampian		G			5		5		1		3				
		F			8		10		1			15	11	3	
		E	1		4		6	6	2	1	1	5	2		
		D	*2		6		3	5	1						
		C	*1		*3		*3	*12	*1	1					
		B			*3		*4	*3	*1						
		A		2	12	9									

* Indicates some overlapping of identical species.

1. *Schubertella*
2. *Thompsonella*
3. *Pseudofusulinella*
4. *Triticites*
5. *Schwagerina*
6. *Pseudofusulina*
7. *Paraschwagerina*
8. *Pseudaschwagerina*
9. *Chalaraschwagerina*
10. *Eoparafusulina*
11. *Cuniculinella*
12. *Klamathina*
13. *Parafusulina*

FIGURE 1.—Numbers of described species of fusulinids in each faunal zone of the McCloud Limestone, and correlation with closely related localities.

sented here by only one species. Accompanying that form are three species of *Schwagerina,* one of which is also present in Zone B; twelve species of *Pseudofusulina,* one common to Zone B; three species of *Pseudofusulinella;* one species of *Paraschwagerina,* also found in Zone B; and one species of *Schubertella,* which ranges into Zone D above.

Of seventeen described species of fusulinids in Zone D, the above-mentioned *Schubertella* is the only species in common with another zone. Zone D contains three species of *Schwagerina,* five of *Pseudofusulina,* six of *Pseudofusulinella,* one of *Paraschwagerina,* two species of *Schubertella,* and undescribed species of *Boultonia.* Yet, distinctive changes in genera and species occurred during and at the close of this period of McCloud Limestone deposition. These differences will be considered later. *Pseudoschwagerina* has not been found in Zone D. The possibility of a hiatus of unknown magnitude between Zones D and E cannot be discounted.

Three new interesting genera of fusulinids appeared during Zone E time, and their morphologic characters indicate that this was a period of at least local evolutionary experimentation among the fusulinids. *Chalaroschwagerina* is represented by one species, *Eoparafusulina* by five species, and *Cuniculinella* by two species. The latter two genera are the earliest of the large fusulinids characterized by cuniculi. Accompanying these three unusual forms are six species of *Schwagerina,* six of *Pseudofusulina,* four of *Pseudofusulinella,* two of *Paraschwagerina,* one of *Pseudoschwagerina,* one of *Schubertella,* and undescribed forms of *Boultonia, Staffella* and *Ozawainella.*

The largest number of species of any zone within the McCloud is found in Zone F. There are forty-eight described species represented among six genera. *Eoparafusulina* and *Cuniculinella,* which got their start in Zone E, flourished during Zone F time, with fifteen species of the former and eleven species of the latter. The other unusual genus of Zone E, *Chalaroschwagerina,* was not found in this zone, but it appears later in Zone G. Accompanying *Eoparafusulina* and *Cuniculinella* in Zone F are ten species of *Schwagerina,* eight species of *Pseudofusulinella,* with distinctive structural features, one species of *Paraschwagerina* (and a rare possible second species left undescribed), and another very unusual new genus, *Klamathina,* with three species. *Klamathina* has not been found in older or younger rocks. Undescribed species of *Boultonia, Staffella,* and *Ozawainella* occur here also.

Because of the great drop in numbers of species of fusulinids from Zone F to Zone G, and because of changes in *Pseudofusulinella,* to be discussed more fully later, it is believed that an important break in sedimentation could explain the change. Skinner and Wilde (1965b) found that on Tombstone Mountain and around the west side of High Mountain in the Shasta Lake Region, thick conglomerate and clastic limestone, as much as 1,050 feet in thickness, comprise the bulk of Zone G. The clastics abruptly overlie limestone beds containing Zone A fossils. Clasts containing fusulinids from all of the older zones of the McCloud are found within this clastic sequence, whereas the matrix contains only Zone G fossils. Indigenous to Zone G are five species of *Schwagerina,* five species of *Pseudofusulinella,* one species of *Paraschwagerina,* and three species of *Chalaroschwagerina.* Again, as in older zones, the genera *Boultonia, Staffella,* and *Ozawainella* also occur in Zone G.

Skinner and Wilde (1965b, p. 15) suggested the following interpretation of events at the close of Zone F deposition: "At or near the close of Zone F time the Tombstone Mountain area appears to have been sharply uplifted and subjected to rapid and deep erosion which essentially destroyed the shelf rocks which had been deposited there. This was followed by local foundering and the rapid accumulation of the limestone conglomerates of Zone G which are now exposed on Tombstone Mountain and around the west side of High Mountain." As will be shown later, this series of events may well have something more than only local significance.

The highest zone of the McCloud, Zone H, has been judged to be Leonardian in age. The only known exposures of this age in the Shasta Lake area are on Tombstone and High Mountains. Here occur three species of *Schwagerina,* two of *Pseudofusulinella,* and at least one of *Parafusulina.* The rocks containing this fauna rest directly upon the thick conglomerates of Zone F; therefore, further subsidence must have taken place in the same area that had been positive at the close of Zone F time.

One surmises from the foregoing that stratigraphic breaks are present in the McCloud Limestone between Zones A and B, D and E, F and G, and G and H. Are these breaks merely the result of local tectonic disturbances or can they be correlated with major breaks in the stratigraphic record?

Conjectured Phylogenetic Trends in *Pseudofusulinella*

Species of *Pseudofusulinella* in the McCloud Limestone of northern California offer an ideal situation for consideration of phylogenetic relationships within that genus because: (1) large numbers of species developed throughout McCloud time; (2) McCloud deposition continued with only occasional interruptions throughout Wolfcampian and into Leonardian time; and (3) changes within species of *Pseudofusulinella* were subtle, so that the total spectrum of change within the genus is discernable.

Ozawa (1967) has discussed phylogenetic relationships of *Pseudofusulinella,* and in the broader sense the present author agrees with Ozawa's understanding of trends within Permian species. Ozawa, however, extended his concept of the genus to include species in the Pennsylvanian which the present writer considers more closely related to *Eowaeringella* Skinner and Wilde (1967), e.g., *Eowaeringella ardmorensis* (Thompson, Verville, and Lokke, 1956), and *Eowaeringella alta* (Verville, Thompson, and Lokke, 1956). One wonders where Ozawa would place *Eowaeringella nevadensis* (Verville, Thompson and Lokke), which was described in the same paper with *E. alta.*

Ozawa (1967) also erected the subgenus *Pseudofusulinella* (*Kanmeraia*) to embrace the more elongate, fusiform species of the genus, and restricted the typical subgenus to the more inflated species with smaller form ratios. This practice is quite similar to that of Ross (1967) who recently divided the genus *Eoparafusulina* into two subgenera based upon similar reasoning. Such separations are of necessity arbitrary and difficult to support, inasmuch as all gradations are easily demonstrated from one group to another. The writer, therefore, rejects these subgeneric categories as taxonomically unrealistic.

In developing a phylogenetic history within *Pseudofusulinella* only those species have been considered which have been described from the McCloud Limestone (Skinner and Wilde, 1965b). The reason is threefold: (1) the present study is restricted to closely controlled sequences of rocks in which physical as well as faunal breaks might be noted; (2) only material immediately available to the writer has been used because assessment of characters is easier; and (3) consideration of important stratigraphic breaks is restricted here to Early Permian, whereas, some species of *Pseudofusulinella* are of Pennsylvanian age. In this respect, Ozawa's study is a very important contribution.

