

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 148, NUMBER 2

Charles D. and Mary Vaux Walcott
Research Fund

THE BRACHIOPOD SUPERFAMILY
STENOSCISMATACEA

By
RICHARD E. GRANT
United States Geological Survey



(PUBLICATION 4569)

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CITY OF WASHINGTON
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Charles D. and Mary Haux Walcott Research Fund

THE BRACHIOPOD SUPERFAMILY
STENOSCISMATACEA¹

BY RICHARD E. GRANT

Geologist, United States Geological Survey

INTRODUCTION

THE Stenoscismatacea constitute a long-ranging and remarkably conservative group of Paleozoic rhynchonelloid brachiopods. Internal structures of the earliest known species in the Middle Devonian differ only slightly from those of species that lived near the end of the phyletic line in the Late Permian. External features underwent moderate, but significant, changes during the history of the group; they provide the basis for its differentiation into 2 families, 4 subfamilies, 11 genera, and more than 200 species.

The superfamily is unified by the presence of a spondylium duplex formed by fusion of the dental plates in the pedicle valve and by a high, spoon-shaped camarophorium in the brachial valve. These two structures differ in detail within the superfamily, but their fundamental form and construction remain nearly unchanged throughout the group.

Families within the Stenoscismatacea are distinguished by presence or absence of a peculiar external marginal fringe that extends from parts of one or both valves. This fringe, here called the stolidium, is absent from genera of the family Atriboniidae n. fam. The stolidium is heralded in earliest genera of that family by slight protrusion of the valve edges in some species, but is not unequivocally present in species earlier than Mississippian members of the family Stenoscismatidae Oehlert (1887). Species in the Stenoscismatidae that occur near the phyletic bifurcation of the two families have the stolidium sporadically present and erratically developed. It becomes an increasingly consistent feature of adult shells through the development of the Stenoscismatinae, and no species of *Stenoscisma*, the culminating Permian genus, lacks a stolidium.

Most genera of the Atriboniidae have no trace of a stolidium, not even the slight protuberance of the valve edges seen in some species of

¹ Publication authorized by the Director, United States Geological Survey.

Devonian *Atribonium* n. gen. In this family the valves meet directly at the anterior and butt against one another, as in most genera of the Rhynchonelloidea.

The general form of stenoscismatacean species is rhynchonelloid, with the typically sharp beak and a foramen that occupies a delthyrium normally constricted by deltidial plates. Internally the relationships are somewhat less obvious, but the spondylium in the pedicle valve generally is conceded to be formed by fusion of rhynchonelloid dental plates (*e.g.*, Kozłowski, 1929), and the crura appear rhynchonelloid. The camarophorium is peculiar to the Stenoscismatacea, but serial sections show clearly that it forms by separation of the ventral edges of the two plates of a septum duplex, which, along with its beginning as an apical swelling of the septum, argues for its development from that septum. The camarophorium is a modification of a normal rhynchonelloid median septum.

The hinge plate is rather conservative in its development through the Stenoscismatacea. Silicified specimens from the Permian of Texas have a finely fimbriate cardinal process, or apical boss, probably for reception of diductor muscles. Serial sections of Devonian and Mississippian specimens also show the fine fimbriation, although less clearly.

The form of the lophophores that extended beyond the calcareous crural processes in the Stenoscismatacea is not known. They may have been helicoid, as in Recent rhynchonelloid genera, but no morphological evidence from the fossils supports this conjecture. The form of the calcareous crura is similar to that of normal rhynchonelloid genera, only longer and more slender, reinforcing evidence from the spondylium and camarophorium that the Stenoscismatacea belong with the Rhynchonelloidea.

Earlier authors believed that the stenoscismataceans are derived from the Pentameroidea (*e.g.*, Weller, 1914), but Kozłowski (1914 and 1929) cited cogent reasons for placing them in the Rhynchonelloidea. Subsequent authors have concurred because similarities between stenoscismatacean and normally rhynchonelloid dental plates, median septum, hinge plate, crural processes, cardinal process, beak form, delthyrium, foramen, and deltidial plates indicate close relationship. Structures in the Pentameroidea that resemble those of the Stenoscismatacea are in opposite valves, and upon close inspection bear little resemblance to them. Furthermore, external profile, manner of valve junction, and especially absence of deltidial plates in the Pentameroidea show lack of relationship with the Stenoscismatacea.

TYPE GENUS

The superfamily is founded upon the genus *Stenoscisma* Conrad (1839), senior objective synonym of *Camerophoria* King (1844,

1846), which in turn is senior synonym of *Camarophoria* King (1850). The type species is *Terebratula schlotheimi* von Buch (1835) from the Middle Zechstein at Pösssneck, Thuringia, (East) Germany. This species is well documented, and specimens of it are distributed widely in museums. However, because it is a highly variable species, differentiation among species of *Stenosisma* and among genera in the Stenosismatacea is somewhat difficult. Although costation seems to be a significant generic character among Devonian and Mississippian members of the superfamily, the single species *S. schlotheimi* has both strongly costate and nearly smooth individuals. Outline also is important in earlier groups, but *S. schlotheimi* ranges from narrowly subpentagonal to widely subelliptical. Consistent features of the type species are its high fold, adult stolidium, long spondylium and camarophorium, and overlapping posterolateral valve edges. These characters tie it to other species of *Stenosisma* and differentiate it from other genera of the superfamily.

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EXTERNAL MORPHOLOGY

SIZE

Evolution.—Genera in the Stenoscismatacea undergo progressive but irregular increase in size from the Devonian through the Permian. The Devonian genus *Atribonium* is small, and none of its species is as large as the smallest species of *Stenoscisma*. However, most species of *Atribonium* are at least as large as, and many are larger than, the Pennsylvanian species *Coledium bowsheri* (Cooper). The smooth Pennsylvanian genus *Psilocamara* Cooper is smaller than the smooth (but sulcate) Permian *Camarophorina* Licharev. The trend toward increase in size among the Stenoscismatacea, therefore, is definite, but not without reversals throughout the history of the group.

COMMISSURE

Description and evolution.—The manner of meeting of the two valves is important in the Stenoscismatacea. Normally the valves butt against one another at the anterior and anterolateral margins, and overlap one another at the posterolateral margins. Two evolutionary changes in the manner of meeting are apparent. In Devonian *Atribonium* the valves tend to butt all the way around the commissure (except, of course, at the hinge). The butting at the posterior slopes is modified by beveling of the valve edges, so that there is slight extension of the outer edge of the brachial valve over the outer edge of the pedicle valve. This is a flange effect rather than actual overlap of the valves. The flanging is more pronounced in the primarily Mississippian genera *Coledium* and *Sedenticellula*. The flanged juncture of the posterolateral margins continues in the Permian genus *Torynechus*, and also occurs in some species of *Stenoscisma*. In most species of *Stenoscisma*, and in Pennsylvanian species of *Coledium*, the posterolateral slope of the pedicle valve is flat and beveled toward the margin, with the corresponding portion of the brachial valve overlapping it, sliding over it as the shell opens and closes. This overlapping of the posterolateral valve edges is especially pronounced in the Mississippian to Permian genus *Camerisma* n. gen. (see Ivanova, 1949, p. 109, fig. 30), and the Permian genus *Cyrolexis* n. gen. (figs. 18, 19).