Species of *Pseudofusulinella* from the McCloud Limestone fall rather logically into four important groups based upon morphological characters (Plate 1). The main characters considered here are length, width, form ratio, tunnel angle, number of whorls, and nature of chomata deposits (Figures 2–7).

Two basic types of chomata deposits are seen in McCloud species of *Pseudofusulinella,* with variations from the two basic types being in degree rather than in kind. The majority of earlier species may be said to have *perched chomata* whereas the majority of the more advanced species may be referred to as having *massive chomata* (Figure 2).

Group I.—(Typical species: *P. meeki* Skinner and Wilde. Elongate-fusiform species with perched chomata). In Zone A of the McCloud Limestone this group includes the following in upward stratigraphic order (Plate 1): *P. prima, P. antiqua, P. meeki, P. ventricosa, P. harbaughi, P. fusiformis,* and *P. thompsoni.* One member of this group, *P. acuminata,* occurs in Zones B and C. Three members of the group *P. fragilis, P. simplex,* and *P. solida* range into Zone D. No species of Group I is known above Zone D, whose top, as mentioned earlier may mark an important stratigraphic break. This coincides with the fact that three new and unusual fusulinid genera, *Chalaroschwagerina, Eoparafusulina,* and *Cuniculinella* appear abruptly in Zone E above. It corresponds also to the base of the Permian sequence near Quinn River Crossing, Nevada.

Group II.—(Typical species: *P. delicata.* Small, rare, very slender-fusiform species with perched chomata). Species of Group II began during Zone A time, possibly developing out of a species such as *P. antiqua.* Two species, *P. delicata* and *P. proba* are known from Zone A. None are known from Zones B and C, but representatives reappeared in Zone D with two known

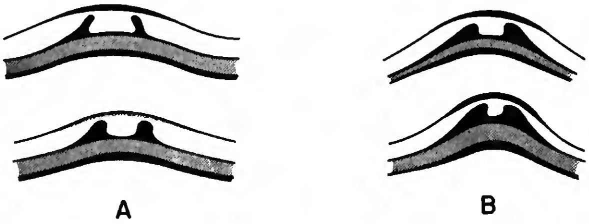


Figure 2.—Two basic types of chomata deposits discussed in this paper: a, perched chomata; b, massive chomata. Many variations and gradations exist.

species, *P. parvula* and *P. acuta*. Zone E has one known representative in *P. spicata*. The youngest known member of Group II, *P. aculeata*, occurs high in Zone F of the McCloud. While being small, *P. aculeata* displays a tendency to massive chomata, although their lateral margins are generally abrupt and blocky rather than sloping. This may well indicate evolution within this small group of species. Interestingly, species of Group II are not found higher than Zone F, whose top corresponds with a suggested major stratigraphic break. Similarly, three unusual fusulinid genera, *Eoparafusulina, Cuniculinella,* and *Klamathina* are not known to range higher than Zone F.

GROUP III.—(Typical species: *P. moorei*. Intermediate, thickly fusiform species with perched chomata). It is appropriate in more than one respect to refer to Group III as intermediate. They comprise species which are generally larger than those of Group II, but they are generally somewhat smaller than species of Group IV. And whereas they display thickly fusiform shapes as those of Group IV, they retain perched chomata and wider tunnels similar to the elongate-fusiform groups.

Pseudofusulinella wheeleri, of Zone A, the earliest species considered to belong to Group III, possibly stemmed off from the species, *P. ventricosa*, or one similar to it. In turn, *P. wheeleri* may have given rise not only to species of Group III but those of Group IV as well. *P. nitida* is the only other species in Zone A belonging to Group III. No species of this group has been found in Zones B, C, or D. But in Zone E there are two representatives, *P. occidentalis* (Thompson and Wheeler), and *P. moorei* that are considered to be typical of the group. The youngest members of Group III are found in Zone F; namely, *P. formosa, P. retusa,* and *P. obtusa*. Advanced characters within these three species are reminiscent of those considered earlier for the Zone F representative of Group II, *P. aculeata*. Indeed, *P. obtusa* is quite similar to *P. montis* (Thompson and Wheeler) in many respects. The latter species occurs in Zone F but belongs in Group IV, the most highly evolved group of all. It may well be that *P. obtusa* and *P. montis* are very closely related species. The fact remains, however, that no representatives of Group III are known above Zone F, whose top, it will be recalled, may represent a major stratigraphic break. This break corresponds with the base of the Coyote Butte Formation of east-central Oregon. In this regard, a point should be made about certain minute, undescribed *Pseudofusulinella* in the Coyote Butte. Those species have not been described to date, although a number of species seemingly are involved. Similar species have been noted also in Permian rocks of the Great Basin and Cordilleran Regions. This is a minute fauna suggestive of origins different from species of Groups II or III.

GROUP IV.—(Typical species: *P. pinguis*. Large, thickly fusiform species with massive chomata.) This last group includes the largest representatives of *Pseudofusulinella* thus far known. In contrast to all three of the preceding groups which have been discussed, species of Group IV have very massive chomata deposits, narrower tunnels, and more volutions on the average. They also constitute the longest ranging group, starting in Zone A (Early Wolfcampian) and ranging into Zone H (Early Leonardian). As a consequence, one can learn a great deal concerning phylogenetic tendencies in *Pseudofusulinella* from a study of the group, but very little concerning stratigraphic breaks. Only one example, which will be mentioned below, may offer evidence for such breaks in the section.

As has been mentioned, Group IV may have developed out of a species such as *P. wheeleri* in Zone A. The only representative of this group in Zone A is *P. splendens*. Representatives occurring in Zones B and C are *P. biconica* and *P. bellula*. Both are handsome representatives of the genus. *P. tumida*, the only representative of Group IV in Zone D is an enigma. It is the largest species of *Pseudofusulinella* known to the writer. It has most of the characteristics of the group, but its chomata deposits are intermediate between perched and massive. It is the only described form which logically might have given rise to younger members of the group, yet it is much larger than any of those that follow. This occurrence coincides with a previously suggested break at the top of Zone D and may be of little understood importance.

Group IV is represented in Zone E again by only one species, *P. solita*; however, Zone F contains four beautiful representatives of the group, *P. rotunda, P. dunbari, P. montis* (Thompson and Wheeler), and *P. optima*. A change is not obvious in the group from Zone F into Zone G, which contains five robust species, *P. pinguis, P. munda, P. venusta, P. decora,* and *P. pulchella*. And again, with no apparent morphological changes, two fine species are present in Zone H, *P. alta* and *P. sera,* the only Leonardian species of *Pseudofusulinella* yet to be described from the McCloud Limestone.

General Evolutionary Trends in Species of *Pseudofusulinella* from the McCloud Limestone

If one considers all forty described species of *Pseudofusulinella* in the McCloud Limestone as a whole, certain interesting evolutionary features become apparent. Some of these have been suggested above under the discussion of the four main groups. Naturally, specific exceptions are obvious throughout the section. Generally, however, through time, chomata deposits of species changed from less well-developed perched deposits to massive (Figure 2), and species developed more whorls (Figure 3), narrow tunnel angles (Figure 4), became shorter (Figure 5), and attained greater

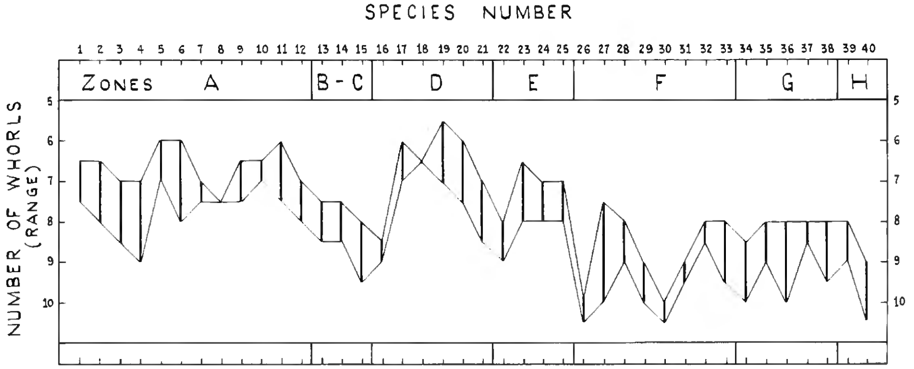


FIGURE 3.—Number of whorls in species of *Pseudofusulinella* from McCloud Limestone.

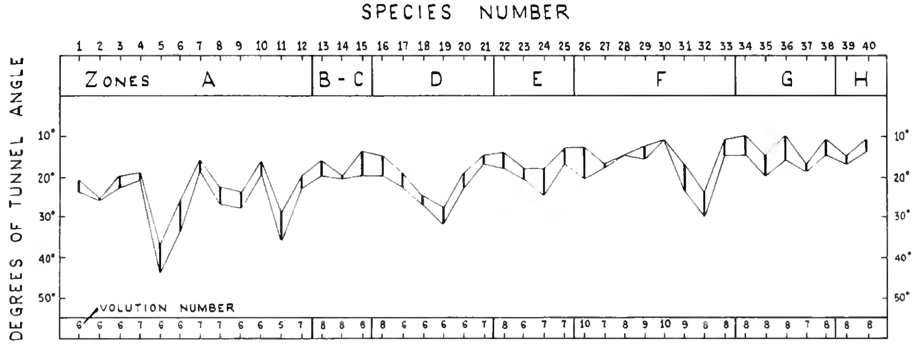


FIGURE 4.—Degrees of tunnel angle in species of *Pseudofusulinella* from McCloud Limestone.

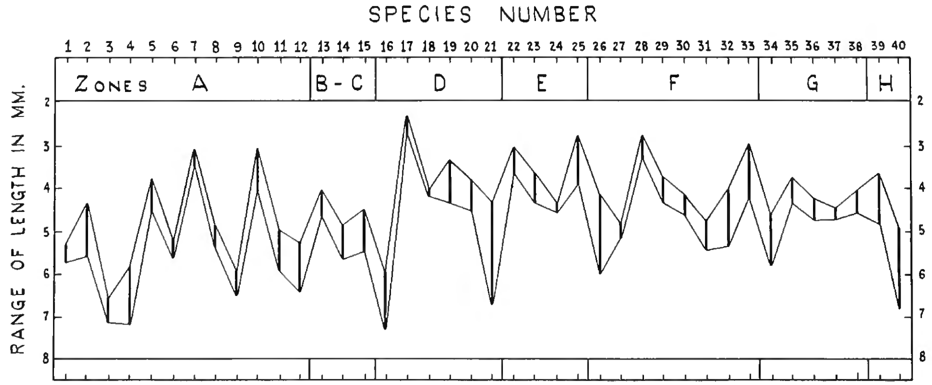


FIGURE 5:—Range of length in species of *Pseudofusulinella* from McCloud Limestone.

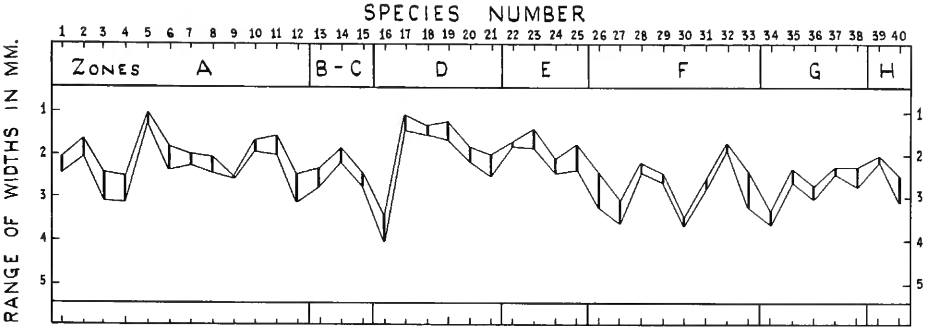


FIGURE 6.—Range of width in species of *Pseudofusulinella* from McCloud Limestone.

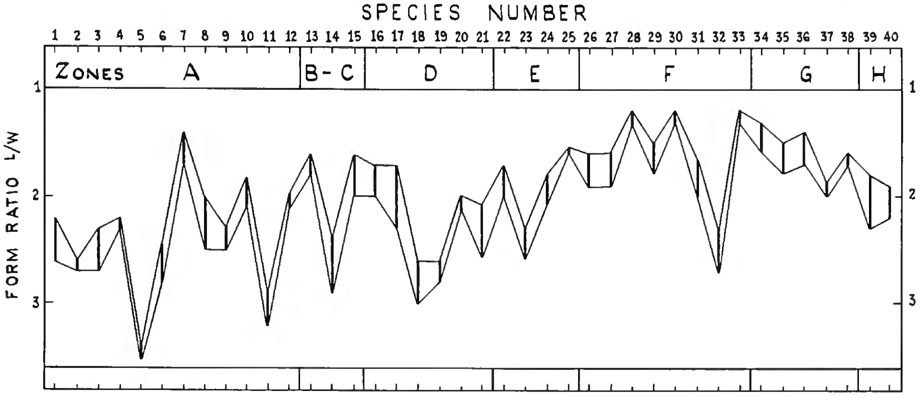


FIGURE 7.—Form ratio L/W in species of *Pseudofusulinella* from McCloud Limestone.

widths (Figure 6); consequently, form ratios became smaller (Figure 7).

Other measurable features have been plotted graphically, but they seem less meaningful; therefore, those plots are not included here. Generally, however, the spirotheca became thicker in time, with the one exception of *Pseudofusulinella tumida* in Zone D which has the thickest spirotheca of all species. The changes in proloculus diameter are interesting in that species which generally have the larger proloculi occur in Zone A and then again in Zones F, G and H. The smaller proloculi occur in the middle zones. Reasons for this are not clear unless it is related to the greater numbers of species in the lowest and highest zones coupled with the above-mentioned fact that species generally are larger higher in the section. Finally, there seemingly was a tendency for species to develop greater numbers of septa per whorl through time although this was not a consistent trend.

Phenetic Versus Phylogenetic Classification

The writer is well aware of the supposed controversy taking place today between so-called "classical taxonomists" and the numerical taxonomists. Cain and Harrison (1960) have defined a phenetic classification as an "arrangement by overall similarity, based on all available characters without any weighting." These authors contrast *phenetic* with *phyletic,* a classification supposedly designed to show the course of evolution with weighting of characters implied.

Actually, weighting is used by both the "classical" and the numerical taxonomist. The former selects, from experience, the most obviously meaningful characters available with which to tell his story. Weighting, then, takes place at the outset, but the characters chosen are usually given equal weighting. The numerical taxonomist selects a group of characters with which to work also, purely for practical reasons, because in the fast approaching day of the optical scanner selections must be made to cope with the infinite number of characters available. The numerical taxonomist also gives equal weighting to the characters chosen. The great value in his approach, however, lies in the fact that the characters receive a more exacting treatment, so that the subjective, or human element is very nearly eliminated.