The anterolateral and anterior margins of the valves butt without overlap in all genera of the Stenoscismatacea; however, the angle of their meeting differs in different genera. In the primarily Devonian *Atribonium* the valves flex abruptly toward one another at the anterior, meeting at nearly a straight angle in adults (they meet at any angle,

acute through straight in juveniles of various stages of growth). In some species the meeting is curved rather than planar, but the butting is direct. Some species, and some individuals within species, have a slight outbending at the very edges of the valves, producing a slight protuberance along the commissure. Although this feature is a matter of individual variation, it seems to herald later development of the stolidium at the valve margins. The same kind of anterior commissure is present in the Permian genus *Torynechus*, complete with the slight protuberance along the commissure, like an abortive stolidium. This slight protrusion is present in species of other genera in different families, e.g., *Uncinulus velifer* Gemmellaro (see discussion of stolidium). In the Permian genus *Septacamera*, the valves butt as in *Torynechus*, but lack the protruding commissure.

In all genera of the Stenoscismatacea except *Atribonium*, *Torynechus*, and *Septacamera*, the valves at the anterior meet at angles less than straight, much as in juveniles of species of *Atribonium*. The most obtuse angle of juncture is in certain species of the primarily Mississippian genus *Coledium*, in which the stolidium first appears. The angle is obtuse in *Psilocamara* (Pennsylvanian-Permian), *Cyrolexis* (Pennsylvanian-Permian) and *Camerisma* (Mississippian-Permian), but is smaller (obtuse to acute) in most species of *Sedenticellula* (Mississippian), *Stenoscisma* (Pennsylvanian-Permian) and *Camarophorina* (Permian). In the Stenoscismatidae, the anterior commissure gave rise to the stolidium (*q. v.*) as an extrusion from the edges of the acutely meeting valve edges.

Taxonomic importance.—The angle of meeting of the anterior and anterolateral margins of the valves in adult specimens is of generic importance in the earliest Stenoscismatacea. Direct butting of the valves nearly in a plane is an important character of *Atribonium*. It is of primary importance, along with costation of the flanks and absence of a stolidium, in distinguishing that genus from *Coledium* and also helps distinguish *Atribonium* from Mississippian *Sedenticellula*, although bifurcation or intercalation of costae in *Sedenticellula* is a more consistent difference. Therefore, the angle of meeting of the valves helps distinguish *Atribonium* from the genera that are most similar to it and occur nearest to it in time.

Other features distinguish *Torynechus* and *Septacamera* of the Permian from *Atribonium*, but the flat anterior surface helps distinguish these two genera from *Stenoscisma*. However, this character is less important in the later stenoscismataceans than in those of the Devonian and Mississippian.

Functional importance.—The angle of meeting of the anterior and anterolateral parts of the commissure probably is related to evolution

of the stolidium in the Stenoscismatidae. The stolidium is present only in genera whose valves meet at an angle less than 180 degrees. However, some species of *Sedenticellula* and the one known species of *Camarophorina* have the valves meeting as in stolidium-bearing species, but they lack the stolidium.

The manner of meeting of the posterolateral parts of the valves also probably is related to presence of a functional pedicle foramen. Ivanova (1949, p. 110) cited the tightly sealed "valve articulation" (inferentially, the posterior articulation) as a character related to unattached living habits. Ivanova's specimens now are believed to belong to *Camerisma* n. gen., which lacks the stolidium but has strong overlap of the valve edges. *Stenoscisma* also has the valves strongly overlapping at the posterolateral slopes, shows the greatest development of the stolidium, and in some species the pedicle foramen is tightly closed. Ivanova suggested that the tightly overlapping articulation in this part of the shell prevented the intrusion of mud as the shell lay agape on the sea floor. Articulated silicified specimens of *Stenoscisma* in the U.S. National Museum collection confirm that the valves could open at the anterior, and remain effectively closed at the posterior by this mechanism (pl. 23, figs. 4, 5).

PLICATION

Description.—All genera of the Stenoscismatacea are plicate at the anterior; the shell is thus divided into three lobes. In all genera except *Camarophorina* Licharev the fold is in the brachial valve and the sulcus is in the pedicle valve, producing a uniplicate shell (Thomson, 1927, p. 58, fig. 17). In *Camarophorina* the fold is on the pedicle valve, producing a sulcate shell. Only *Camarophorina* and *Psilocamara* have the median plication entirely unmodified by costae.

Juveniles of all genera of the superfamily have the anterior commissure nearly rectimarginate. The fold or sulcus normally begins more than 5 mm. anterior to the beaks, and is well developed only on adult shells. The median plication is not prominent in any genus of the Stenoscismatacea, in the sense that it is prominent from beaks to anterior margins as in groups like the Spiriferacea; its shape and strength (either uniplicate or sulcate) are typically rhynchonelloid.

Taxonomic importance.—Normal uniplication of the brachial valve is not generically significant within the Stenoscismatacea; only the sulcation of *Camarophorina* is significant. Details of the shape and height of the fold distinguish genera and/or species, but plication itself is not distinctive.

Evolution.—All genera and species in the Stenoscismatacea are mesially plicate, without consistent modifications of that character

throughout the range of the group. Persistence of this feature throughout the superfamily constitutes evidence for its relationship with the Rhynchonelloidea; it leads the search for ancestors and descendants to genera that are similarly folded.

Sulcation.—Only *Camarophorina* among the Stenoscismatacea has the fold in the pedicle valve. This condition occurs in many groups of brachiopods. A few examples include *Sanjuania* Amos (Mississippian), *Paranorella* Cloud (Permian), *Norella* Bittner, *Rhynchonella retractifrons* Bittner (Triassic), and the Recent genus *Neorhynchia* Thomson among the Rhynchonellacea; *Brachymimulus* Cockerell (Silurian) in the Triplesiaea, *Parenteletes* R. E. King (Pennsylvanian-Permian) in the Dalmanellacea, and *Centronella* Billings (Devonian), *Pseudoglossothyris* Buckman (Jurassic) and the modern genus *Abyssothyris* Thomson in the Terebratulacea. Recurrence of sulcation in various groups throughout the history of the Brachiopoda indicates no more than generic importance.

COSTATION

Costation is a typifying but not identifying character of genera within the Stenoscismatacea. The general trend is toward increasing strength of costation within the superfamily, but earliest known genera are costate, and least costate genera are midway in the range of the superfamily. However, evolutionary trend in the Family Stenoscismatidae (fig. 3) is toward increasing strength and extent of costation.

Description.—Costae are present in some genera of the Stenoscismatacea, absent from others. They are strong or weak, begin at the beaks or anterior to the beaks, and occupy the fold or the flanks, or both. Normally the costae are simple, V-shaped, without bifurcation or intercalation. Only the genus *Torynechus* has narrow ridgelike costae that increase in number anteriorly by intercalation. *Camarophorinella* and some species of *Stenosisma* have occasional bifurcating costae, especially at the sides of the fold and sulcus; *Sedenticellula* has narrow, frequently bifurcating costae.

Costae normally increase in height toward the anterior of the shell, but in *Torynechus* and *Septacamera* they are broader and flattened on the anterior slope; in the former, each costa has a median furrow instead of a crest, essentially doubling the number of ribs, as in *Uncinulus* or *Rhynchopora*. The ends of costae project like sharp teeth, serrating the commissure. Externally these serrations produce deep indentations in the edge of the stolidium where it joins the shell.

Taxonomic importance.—Costae are important taxonomically on two levels. Their presence or absence is important generically; costae are present in most genera of the Stenoscismatacea, but they are absent

in *Camarophorina* Licharev, *Psilocamara* Cooper, and normally absent in *Camerisma* n. gen.

On the specific level the strength and distribution of costae are important. In *Atribonium* n. gen., their relative strength on fold or flanks is significant. In *Stenoscostisma* Conrad, their beginnings on the umbones are important; in *Sedenticellula* Cooper, their relative strength and bifurcations distinguish species. In *Coledium* n. gen., the relative strength of costae on the fold and flanks helps to determine species.

Evolution.—Costae show progressive increase in strength through the development of the Stenoscostimatidae, but they exhibit no definite trend within the Atriboniidae. Costae are relatively weak and developed only anteriorly in the Devonian *Atribonium*, but they are numerous and narrow in the Mississippian *Sedenticellula*. Costae begin far anterior in the atriboniid *Cyrolexis* n. gen. which occurs primarily in the Permian. *Camarophorinella* Licharev has moderately strong costae; others of the family are smooth or nearly smooth.

Among the Stenoscostimatidae, costae exhibit an erratic but persistent trend toward increase in size and extent, from the Mississippian through the Permian. The earliest known genus with a stolidium is *Coledium* n. gen. (Mississippian) which has some smooth species, and some whose costae commonly begin about midlength on the shell. Costae in *Stenoscostisma* Conrad increase in strength from the earliest known species in the Lower Carboniferous of Britain, through Permian species of Germany, the Urals, Timor, and North and South America. The type species, *S. schlotheimi* (von Buch), has individuals with weak, nearly absent costae, and others with relatively strong costae; however, nearly all have costae beginning several millimeters anterior to the beaks (pl. 21).

Species of *Stenoscostisma* from the Permian of Timor (Broili, 1916) have strong or weak costae; species from Texas have costae ranging from short and anterior, like those on *S. schlotheimi* (e.g., *S. thevenini* (Kozłowski) in King, 1931) to those that cover the entire shell, excepting only the extreme posterior, as in *S. venustum* (Girty), *S. kalum* Stehli, and *S. multicostum* Stehli.

THE STOLIDIUM

Description.—The broad frill or skirt around the anterior and anterolateral commissures of genera of the Stenoscostimatinae is here termed the stolidium, from the Greek stolidion: a skirt. The stolidium is present only on adult specimens, where its form varies greatly among the species (see pls. 22, 23; fig. 2). It is narrow in species of *Coledium* n. gen., but normally it is broad in species of *Stenoscostisma*, reduced in

Torynechus, and absent from *Septacamera*. It is absent from the posterolateral slopes of all species, and normally is widest on the crest of the fold and the highest parts of the flanks. In most species it is absent or very narrow on the sides of the fold, but in a few species of *Stenosisma* it is well developed there on some individuals.

The stolidium may be convex or concave in either direction, or may be slightly wavy, but normally the stolidia of the two valves conform to one another. They bear growth lines whose concentricity appears to be a continuation of the pattern on the valves themselves. Their inner surfaces have pallial markings, normally with one or more sets of bifurcations. Many specimens show evidence of former presence of several stolidia on each valve. These appear to have broken off as the valves grew along their edges, with new stolidia progressively replacing those that were bypassed by lengthening of the shell (pl. 20, fig. 2). This indicates that the stolidia grew much faster than the valves themselves, and that numerous growth lines on the stolidium correspond to few on the shell. The stolidium seems to have been strengthened or perhaps continually repaired by the mantle as long as it grew from the commissure. In order for the shell to grow, however, the mantle either had to split (branch), retract, or slough off the part along the stolidium, thus abandoning previous stolidia in favor of growth of a new pair along the subsequent valve margins.

Silicified specimens of *Stenosisma* from the Permian of West Texas have the stolidium in various positions on the two valves. For example, *S. kalum* Stehli (pl. 19, fig. 4) has the stolidium on the fold of the pedicle valve, but the stolidium of the flanks is on the brachial valve. Most other species are like *S. venustum* (Girty), with a stolidium on fold and flanks of both valves (pls. 22, 23).

Function.—The function of the stolidium is a matter for conjecture. Stehli (1954) suggested that it served as a support for the shell as it lay on a soft substrate. This hypothesis was supported indirectly by Ivanova (1949) who gave evidence that *Stenosisma* lived free on the sea floor, but who did not mention presence of the stolidium (her specimens probably belong to *Camerisma* n. gen.). Ivanova's evidence was in the blocking of the pedicle foramen by the beak of the brachial valve. Many specimens from the Permian of Texas and of Timor in the U.S. National Museum collection also have the pedicle foramen completely closed by the strong curvature of the beak of the pedicle valve which presses closely on the brachial umbonal region. This condition normally occurs in large adult specimens that have the stolidium (e.g., *S. purdoni*, pl. 20); normally the foramen is open and presumably functional in immature specimens that lack the stolidium. Although this relationship suggests that the stolidium had something to

do with the free living habit of the adult stenoscismatid, it does not necessarily mean that the stolidium supported the shell on the substrate. However, this seems to be the most reasonable hypothesis.

An alternate explanation is that the stolidium had a function in the sexual maturity of the individual, perhaps as a producer or place of attachment for clusters of eggs, and that its relationship to the constricted foramen is entirely coincidental. This idea is supported by large adult specimens with full-grown stolidia that also have the pedicle beak nearly straight and the foramen open as, for example, specimens of *S. venustum* (Girty) (pls. 22, 23). Such specimens are in the minority, but are fairly common. However, presence of a foramen does not necessarily mean that the pedicle was functional or that the shell continued to attach by it.