It is absolutely impossible to define species among extinct fossil groups on the same basis as with living forms; that is, in the sense of interbreeding populations. Good approximations are possible, but that is all. Blackwelder (1964, p. 22) has pointed out that "one of the tasks of taxonomy is to identify specimens, and identification consists of determining the correct place of the specimen in the prior classification by means of its comparative attributes. A reproductive definition of a species would nearly always make identification impossible. . . Our entire taxonomic system is based on the assumption that species can be segregated and classified on the basis of the attributes of the individuals. No other basis for species *can* be mixed into that system, and all efforts so far have been futile."

Data presented in the present study are not intended to represent proof of phylogenetic relationships in *Pseudofusulinella.* After all is said, species, or phylogenetic schemes, are never sacred, they are man-made. *Homo sapiens* was determined by *Homo sapiens,* and this might be the strongest argument for separating ourselves from other, earlier humanoids! The best, still, that can be suggested is that a species is what a competent taxonomist decides to call a species.

The "phylogenetic" relationships shown in the present paper might just as easily be called "phenetic," but the important point for consideration is not what something is called, but what one does with the information.

Correlation of McCloud Events With Other Important Wolfcampian Sequences in the United States

Attempts to correlate breaks within the stratigraphic record should be accompanied always with a great deal of caution. It should be emphasized here that catastrophic diastrophism is not intended to explain the seemingly widespread nature of the stratigraphic breaks noted in the McCloud. Possibly none of the correlative events occurred at precisely the same time; and, in many areas, certain fusulinid species continued living much as they had before. But the end effect of major tectonic disturbances which, no doubt, occurred over a relatively short span of geologic time, left undeniable evidence in the sediments and the fossils.

Correlative Exposures in the Pacific Northwest

Exposures of Permian limestone containing fusulinid faunas identical with portions of the McCloud Limestone (Figure 1) have been reported by Skinner and Wilde (1966a) from near Quinn River Crossing in northwestern Nevada, the Coyote Butte Limestone of the Suplee area, east-central Oregon, (1966b) and from exposures near Kettle Falls and Republic, in northeastern Washington (1966c). Exposures near Quinn River Crossing correlate with Zones E, F, and G of the McCloud. Base of the Quinn River sequence corresponds roughly with a suggested stratigraphic break between Zones D and E in the McCloud, and its top seemingly corresponds to the Wolfcampian-Leonardian boundary of the McCloud section.

Exposures near Kettle Falls and Republic in northeastern Washington are actually large limestone pods or lenses within the Permian Mission Argillite; consequently, tops and bottoms may mean very little. The contained fusulinids indicate that these exposures correlate roughly with Zones F and G of the McCloud of northern California. The base of these exposures does not seem to correspond with any of the suggested major breaks of the McCloud sequence, but the top appears to be related to the Wolfcampian–Leonardian boundary.

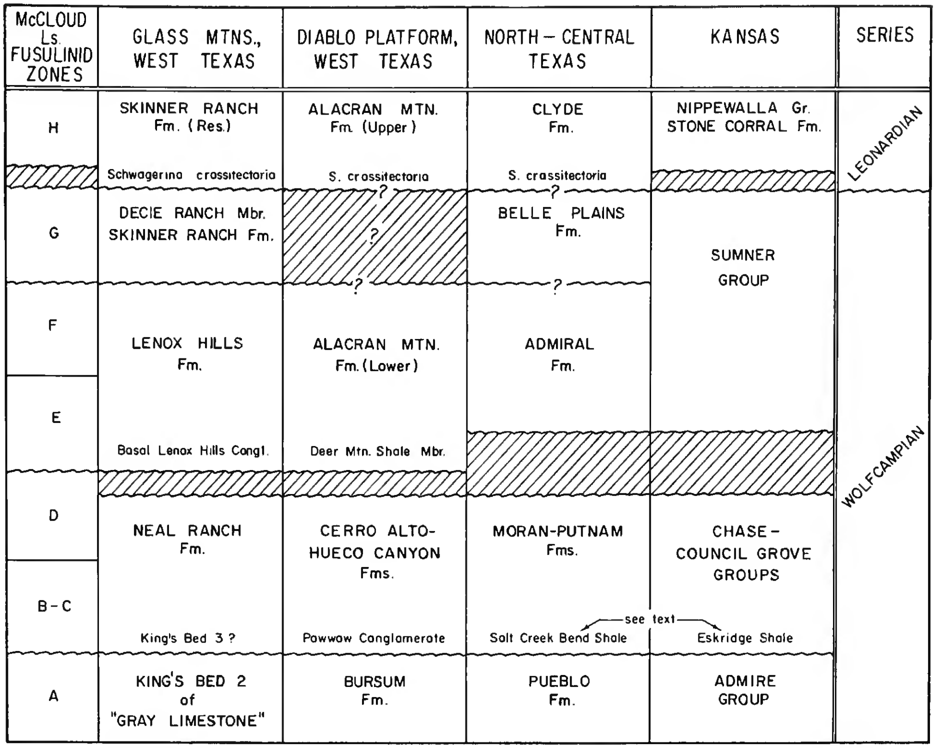
Exposures of the Coyote Butte Limestone of east-central Oregon contain fusulinids that correlate with Zone G of the McCloud. Thus, the base corresponds roughly with a major stratigraphic break between Zones F and G, and the top apparently is close to the Wolfcampian–Leonardian boundary.

Here, then, one sees some evidence of widespread stratigraphic and physical breaks in Early Permian strata over portions of the Pacific Northwest. Can such breaks be recognized in more remote regions where fusulinid faunas are quite different, especially at the specific level?

Glass Mountains, Texas

Because of the evidence that has been accumulated in recent years by Dunbar and Skinner (1937), Ross (1959, 1963), and Wilde (1962), rather precise age dating of the type Wolfcampian of the Glass Mountains of Texas is now possible. It is here also that important stratigraphic breaks have been determined.

Ross (1959, 1963) divided the Wolfcampian into a lower Neal Ranch Formation separated by unconformities at its base and top, and an upper Lenox Hills Formation, which he considered to lie also in unconformable relationship to the Leonardian rocks above (Figure 8).



McCLOUD Ls. FUSULINID ZONES	GLASS MTNS., WEST TEXAS	DIABLO PLATFORM, WEST TEXAS	NORTH-CENTRAL TEXAS	KANSAS	SERIES
H	SKINNER RANCH Fm. (Res.) Schwagerina crassitectoria	ALACRAN MTN. Fm. (Upper) S. crassitectoria	CLYDE Fm. S. crassitectoria	NIPPEWALLA Gr. STONE CORRAL Fm.	LEONARDIAN
G	DECIE RANCH Mbr. SKINNER RANCH Fm.	?	? BELLE PLAINS Fm. ?	SUMNER GROUP	WOLFCAMPIAN
F	LENOX HILLS Fm.	ALACRAN MTN. Fm. (Lower)	ADMIRAL Fm.		
E	Basal Lenox Hills Congl.	Deer Mtn. Shale Mbr.			
D	NEAL RANCH Fm.	CERRO ALTO-HUECO CANYON Fms.	MORAN-PUTNAM Fms.	CHASE-COUNCIL GROVE GROUPS	
B-C	King's Bed 3 ?	Powwow Conglomerate	Salt Creek Bend Shale see text	Eskridge Shale	
A	KING'S BED 2 of "GRAY LIMESTONE"	BURSUM Fm.	PUEBLO Fm.	ADMIRE GROUP	

FIGURE 8.—Correlation of McCloud fusulinid zones with other lower Permian sequences.