Another possibility is that the stolidium did not support the shell, but functioned as a respiratory and/or auxiliary feeding organ when the shell was partly buried. Ivanova (1949, fig. 30) presented a drawing in support of her hypothesis that the shell lay with at least the umbonal region of the pedicle valve in the substrate. She cited the great thickness of the part of "*Camarophoria*" *pentameroides* Tschernyshev in support of her reconstruction. Although silicified shells of *Stenosisma* show no great thickening of the pedicle valve, the shell probably would have become partly buried at the posterior after its release from the juvenile attached condition. In such a position the projecting stolidium could gather oxygen, or perhaps trap food by providing a mucus layer or by channeling the in- and ex-currents. In addition, opening and shutting of the shell would cause the two stolidia to create currents at the commissure that could either stir in food particles or flush out invading sediment. Setae probably extended from the troughs between the costae at the valve margins, projecting between the stolidia of the two valves. They may account for some of the grooves, although probably those that bifurcate on the surface of the stolidia are continuations of pallial marks within the shell.

Available evidence does not indicate clearly the function of the stolidium. Its shape is too random and it seems to be too thin to have functioned as a mechanism that enabled the brachiopod to "flutter" through the water like a *Pecten*. Its pallial markings might have supported the respiratory or reproductive functions, but they also may have merely supplied nourishment to the mantle that produced the stolidium.

Taxonomic importance.—The presence or absence of the stolidium is a major consideration in dividing the Stenosismatacea into two families. Genera in which the stolidium is present constitute the family Stenosismatidae Oehlert (1887); they range from the Late Devonian

through the Permian. Genera that lack the stolidium are included in the family Atriboniidae n. fam. that ranges from Early or Middle Devonian through the Permian.

Species of the genus *Coledium* n. gen. that occur in the Upper Mississippian (Chester) are near the morphologic division between the two families. The stolidium is narrow and may be absent from some individuals (i.e., it is not preserved on all specimens), but the shape of the shell is similar to that of smooth specimens of *Stenosisma schlothemi* (von Buch) from the Permian of Germany. Devonian and Early Mississippian species of *Coledium* normally lack the stolidium.

Presence of a stolidium, while important within the Stenosismatacea, is not a defining characteristic of that superfamily. Many genera in other groups have similar structures that may well be homologous or have served the same function. Several genera within the Triplesiacea have marginal frills; examples are *Streptis* Davidson, *Cliftonia* (*Cliftonia*) Foerste, *C. (Plectotreta)* Ulrich and Cooper, and *C. (Oxoplecia)* Wilson, all of which are described and illustrated by Ulrich and Cooper (1936). Among the Athyridae, *Athyris* M'Coy and *Actinoconchus* M'Coy have frills on many of the growth laminae, beginning with some of the earliest. Apparently stolidia were not features of maturity in these genera (for illustrations see Sarycheva (editor), 1960). The common genus *Atrypa* Dalman also has frills on juvenile as well as adult parts of the shell (Fenton and Fenton, 1932; Cooper, 1944).

Among groups more nearly related to the Stenosismatacea, the rhynchonelloid genus *Sphaerirhynchia* Cooper and Muir-Wood has a rudimentary protuberance at the commissure, reminiscent of the incipient stolidium of many species in the Atriboniidae and many specimens of *Coledium*. *Uncinulus velifer* Gemmellaro (1899, pl. 26) has a similar structure and, except for its typically rhynchonellacean dental plates and median septum, it might be assigned to the Stenosismatacea.

The trail on many productaceans may be analogous to the stolidium of the Stenosismatacea, although in most genera it appears to have formed in a different way. Instead of being a fundamental change in direction of growth of both valves, normally the trail is a continuation of the pedicle valve, with corresponding conformity of the edge of the brachial valve. *Institella* Cooper and *Limbella* Stehli, however, have a marked change in direction of growth of the pedicle valve to form a relatively broad and flexuous marginal frill (Muir-Wood and Cooper, 1960), much as in the strophomenacean genera *Leptaena* Dalman and *Limbimurina* Cooper (see Cooper, 1956b, p. 820, 851).

Evolution.—Devonian species in the Stenosismatacea lack the stolidium, as do most species in the Mississippian. However, the margins

of the valves in several Devonian and Mississippian species of *Atribonium* protrude slightly instead of butting against one another directly, apparently presaging later development of the stolidium. The earliest species in which the stolidium developed beyond a slight protuberance are species of *Coledium* that occur in the Upper Mississippian. In these the stolidium may have developed only on an individual basis, or perhaps was present only on mature adults as in later species. It is not preserved on all specimens, but because all known specimens of these species are calcareous, none can be etched free to expose the stolidium that might have been present.

From its beginning as a mere out-pushing of the valve margins in Devonian and Early Mississippian species of *Coledium*, the stolidium became a definite extension of the valves in Late Mississippian species. Its breadth increased progressively until in Permian species of *Stenoscisma* it is rather broad and occupies the crests of fold and flanks of many species; it is continuous around the anterior margins of several species, connecting fold with flanks. The stolidium is greatly reduced in the Permian genus *Torynechus*, appearing only as a ridge along the anterior commissure. It is completely absent in Permian *Septacamera*, which is assigned to the Stenoscismatidae because of its apparent relationship to *Torynechus*.

Ontogeny.—The stolidium is absent from juvenile specimens shorter than 5 mm. and rare in specimens shorter than 20 mm. Species in genera of the stolidium-bearing Stenoscismatidae range in maximum length from about 20 mm. to more than 40 mm., but normally the stolidium is present only in adult specimens that are at least two-thirds the maximum size of the species. The stolidium does not appear to be an ontogenetically enlarging structure that is small on young adult specimens and larger on mature or gerontic individuals. Rather, it appears full grown on specimens that have it, and as the shell increased in size the stolidium broke off and was replaced by subsequent fully developed stolidia.

Relationship of foramen to stolidium.—Most specimens in species that have a well-developed stolidium also have the foramen reduced either by deltidial plates or by tight apposition of the two beaks. This relationship is best illustrated in *Stenoscisma*; all known species have the stolidium on mature specimens, and there is a marked trend among Permian species for the pedicle valve to curve tightly against the brachial valve. This trend is well expressed in species from the Glass Mountains, Tex., where Late Permian (Guadalupe) species with a broad stolidium have the foramen completely closed. The same relationships hold in Late Permian species from Timor (pl. 20). In contrast, the two genera of Stenoscismatidae in which the stolidium is reduced or absent, *Torynechus* and *Septacamera*, have the pedicle beak

nearly straight, and the delthyrium is bounded by small deltidial plates that leave the foramen open.

The inverse relationship of foramen to stolidium holds only for the Stenoscismatidae. In the Atriboniidae, the same trend toward closing of the foramen is apparent, but no stolidium is present.

DELTHYRIUM AND DELTIDIAL PLATES

Description.—The delthyrium is triangular in all species in the Stenoscismatacea. It varies in the manner and extent of constriction by deltidial plates, and by curvature of the pedicle beak over the brachial beak. The delthyrium in *Atribonium* (Devonian) is constricted in the normal rhynchonelloid manner by a pair of conjunct deltidial plates. In *A. cooperorum* n. sp. the delthyrium is so constricted by conjunct plates that the foramen would be nearly completely closed were it not for penetration of the foramen into the apex of the beak. In *Atribonium* the foramen is kept open either by slight constriction by the deltidial plates or by incursion of the foramen into the beak of the pedicle valve. In other genera of the superfamily the delthyrium is either unmodified and unconstricted, constricted only sporadically by deltidial plates, or constricted by tight curvature of the pedicle beak onto the brachial umbonal region.

Function.—The delthyrium primarily afforded an opening by which the pedicle could emerge from the ventral valve to attach the shell to the substrate. Some specimens of *Stenoscisma* with disjunct deltidial plates have the foramen nearly or entirely closed by tight apposition of the two beaks. Other specimens, especially of Permian species, have the size of the foramen reduced by the deltidial plates. Apparently the pedicle of many Permian species was not functional; this conclusion also was reached by Ivanova (1949) from study of Permo-Carboniferous specimens (of *Camerisma* n. gen.) from the Moscow Basin.

Evolution.—The earliest known stenoscismatacean, Devonian *Atribonium*, has a typically rhynchonelloid delthyrium, constricted by a pair of small, disjunct or conjunct deltidial plates; the foramen appears to have been able to accommodate a pedicle in all individuals of all species. Likewise, no known specimen of *Atribonium* has a stolidium, and none has the valves overlapping at the posterolateral margins.

Species in subsequent genera of the superfamily (except *Camerisma* and *Cyrolexis*) have individuals with the foramen open and others with it closed either by the deltidial plates or by the brachial umbo. This variable condition occurs even in *Stenoscisma* in which adults of all species invariably bear stolidia. In *Camerisma* and *Cyrolexis*, all known specimens have the foramen tightly sealed by apposition of the umbones.

INTERNAL MORPHOLOGY THE CAMAROPHORUM

Definition.—For many years prior to 1929 paleontologists had referred to the internal structure on the crest of the median septum of the brachial valve of *Stenosisma* as a “cruralium,” although many noted its difference from the normal cruralium of the Camarotoechiinae (e.g., Weller, 1914). Kozłowski (1929) demonstrated its difference from that structure, and designated it the camarophorium. The name was derived from the name of the genus *Camarophoria* King (1850), equivalent of *Camerophoria* King (1844) and *Stenosisma* Conrad (1839). Cooper (1956a), who was familiar with Kozłowski’s paper, inadvertently (oral communication, 1960) coined the term “torynidium” for the same structure. Because the earlier term was well established, and unambiguous, it is here retained. Its spelling is based on the correct etymology of *Camarophoria*.

Description.—The camarophorium, as defined by Kozłowski (1929), includes both the median septum of the brachial valve and the expansion of its crest into an elongate trough (pls. 22–24; fig. 1). It does not include the short plate that unites the posterior part of the midline of the trough with the underside of the hinge plate. That plate, separate from the camarophorium itself, is called the intercamarophorial plate (Licharev, 1936).

The septum is a normal septum duplex, as shown by Kozłowski (1929) and by serial sections of specimens of *Atribonium* (fig. 7c), *Coledium* (fig. 21), *Stenosisma* (fig. 25), *Cyrolexis* (pl. 6, figs. 4, 4a), and *Camerisma* (fig. 11c; pl. 8, fig. 2a). The expansion of the crest of the septum forms a trough that broadens slightly toward the anterior and normally is extended slightly at the anterior midline. The crest of the septum, and consequently the base of the trough, curves gently ventrally forward, giving the trough the shape of a shallow spoon. The combination of trough and septum constitute the camarophorium.

The intercamarophorial plate extends from the underside of the hinge plate to intersect the midline of the trough of the camarophorium (Kozłowski, 1929). It is present only in the posterior half to two-thirds of the camarophorium, its anterior extent in some genera is only slightly greater than that of the hinge plate from which it derives. The anterior of the camarophorium is simply spoon-shaped, without a median septum or ridge.

The septum of the camarophorium is present in the extreme poste-

rior of the brachial valve. The trough-shaped crest also originates in the apex of the valve and, in some species and some individuals, intersects the floor of the valve there. However, it normally begins slightly above the valve floor and increases in height anteriorly so that the trough begins slightly anterior to the beginning of the septum itself.

Ontogeny.—Kozłowski (1929) demonstrated that the trough capping the septum to form the camarophorium is an expansion of the septum, not a separate structure imposed upon it. Serial sections of several specimens of Devonian species of *Atribonium* (fig. 5; pl. 3, fig. 1E) show that the camarophorium begins as a small swelling on each side of the crest of the median septum, at or very near the apex of the brachial valve. Sections in which the duplex character of the septum is obscured show the trough as a small bulb at the top of the septum; more favorable sections show it to be an expansion of each side of the septum. Its rounded cross-section flattens anteriorly, and about 1 mm. from the beak it is a platform with a nearly flat cross-section (fig. 5c). Farther forward the platform becomes concave toward the pedicle valve, and from there nearly to its anterior termination it becomes more deeply concave. Near the anterior end it shallows rapidly, terminating between one-fourth and one-half the shell length in different species. The trough of the camarophorium extends slightly beyond the anterior edge of the septum; the edge of the septum normally is concave forward, with slight extension as a ridge along the floor of the valve and along the base of the trough.

Origin.—If the adductor muscles attached within the camarophorium (see discussion of musculature), that structure functioned in effect as an elevated floor of the valve. An elevated or detached valve floor that serves as a muscle attachment is not peculiar to the Stenoscismatacea, but is found in either valve of several other groups of brachiopods. Genera with the floor detached in the pedicle valve are *Parentcletes* King (1931) among the Dalmanellacea and *Orthotetella* King (1931) among the Orthotetacea. *Mystrophora* Kayser has a muscle platform in the brachial valve as in the Stenoscismatacea.

The camarophorium is not simply a detached and elevated area of the valve floor, despite its probable function as a muscle attachment. If it originated by progressive elevation of the muscle area, the fibers of its septum would be expected to be continuous with those of the valve floor. Instead, the septum of the camarophorium wedges into the floor quite discontinuously, and only secondary shelly matter that thickens both floor and septum is continuous from one to the other (e.g., in *Camerisma*, fig. 12). The camarophorium grew anteriorly from the cardinal region beneath the hinge plate, and may have usurped the muscle carrying function from the floor. Possibly a septum duplex

developed first in the history of the group, and then its plates spread to form the camarophorium, to provide more surface for muscular attachment. Solution of this problem awaits discovery of earlier or ancestral Stenosismatacea.