In recognizing these breaks, Ross placed Bed 2 of the "Gray Limestone" of King (1930) in the underlying Gaptank Formation of Pennsylvanian age, although he recognized an unconformity also at the base of the "Gray Limestone." The writer has observed these same unconformable relationships; but because of the presence of Wolfcampian species of *Triticites* and *Schwagerina* in Bed 2, a Wolfcampian age assignment for the unit seems most logical. Apparently Ross had none of these in his collections.

Bed 2 of the "Gray Limestone" is considered at present to correlate with some portion of Zone A of the McCloud Limestone. It is of interest to note that undescribed species of *Pseudofusulinella* have been found in the "*Uddenites* zone" of the underlying Gaptank Formation at Wolf Camp, but none have been found in Bed 2 of the overlying "Gray Limestone." The "*Uddenites* zone" is of Pennsylvanian (Virgilian) age; and species of *Pseudofusulinella* are known in the Great Basin Region of the western United States in beds of the same age.

The Neal Ranch Formation correlates roughly with Zones B, C, and D of the McCloud sequence. Interesting similarities and differences may be noted among the fusulinids of the two sequences. In the McCloud sequence, *Triticites* is not known above Zone A, but species of the genus are present in the Neal Ranch of the Glass Mountains. Similarly, *Pseudofusulinella* is abundant in McCloud Zones B, C, and D, but it has not been found in the Neal Ranch. In fact, *Pseudofusulinella* has not been found above the "*Uddenites* zone" of the Gaptank Formation in the Glass Mountains. Genera in common, however, are numerous. Species of *Schwagerina, Pseudofusulina, Paraschwagerina, Pseudoschwagerina,* and *Schubertella* occur in both, and a number of similar species may be noted in Table 1.

Correlation of the Lenox Hills Formation with Zones E and F of the McCloud Limestone is also judged to be quite acceptable, although certain local problems arise which need further explanation. The Lenox Hills Formation was referred to as constituting the "assemblage-zone of *Monodiexodina linearis*" by Wilde (1962) because of the widespread occurrence of the species in rocks of an equivalent age elsewhere as well as its dominance in the Lenox Hills of the Glass Mountains.

TABLE 1.—*Similar species in Neal Ranch Formation and McCloud Zones B, C, D.*

Neal Ranch Formation	*McCloud Zones B, C, D*
Paraschwagerina gigantea Dunbar and Skinner	*Paraschwagerina magna* Skinner and Wilde
Pseudoschwagerina uddeni Dunbar and Skinner	*Pseudoschwagerina californica* Skinner and Wilde
Pseudofusulina huecoensis Dunbar and Skinner	*Pseudofusulina soluta* Skinner and Wilde
Schwagerina pugunculus Ross	*Schwagerina acuminata* Skinner and Wilde

Monodiexodina has not been discovered in the McCloud Limestone, but a very closely related genus, *Eoparafusulina,* is represented by twenty species, and these species occur only in Zones E and F. Zone E concontains five species and Zone F contains fifteen species.[1]

The main zone fossils of the Lenox Hills Formation, other than *Monodiexodina linearis* (Dunbar and Skinner), are *Pseudoschwagerina gerontica* Dunbar and Skinner, *Pseudoschwagerina convexa* Thompson, *Schwagerina laxissima* Dunbar and Skinner, *Schwagerina diversiformis* Dunbar and Skinner, and *Schwagerina nelsoni* Dunbar and Skinner. The latter species more rightly belongs in the genus *Chalaroschwagerina* Skinner and Wilde, and is here so placed.

Schubertella kingi Dunbar and Skinner ranges throughout the Wolfcampian of the Glass Mountains and, therefore, is not confined to the Lenox Hills Formation. It occurs however, only in Zone E of the McCloud of California. As mentioned previously, *Triticites* does not occur higher than Zone A of the McCloud sequence. Numerous abraded specimens of *Triticites* have been found in Lenox Hills strata, but in all known instances the specimens appear to have been reworked from Neal Ranch and older beds.

By reference to some of the fusulinids listed above, comparisons are shown for correlation purposes in Table 2.

The question arises logically as to whether Zone G of the McCloud Limestone, the highest Wolfcampian of the sequence, has an equivalent counterpart in the Glass Mountains. Admittedly, the correlation might be considered rather hazardous, but it is suggested that the Decie Ranch Member of the Skinner Ranch Formation (Cooper and Grant, 1964) correlates with at least a portion of Zone G of the McCloud Limestone. Wilde (1962) considered the sequence now known as the Decie Ranch Member at Dugout Mountain in the western Glass Mountains to belong in the Wolfcampian rather than the Leonardian.

The Decie Ranch Member is dominated by the following species of fusulinids: *Schwagerina hessensis* Dunbar and Skinner, *Schwagerina hawkinsi* Dunbar and Skinner, and *Schwagerina dugoutensis* Ross. The latter is quite similar to *Schwagerina amoena* Skinner and Wilde and *Schwagerina eximia* Skinner and Wilde of the McCloud. *Schwagerina hawkinsi* is a transitional species between *Schwagerina* and *Chalaroschwagerina* and it compares favorably with *Schwagerina corpulenta* Skinner and Wilde as well as *Chalaroschwagerina tumentis* Skinner and Wilde both of which occur in Zone G of the McCloud.

Monodiexodina linearis (Dunbar and Skinner) has been cited also as occurring in the Decie Ranch Member, as well as higher in the Leonard (Ross, 1962). The writer has made similar observations, although reworking and faulting leave doubts about some occurrences. One would not expect the highest collection reported by Ross to be indicative of an indigenous occurrence, but presence of the species at a number of localities in the Decie Ranch Member only strengthens the argument that this member is of Wolfcampian age.

Diablo Platform, Texas

For purposes of discussion, Diablo Platform is used here to refer to the area of the Sierra Diablo, Hueco, and Franklin Mountains of western Texas. Thompson (1954) and Williams (1963) have discussed the Wolfcampian stratigraphy of the Hueco Mountains and they have described the fusulinid faunas. Wilde (1962) discussed the Permian stratigraphy of the Sierra Diablo and suggested correlations with the Glass Mountains

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[1] The species described recently by Ross (1967) as *Eoparafusulina allisonensis* Ross from the Neal Ranch Formation near Gaptank, eastern Glass Mountains, does not belong in that genus, but in *Alaskanella* Skinner and Wilde, which Ross considered a synonym of *Eoparafusulina.*

TABLE 2.—*Similar species in Lenox Hills Formation and McCloud Zones E and F.*

Lenox Hills Formation	*McCloud Zones E and F*
Monodiexodina linearis (Dunbar and Skinner)	*Eoparafusulina thompsoni* Skinner and Wilde
Pseudoschwagerina gerontica Dunbar and Skinner	*Pseudoschwagerina robusta* (Meek)
Chalaroschwagerina nelsoni (Dunbar and Skinner)	*Chalaroschwagerina obesa* Skinner and Wilde

sequence on the basis of fusulinid assemblage zones. Stewart (1963) described some of the fusulinids in the Sierra Diablo section. Dunbar and Skinner (1937) described fusulinids from the Sierra Diablo, Hueco, and Franklin Mountains; and Williams (1966) recently discussed the stratigraphy and described fusulinids from the Franklin Mountains Wolfcampian section.