Evolution.—The camarophorium appears fully developed in the earliest known genus of the group, the Devonian *Atribonium* where it is comparatively short and its crest is not strongly curved ventrally (fig. 4; pl. 1, figs. 8, 9). Subsequent genera of the group have the camarophorium somewhat more strongly curved in longitudinal profile than does *Atribonium*. That is, the septum of the camarophorium is proportionately higher at its anterior (*see* figs. 20, 23; pl. 6, fig. 5; pl. 9, fig. 2b).

The spoon or trough of the camarophorium normally is narrowly separated from the hinge plate. The two structures are connected in most genera by the intercamarophorial plate. In *Psilocamara* Cooper, the intercamarophorial plate is absent; in *Cyrolexis* n. gen., it is absent or very thin and short; and in *Camarophorinella* Licharev, the hinge plate is divided medially, no intercamarophorial plate is present, and the edges of the camarophorial trough join the underside of the hinge plate.

Taxonomic importance.—Presence of the camarophorium in the brachial valve, along with the spondylium of the pedicle valve, is diagnostic of the superfamily Stenosismatacea. Spondylia are present in many groups as modifications of dental plates. For example, *Geyerella* is separated from *Meekella* among the Orthotetacea by coalescence of dental plates into ventral spondylium. However, the dorsal camarophorium is known only in the Stenosismatacea.

THE SPONDYLIUM

Description.—The spondylium of the pedicle valve is formed by convergence and fusion of the two dental plates just above the floor of the valve (pl. 6, figs. 4, 4a; pl. 8, fig. 2a; and Kozlowski, 1929). It is a deep boat-shaped trough in the posterior part of the valve, becoming shallow and scoop-shaped anteriorly where the dental plates terminate and only the base persists (pl. 23, figs. 1, 2, 3; fig. 2).

Evolution.—Normally the spondylium is elevated above the floor by the septum duplex that is formed by coalescence of the dental plates. However, many species contain individuals in which the dental plates extend to the floor of the valve in the extreme apex, but coalesce and are elevated at a distance less than a millimeter to the anterior. Such individuals are most frequent in early genera such as Devonian *Atribonium*, Devonian and Mississippian *Coledium*, and Mississippian *Sedenticellula*; the sessile condition of the spondylium continues far-

these anterior in the last genus. Elevated and sessile spondylia appear throughout the range of the Stenoscismatacea.

Function.—The interior (concave) side of the spondylium seems to be smoother than the floor of the shell in silicified Permian specimens of *Stenoscisma*. This smooth area probably was formed by seating of muscles (for evidence, see discussion of musculature).

Taxonomic importance.—Spondylia produced by fusion of dental plates are present in many groups (e.g., genera of the Pentameracea, Tetracameridae, Rhynchotetridae, some Orthotetacea). Presence of a spondylium is not a defining character for the Stenoscismatacea unless accompanied by a camarophorium in the brachial valve; were a genus to be found containing a camarophorium but not a spondylium, it might be included with the Stenoscismatacea.

Insertion.—The median septum of the spondylium is inserted into the valve floor like a wedge; its fibers are not continuous with those of the floor, and it is not derived from the floor. This peculiar insertion was described by Licharev (1936, p. 57, fig. 1) and is shown here in plate 6, figs. 4, 4a; plate 17, fig. 5a; and figures 11–13 and 31. It is in direct contrast to the normal form of median septum where the fibers of the shell wall can be traced continuously from the valve floor to the side of the septum. The normal form of growth of septa was described for billingsellids and clitambonitids by Kozłowski (1929, p. 121–132, figs. 37–38) and illustrated by photographs of transverse sections of orthoids by Schuchert and Cooper (1932). Both of these works also illustrate the manner of growth of the septum of the spondylium in pentameroids, where it wedges into the shell material of the valve floor as in the Stenoscismatacea.

The similar manner of insertion of the septum of the spondylium of the pentameroids and the stenoscismataceans might argue for close phylogenetic relationships between the two groups. Earlier workers (e.g., Girty, 1909) classified the stenoscismatids with the pentameroids, largely on the basis of similarity of the camarophorium and the spondylium with the elevated spondylia of the pentameroids. Later authors (e.g., Kozłowski, 1929; Muir-Wood, 1955) include the Stenoscismatacea with the Rhynchonelloidea because of their crura and characteristic rhynchonelliform pedicle beak (see discussion of classification).

The spondylium of the Pentameroidea is different in shape from the spondylium and camarophorium of the Stenoscismatacea and, according to Schuchert and Cooper (1932), pentameroid cardinalia are not homologous to those of the Rhynchonelloidea. Similarity in the manner of insertion of septa in the two groups may reflect mechanical rather than phylogenetic causes. Cross-sections of a *Meekella* in which the

dental plates join at the floor show similar wedged insertion of the fused plates into the valve floor. The same is true of *Ombonia* and *Geyerella* whose dental plates fuse well above the floor to form a distinct spondylium on a septum duplex. These Orthotetacea certainly are remotely related to the Pentameroidea and the Stenosismatacea, their only similarity is in formation of the spondylium by fusion of dental plates and consequent wedgelike insertion of the resulting septum duplex into the valve floor. Therefore, wedged insertion may mean that the septum is derived from structures above the valve floor (i.e., dental plates or cardinal structures), rather than from the floor itself, and therefore must attach to the floor by insertion.

The septum of the camarophorium inserts in the same way, indicating formation by tissues independent of the valve floor. This is in contrast to the low septum and "cruralium" of *Cupularostrum* (olim *Camarotoechia*) whose calcareous fibers are continuous with those of the valve floor indicating derivation from the floor and growth toward the hinge plate rather than derivation from the cardinalia (or independent tissue) and growth toward the floor.

Kozłowski (1929, p. 131) called the spondylium of *Stenosisma* (then *Camarophoria*) a typical spondylium duplex. By this he meant a spondylium that is formed of two plates that unite with an interseptal lamina between them (1929, p. 125). Licharev (1936, p. 66) clarified this concept as applied to the Stenosismatacea, emending it to mean a septum formed of two distinct plates. No interseptal lamina was observed in any of my serial sections, only the dark line where the two plates of the septum meet. Therefore, the term "duplex" is used here in Licharev's sense, rather than in Kozłowski's (unless by interseptal lamina Kozłowski meant merely a plane of joining).

MUSCULATURE

Muscle marks are not strongly impressed in the Stenosismatacea; they are invisible in most specimens. However, a few valves in the U.S. National Museum's large collection of silicified specimens of *Stenosisma* and *Torynechus* from the Permian of Texas have light marks of muscle attachment in the concave surfaces of the camarophorium and the spondylium. These marks support the contention of King (1850, p. 115) supported by Licharev (1936, p. 65) and Cooper (1956a, p. 521) that the adductor muscles attached within the camarophorium (fig. 1). In addition, the inner surfaces of the camarophorium and spondylium are smooth in many valves where individual muscle marks are not distinguishable. Their smoothness contrasts with the rougher or pitted nature of the valve floors, the sides of the septa, and the convex surfaces of the camarophorium and spondylium. Originally

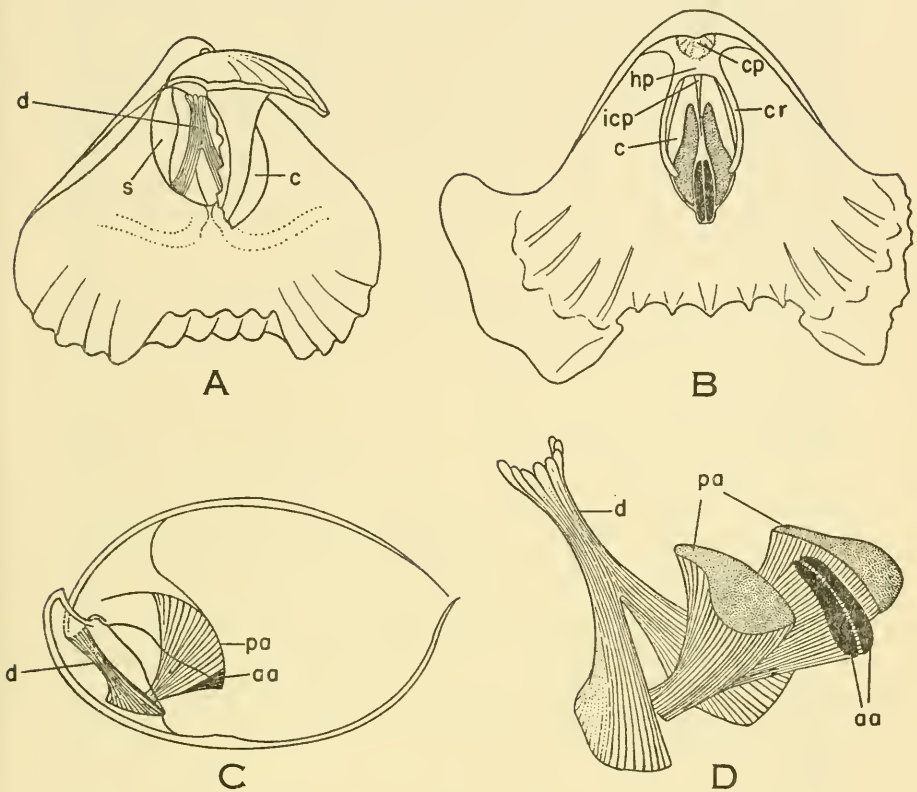


FIG. 1.—Reconstruction of arrangement of principal muscles in *Stenoscismatacea* based on *Stenoscisma*.

A. Interior of pedicle valve and cutaway brachial valve showing seating of paired proximal end of diductor within spondylium: c—camarophorium; d—diductor muscle; s—spondylium.

B. Interior of brachial valve showing areas of attachment of adductor muscles: blackened area is paired anterior adductor, stippled area is paired posterior adductor: c—camarophorium; cp—cardinal process; cr—crus; hp—hinge plate; icp—intercamarophorial plate.

C. Side view along midline, showing mechanical arrangement of muscles: diductor muscle (d) extends from cardinal process to spondylium; anterior adductor (aa) and posterior adductor (pa) muscles extend from midline of spondylium to camarophorium.

D. Reconstruction of muscles, enlarged and spread to show arrangement: diductor (d) single at cardinal process, paired in spondylium; adductor single in spondylium, dividing in camarophorium to form posterior adductors (pa) and anterior adductors (aa), surfaces of attachment blackened or stippled corresponding to pattern of attachment areas in figure B.

the entire inner chamber of the brachiopod shell probably was smooth, but the areas where muscles attached seem to weather or silicify in a manner that produces a smoother ultimate surface.

The spatulate outline of the camarophorium is similar to that of the muscle area in many brachiopods. Apparently the anterior adductor muscles attached in a narrow band along each side of the midline, beginning just anterior to the intercamarophorial plate, and extending anteriorly onto the small, toothlike median extension of the spoon of the camarophorium. The posterior adductors attached lateral and posterior to the smaller pair of muscles, apparently utilizing the anterior part of the intercamarophorial plate for additional surface. Lateral boundaries of the posterior adductor muscle marks have not been observed; probably the muscles attached over the remainder of the concave surface of the camarophorium.

Davidson (1853, p. 96) suggested that the adductor muscles attached near the base of the septum of the camarophorium. If they attached there, the spoon of the camarophorium would have acted as a "spreader" for the muscles, and they could have attached in the deep transverse groove on each side of pedicle valve floor. Several objections to this possible arrangement are apparent. The surfaces of the transverse grooves do not resemble those of muscle areas in other groups of brachiopods; they do not appear to be muscle marks or tracks. Instead they are like the remainder of the valve floor and probably represent pallial grooves or gonocoels. Moreover, no muscle marks are apparent on the septum or the convex surface of the camarophorium.

Further objection to Davidson's proposed muscle arrangement is in its radical departure from that of all other groups of brachiopods. The adductors in this pattern must necessarily attach lateral to the diductors in the pedicle valve, because the spondylium would have confined the diductors too narrowly for them to have occupied the entire width of the transverse grooves in the floor. The same would be true if they attached to the outer surface of the spondylium (where no muscle marks have been observed) rather than within it. The normal arrangement in all other groups that have these sets of muscles is for the adductors to be doubly paired in the brachial valve, but single-paired and median in the pedicle valve. Furthermore, no division into anterior and posterior adductors seems possible with the proposed arrangement. These departures from the normal pattern for muscles in brachiopods seem too extreme to accept without convincing evidence.

If the adductor muscles attached within the camarophorium, they also must have attached within the spondylium of the pedicle valve.

Adductor muscles typically unite and attach singly along the median line in the pedicle valve of brachiopods. An elongate area like a muscle mark was observed along the midline of the floor of the spondylium in several silicified valves of *Stenoscisma*. This area is narrow, but seems to cover sufficient surface to accommodate the united adductor, which is proportionately small in most brachiopods. The remainder of the inner surface of the spondylium probably seated the proximal end of the pedicle, the pedicle adjustor muscles, and the paired ventral ends of the diductor muscle.

The diductor muscles attached to the fimbriate, knoblike cardinal process on the hinge plate near the apex of the brachial valve. This seat for muscular attachment has been observed in all groups in the Stenoscismatacea. It is especially large and deeply grooved in silicified Permian specimens of *Stenoscisma*, where it can be observed directly rather than in cross-section. It is large enough in all genera to have accommodated a large and powerful set of muscles. Normally the diductor divides to form two muscle marks in the pedicle valve. In this superfamily they apparently attached to the inside surfaces of the dental plates that form the spondylium.