The oldest Permian rocks of the Diablo Platform are exposed in the Hueco Mountains and have been referred to the Bursum Formation, described originally by Wilpolt, McAlpin, Bates, and Vorbe (1946) from exposures in the Hansonburg Hills, Socorro County, New Mexico. At the type locality the Bursum represents a zone of transition between dominantly marine Pennsylvanian strata and predominantly continental redbeds of Permian age (Bachman, 1968). Beds occupying this same faunal and similar lithologic transitional position between the Pennsylvanian and Permian of other areas in New Mexico have been given local formation names. For example, Otte (1959) gave the name Laborcita Formation to such beds in the northern Sacramento Mountains; and Stark and Dapples (1946) introduced the name Aqua Torres Formation for a similar unit in the Los Pinos Mountains.

Thompson (1954) reported a number of species from the Bursum at several localities in New Mexico. From Abo Canyon he cited *Triticities* (*Leptotriticites*) *eoextentus* (Thompson), *Triticities creekensis* Thompson, *Schwagerina pinosensis* Thompson, and *Schwagerina grandensis* Thompson[?]. All but *S. pinosensis* were reported from the Oscura Mountains. From the Robledo Mountains, Thompson also reported *Pseudofusulina robleda* Thompson, *Leptotriticities* aff. *glenensis* (Thompson), and *L. hughesensis* (Thompson).

In the Hueco Mountains, the Bursum beds contain *Triticities cellamagnus* Thompson and Bissell and *Schwagerina grandensis* Thompson[?] (Thompson, 1954, Williams 1963). From the Laborcita Formation of the Sacramento Mountains, Steiner and Williams (1968) have recently identified *Triticites creekensis* Thompson, *T. ventricosus* (Meek and Hayden), *T.* (*Leptotriticites*) *americanus* (Thompson), *Schwagerina campensis* Thompson, and *Schwagerina emaciata* (Beede). All of these species are widespread in Early Wolfcampian rocks from many areas of the United States.

Already mentioned is the fact that *Pseudofusulinella* is not known in Permian strata of the southwestern and mid-continental United States. *Leptotriticites* Skinner and Wilde (1965a), fulfills a role in the Permian of these mentioned regions similar to that of *Pseudofusulinella* in the western provinces; that is, the two apparently occur exclusive of each other throughout the Wolfcampian in their respective areas.

Species of *Triticites* in the Bursum equivalents are well-developed members of the genus, but they have not attained the evolutionary development of some of the species of Zone A of the McCloud Limestone, which, as mentioned earlier, exhibit features transitional between *Triticites* and *Schwagerina.* Simple species of *Schwagerina* do occur in Bursum equivalents, so that the conclusion seems justified that Bursum beds and Zone A of the McCloud are at least approximately equivalent.

Williams (1963) has given formational status to the Lower, Middle and Upper divisions of the Hueco Limestone of the Hueco Mountains, recognized originally as mappable units by King, King, and Knight (1945). In ascending order these are the Hueco Canyon, Cerro Alto, and Alacran Mountain Formations. In the same paper, Williams described the fusulinid faunas of the Hueco Group. Later Williams (1966) recognized the same threefold separation of the Hueco Group in the Franklin Mountains and described the fusulinids.

The lowest of the three formations in the Hueco Mountains, Hueco Canyon, is separated from the Bursum beds by an unconformity. This surface of unconformity is marked by the Powwow Member of the

Hueco Canyon Formation, a basal conglomerate and red-bed sequence. The Powwow is widespread at the surface on the Diablo Platform, and is recognized in the subsurface, especially over major regional highs such as the Central Basin Platform, which separates the Midland and Delaware basins. By its very nature, the Powwow Member varies a great deal in thickness, lithology, and stratigraphic relationship to underlying Bursum equivalents (Thompson, 1954). In the vicinity of the Hueco Mountains, the Powwow surface of unconformity truncates older and older beds from north to south. Williams (1963) reports the presence of beds containing a *Pseudoschwagerina* fauna beneath the uncomformity at one locality in the Hueco Mountains. In the Sierra Diablo the Powwow at the base of the Hueco Group is about the same age as the basal Lenox Hills conglomerate in the Glass Mountains (Wilde, 1962). This fact prompted Wilde to suggest an approximate time equivalency for the two clastic units, while at the same time recognizing differences in age from place to place. On the accompanying correlation chart (Figure 8), the time-transgressive character of the Powwow is not indicated, but the Powwow is shown in the correct position of its type section in Powwow Canyon, Hueco Mountains.

Fusulinids from the Powwow Member were described first by Dunbar and Skinner (1937), and more recently by Williams (1963). Williams identified *Schwagerina emaciata* (Beede), *Schwagerina bellula* Dunbar and Skinner, and *Triticites powwowensis* Dunbar and Skinner. The latter is considered a primitive species of *Schwagerina* by the writer, and is not greatly different from transitional forms that occur in lower, McCloud beds in California. It occurs also in Bed 8 (King, 1930) of the type section of the Neal Ranch Formation in the Glass Mountains.

At least four other well-known species of fusulinids occur in the Hueco Canyon Formation which also occur in the Neal Ranch Formation of the Glass Mountains. These are *Pseudoschwagerina uddeni* (Beede and Kniker), *P. beedei* Dunbar and Skinner, *P. texana* Dunbar and Skinner, and *Pseudofusulina huecoensis* (Dunbar and Skinner). Correlation of the Neal Ranch fauna with Zones B, C, and D of the McCloud has already been discussed.

Further evidence for correlation of the Hueco Canyon Formation with the above-mentioned zones of the McCloud is shown in Table 3.

In the present paper the overlying Cerro Alto Limestone of the Hueco Mountains is correlated also with some portion of McCloud Zones B, C, and D. It is recognized, however, that there are difficulties in making such a correlation. Only two species of fusulinids, *Schwagerina eolata* Thompson, and *S. neolata* Thompson, occur in the Cerro Alto, and direct comparisons cannot be made with accuracy to other described species. On the other hand, the Cerro Alto is separated from most of the overlying Alacran Mountain Formation by a prominent series of red beds, the Deer Mountain Member of the Alacran Mountain. Intrusion of this lithic unit across older beds of normal marine deposition denotes a major regression. Above the Deer Mountain Member the Alacran Mountain contains a fine Lenox Hills fusulinid fauna. It seems obvious, therefore, that the Deer Mountain marks the stratigraphic break between the Neal Ranch and Lenox Hills formations of the Glass Mountains, and, in turn, between Zones D and E of the McCloud Limestone of northern California. Species very similar to, if not identical with *Schwagerina neolata* and *S. colata* occur in King's (1930) Beds 8 and 15, respectively, in the type Neal Ranch Formation of the Glass Mountains.

All of the main zone species of the Lenox Hills except *Monodiexodina linearis* (Dunbar and Skinner) occur in the Alacran Mountain; *Pseudoschwagerina gerontica* Dunbar and Skinner, *P. convexa* Thompson, *Chalaroschwagerina nelsoni* (Dunbar and Skinner), and *Schwagerina diversiformis* Dunbar and Skinner.

It has been stated earlier that the formations described in the Hueco Mountains have been recognized also in the Franklin Mountains (Williams, 1966). The fusulinid faunas are also the same. Similarly, the fusulinid faunas are known in the Sierra Diablo

TABLE 3.—*Similar species in Hueco Canyon Formation and McCloud Zones B, C, D.*

Hueco Canyon Formation	McCloud Zones B, C, and D
Schwagerina bellula Dunbar and Skinner	*Schwagerina pseudoprinceps* Skinner and Wilde
Schwagerina knighti Dunbar and Skinner	*Schwagerina pseudoprinceps* Skinner and Wilde
Paraschwagerina shuleri Williams	*Paraschwagerina fairbanksi* Skinner and Wilde

(Wilde, 1962), but the formational units have not been separated. It is probable, however, that only Alacran Mountain equivalents are present in the Sierra Diablo.

North-Central Texas

Many attempts to correlate rock units of the north-central Texas Wolfcampian with those of other areas have generally proved to be unsatisfactory insofar as fusulinid faunas are concerned. The conclusions presented here, for example, are at variance with those of Ross (1963, p. 43), his work being about the most recent to deal with the problem.

As regards the Bursum equivalents in north-central Texas sequence, the writer generally agrees with Ross that the Pueblo Formation is approximately coeval. The presence of *Triticites creekensis* Thompson, *T. ventricosus* (Meek and Hayden), and *Schwagerina campensis* Thompson, in the Pueblo Formation, along with numerous species of *Leptotriticites,* is reminiscent of the Laborcita fauna (Williams, 1966) mentioned previously.

Top of the Pueblo Formation as defined does not seem to be the most logical place to draw the boundary between Bursum and McCloud Zone A events on a purely lithologic basis. A prominent sandstone overlain by an equally prominent red-shale sequence some 25 to 50 feet below the top may mark this boundary. These beds comprise the upper half of the Salt Creek Bend Shale Member. Comparison of the Pueblo fauna and that of Zone A is difficult. It is true, however, that both contain a dominant *Triticites* fauna. Moreover, the few species of *Schwagerina* in the Pueblo Formation are quite simple and not highly developed.

Ross (1963) believed that the Neal Ranch was represented in north-central Texas by a hiatus. This is difficult to reconcile with the fusulinid evidence. The Gouldbusk Limestone Member of the Moran Formation contains *Pseudoschwagerina texana* Dunbar and Skinner, *Schwagerina complexa* Thompson, *Pseudofusulina*[?] *moranensis* Thompson,[2] and other undescribed species. The two first-named species are common to abundant in King's beds 13 to 15 of the type Neal Ranch in the Glass Mountains, and *Pseudoschwagerina texana* occurs in the Hueco Canyon Formation of the Hueco Mountains.

The Putnam Formation, which overlies the Moran Formation in the north-central Texas sequence contains few species of fusulinids. In the top of the Putnam, however, the Coleman Junction Limestone Member contains *Schwagerina colemani* Thompson, a species comparable in development to *Schwagerina emaciata* (Beede).

Fusulinids have not been reported from the Admiral Formation of the north-central Texas section. Recently Myers (1968) described *Schwagerina crassitectoria* Dunbar and Skinner and *S. guembeli* Dunbar and Skinner from the Leonardian Clyde Formation, which is separated from the Admiral by the Belle Plains Formation. Because the *Schwagerina crassitectoria* fauna marks an important zone near the base of the Leonardian over a wide area (Figure 8), it seems entirely possible that the Admiral is equivalent to Zones E and F of the McCloud (Lenox Hills, Alacran Mountain); and that the Belle Plains occupies the position of McCloud Zone G (Decie Ranch). This view is similar to that of Roth (in Dunbar et al., 1960, p. 1788) who believes that the Wolfcampian–Leonardian boundary falls within the Belle Plains Formation rather than at its base.

Kansas Section

Very little difference exists between the eastern Kansas Wolfcampian and that of north-central Texas. Identical species of fusulinids occur throughout, and the cyclic sedimentational pattern is similar.

Moore (1936) placed the boundary between the Pennsylvanian and Permian of Kansas just above the

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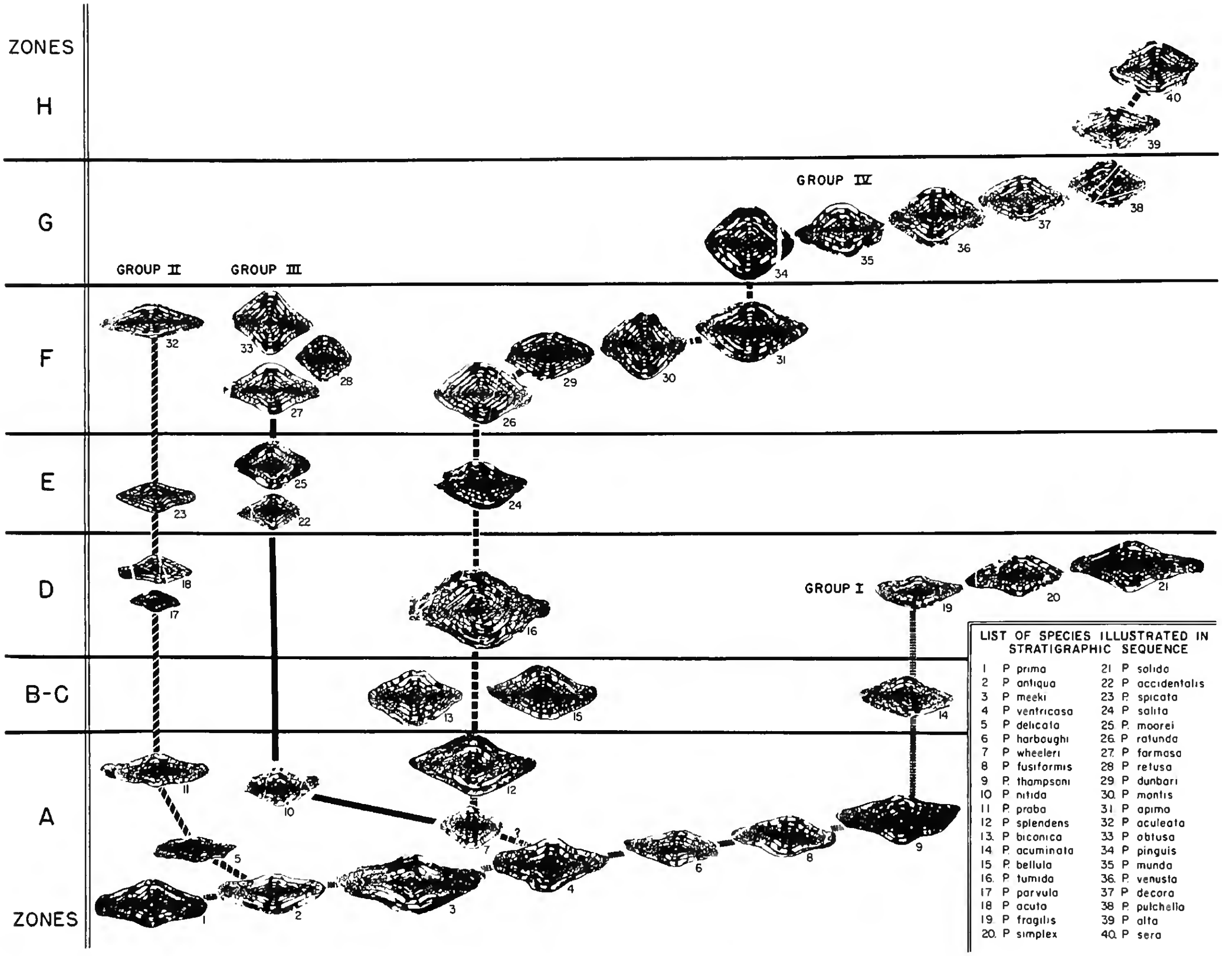
[2] A number of species referred to *Pseudofusulina* Dunbar and Skinner by Thompson (1954) obviously do not belong to that genus. Skinner and Wilde (1965b, 1966d) have offered conclusive evidence that *Pseudofusulina* sensu stricto has a rugose spirotheca, and is a senior synonym of *Rugosofusulina* Rauser. The species described by Thompson (1954) as *Pseudofusulina* possess certain unique characters which place them between typical *Schwagerina* Moeller and *Pseudoschwagerina* Dunbar and Skinner. Low, rounded septal folds, tightly coiled juvenaria followed by some inflation of outer whorls, and chomata in the two inner volutions are similar to *Pseudoschwagerina texana* Dunbar and Skinner. Lack of well-defined inflation and thickness of spirotheca are more like *Schwagerina.* Such forms are hereby assigned a new generic name, *Stewartina,* in honor of Wendell J. Stewart of Midland, Texas. Type species is chosen as *Pseudofusulina*[?] *moranensis* Thompson, 1954 (p. 69, pl. 39: figs. 1–7; pl. 40: figs. 1–9). Other species assigned here to the new genus, *Stewartina,* are *Pseudofusulina loringi* Thompson (1954) *Pseudofusulina robleda* Thompson (1954), *Schwagerina laxissima* Dunbar and Skinner (1937).



LIST OF SPECIES ILLUSTRATED IN STRATIGRAPHIC SEQUENCE

1	P prima	21	P solida
2	P antiqua	22	P occidentalis
3	P meeki	23	P. spicata
4	P ventricosa	24	P salita
5	P delicata	25	P. moorei
6	P harbaughi	26.	P rotunda
7	P wheeleri	27.	P formosa
8	P fusiformis	28	P retusa
9	P. thompsoni	29	P dunbari
10	P nitida	30.	P montis
11	P. proba	31	P opima
12	P splendens	32	P aculeata
13.	P biconica	33	P obtusa
14	P. acuminata	34	P pinguis
15	P. bellula	35	P munda
16.	P. tumida	36.	P. venusta
17	P parvula	37	P decora
18	P acuta	38	P. pulchella
19.	P fragilis	39	P alta
20.	P simplex	40.	P sera

PLATE 1.—Conjectured evolutionary trends in species of *Pseudofusulinella* in McCloud Limestone, Northern California. Group I: elongate-fusiform species with perched chomata; range, Zones A–D. Group II: small, rare, very slender-fusiform species with perched chomata; range, Zones A–F. Group III: intermediate, thickly fusiform species with perched chomata; range, Zones A–F. Group IV: large, thickly fusiform species with massive chomata; range, Zones A–H. Species number 22, *P. occidentalis,* and number 30, *P. montis,* were described by Thompson, Wheeler, and Hazard (1946); all others shown here were described by Skinner and Wilde (1965).

Brownville Limestone. The choice was somewhat arbitrary inasmuch as channel sandstones mark disconformities above and below the Brownville. Recently, however, Douglass (1962) has described *Triticites* (*Leptotriticites*) *brownvillensis* (Douglass) from the Brownville. Accumulated evidence (Skinner and Wilde, 1965) indicates that *Leptotriticites* is apparently restricted to the Wolfcampian. It, therefore, seems best that the boundary be drawn below the Brownville. A somewhat similar situation exists in the Texas sequence. The Belknap Limestone of the Brazos River section, heretofore considered to be of Pennsylvanian age, contains *Leptotriticites extentus* (Thompson) and *L. eoextentus* (Thompson) and *Schubertella kingi* Dunbar and Skinner (Kauffman and Roth, 1966). This fauna is also present in the "Waldrip No. 1" of the Colorado River section. The Belknap and "Waldrip No. 1" are judged to be equivalent, and Wolfcampian rather than Pennsylvanian in age.

Strictly on the basis of fusulinid occurrences one is rather moved to carry the top of McCloud Zone A events in the Kansas section to the base of the Eskridge shale in the middle of the Council Grove Group. This has the immediate advantage of correlating their containing beds with widely occurring species of fusulinids. *Leptotriticites americanus* (Thompson) occurs in the Americus Limestone Member of the Foraker Limestone (Council Grove Group) of Kansas, and in the Laborcita Formation of New Mexico. *Leptotriticites eoextentus* (Thompson) occurs in the Americus, the Bursum Formation of New Mexico, and in "Waldrip No. 1" of the Pueblo Formation of Texas. *Leptotriticites hughesensis* (Thompson) is found in the Hughes Creek Shale Member of the Foraker of Kansas and in the Bursum Formation of New Mexico. *Triticites meeki* (Moeller) occurs in the Foraker of Kansas and Pueblo Formation of Texas. *Triticites ventricosus* (Meek and Hayden) occurs in the Laborcita of New Mexico, Foraker of Kansas, and Pueblo of Texas. *Triticites creekensis* (Thompson) is found in the Laborcita and Bursum of New Mexico, and the Pueblo of Texas. *Schwagerina longissimoidea* (Beede) occurs in the lower half of the Council Grove of Kansas and the Pueblo of Texas. All of the above mentioned have been found in other localities, but only those which relate to the present discussion are given here.

One of the immediate disadvantages in correlating McCloud Zone A with beds in Kansas all the way to the base of the Eskridge shale is that *Paraschwagerina kansasensis* (Beede and Kniker) occurs in the Neva Limestone just beneath the Eskridge. Occurring with *P. kansasensis* are three advanced species of *Leptotriticites* and *Schwagerina longissimoidea* (Beade). *P. kansasensis* occurs in King's Beds 4 and 5 of the type section of the Neal Ranch Formation of the Glass Mountains, Texas. Bed 4 of King's Section 24 at Wolfcamp (King, 1930, p. 55) lies only eight feet above the "Lower Gray Limestone," or Bed 2. So the correlation proposed here is probably not too far out of line with the true facts of the matter. Greater precision than this would not be expected on such a regional scale.

Remainder of the Council Grove and overlying Chase Group in the Kansas sequence correlates easily with the north-central Texas Moran and Putnam formations, and by inference, with Zones B, C, and D of the McCloud of California. In fact, there seems to be a very close correlation between the Florence Limestone of Kansas and Gouldbusk of Texas. Both units contain *Pseudoschwagerina texana* Dunbar and Skinner and *Stewartina moranensis* (Thompson).

McCloud Zones E, F (Lenox Hills), and G (Decie Ranch) apparently are missing from the Kansas section, although faunal evidence is lacking, so that it is difficult to be certain. It is possible that practically all of the overlying Sumner Group, now considered to be of Leonardian age, is actually Late Wolfcampian. Merriam (1963) reports a well-recognizable unconformity at the base of the Stone Corral Formation, the top unit of the Sumner Group. This unconformity could actually represent the Wolfcampian-Leonardian boundary. If most of the Sumner Group actually is Wolfcampian rather than Leonardian in age, this would have important implications for correlation of many Early Permian sequences throughout the mid-continent and eastern Rocky Mountain regions.

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Index to Genera and Species

(New taxa and principal entries in italics)

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