The muscle arrangement described here is illustrated in figure 1. It provides a set of very short adductor muscles and a longer diductor than in Davidson's arrangement. The camarophorium served as a long lever for the closing of the shell and, although it appears to be a fragile platform, surprisingly great strength is indicated by its frequency of preservation in fossil shells. All specimens that were sectioned serially had the camarophorium intact, and this could not be determined prior to making the section. A great majority of specimens in the large collection of silicified Permian shells from Texas in the U.S. National Museum contains a complete camarophorium or a large part of one in open shells or single brachial valves where it can be observed. The camarophorium is heavily thickened by secondary shell material in some genera, notably *Camerisma*; this probably added greatly to its strength.

The gape is very narrow in articulated specimens of *Stenoscisma* that could be manipulated, and the close similarity of other shells in the Stenoscismatacea indicates that a narrow gape is characteristic. The short adductors and large lever system postulated by the proposed muscle arrangement probably provided a quick closing action by the striated portions of the adductors and a rather powerful locking action by the smooth portions, if the adductors were thus divided (Rudwick, 1961, p. 1021). The long, nearly straight diductor, attached well posterior to the hinge teeth, provided a relatively efficient system for open-

ing the shell narrowly, possibly against the confining action of sand or mud (in free-living forms) and certainly against the force exerted by the water against motion by the broad stolidia in *Stenoscisma*.

HINGE PLATE AND CARDINAL PROCESS

Description.—The hinge plate in all genera of the Stenoscismatacea is typically rhynchonelloid, supporting inclusion of that superfamily within the Rhynchonelloidea. The hinge plate varies in length, but normally it is rather flat, with a fimbriate swelling at the apex, and a pair of brachial processes extending from the anterior edge. Normally, the plate is undivided, but it is anteriorly recessed in *Cyrolexis*, and deeply split in *Camarophorinella*.

Paired crural processes extend forward from the anterior edge of the hinge plate. They are slender and bow distally while curving ventrally, roughly following the edges of the camarophorium. Their coincidence with the shape of the camarophorium is only approximate; they curve more strongly toward the pedicle valve (pl. 21, fig. 13; pl. 22, fig. 3a; pl. 23, fig. 4, 5; pl. 24, fig. 10). In most specimens their length is roughly that of the camarophorium, but in many they are slightly shorter or longer (see discussion of crura, below).

Functions.—The brachial attachment for the diductor muscles is not a cardinal process in the sense in which that term applies to members of the Productoidea or the Strophomenoidea; rather it is a swelling in the apical part of the hinge plate that includes a small part of the apex of the valve. The knob is shallowly fimbriate radially, and there is little doubt that it served as an attachment for muscles that opened the shell.

CRURA

Description.—The two processes that extend anteriorly from the hinge plate are here called the crura (following Cooper, 1956a, p. 521) although they are longer and more slender than the crura of many other rhynchonelloids. They extend forward about the same distance as the crest of the camarophorium and their curvature reflects approximately the course of the edges of the trough. Posteriorly they are subparallel, not strongly curved ventrally, and rather near one another. They bow distally toward the anterior, and curve ventrally somewhat more strongly than the trough of the camarophorium, nearly touching the edges of the spondylium in some specimens; this is shown in figure 1 and in plates 22–24.

Function.—It is doubtful that the crura supported the fleshy lophophore. The body of the brachiopod probably occupied the space within and immediately outside the chamber formed by the spondylium and

camarophorium. The crura also help outline this chamber and probably helped support the body wall of the animal. As in living rhynchonelloids, the lophophore probably extended anteriorly from the anterior body wall, and its support probably was fleshy, with the crura lending support only to its base (Hyman, 1959).

LOPHOPHORE

The form of the lophophore cannot be observed directly because it was not supported by a calcareous brachidium. However, if the Stenoscismatacea are correctly classified as Rhynchonelloidea, the lophophore probably was spirolophous, as in Recent representatives of that group (Hyman, 1959).

Rudwick (1962), in his analysis of the forms of the lophophores of Recent brachiopods, called attention to Hancock's (1859) observation that the various shapes are efficient to organize the requisite length of lophophore to accommodate the number of filaments needed to feed the organism at any particular stage of growth. Rudwick explained that they must be arranged so that the filter chamber (the mantle cavity) is divided into effectively isolated inhalent and exhalent chambers, each with its own aperture. The spiroloph develops from the trocholophus stage through the schizolophe, each of the two earlier stages providing sufficient filamentous surface to feed the growing animal.

Possibly all adult Stenoscismatacea were spirolophous. However, the evolutionary increase in size, primarily exhibited in the Stenoscismatidae and suggested less strongly in the Atriboniidae, might mean that the small early species could have fed efficiently with a schizolophus lophophore (Rudwick, 1962, p. 598, fig. 6).

PALLIAL MARKINGS

Description.—Pallial markings in adult shells of the Stenoscismatacea begin about one-third the distance from the beak to the anterior margin. A deep transverse groove, probably a gonocoel, extends from the anterior edge of the median septum of the pedicle valve to each side of the valve. The groove is rather deep in Permian silicified shells in which it has been observed, and its anterior edge is a low ridge. Posterior to this pair of grooves there are no clearly distinguishable pallial marks.

Pallial marks begin anterior to the transverse gonocoels as a pair of shallow *vascula media*, one on each side of the median line. Each vasculum bifurcates a few millimeters anterior to its beginning, and each pair from this dichotomy also branches about the same distance forward. Similar branching takes place at nearly equal intervals anteriorly, with about three or four dichotomies behind the margins of the

valves. Branching is such that it produces one pallial line to go through each costal trough (fig. 2). Anterior to the shell margin in the Stenoscismatidae the pallial marks continue to dichotomize, with one or two bifurcations taking place on the stolidia. The pallial pattern was well illustrated by King (1850, pl. 8).

Function.—The transverse grooves that cross the pedicle valve from the anterior edge of the median septum to the sides of the valve probably seated some portion of the gonads (Williams, 1956, p. 272 *et seq.*). The body of the brachiopod, and the major portion of the gonads probably occupied the area posterior to the transverse grooves (*see* Williams, 1956, p. 272 *et seq.*).

The shallow vascula that bifurcate several times in their anterior course onto the stolidia are termed pallial marks. Normally, this term refers to irregularities in the mantle edge, but here it is employed in its general sense for shallow branching lines on the interior surfaces of the valves. Those in the Stenoscismatacea may be genital, or perhaps respiratory, but their thinness, symmetrical bifurcation, and extension out onto the stolidia indicate a possible circulatory function.

Taxonomic importance and evolution.—Pallial marks are clear only on silicified Permian specimens in the Stenoscismatacea, but on them the pattern seems rhynchonelloid. Among Permian species of *Stenoscisma* they show no significant change, so I consider it unlikely that

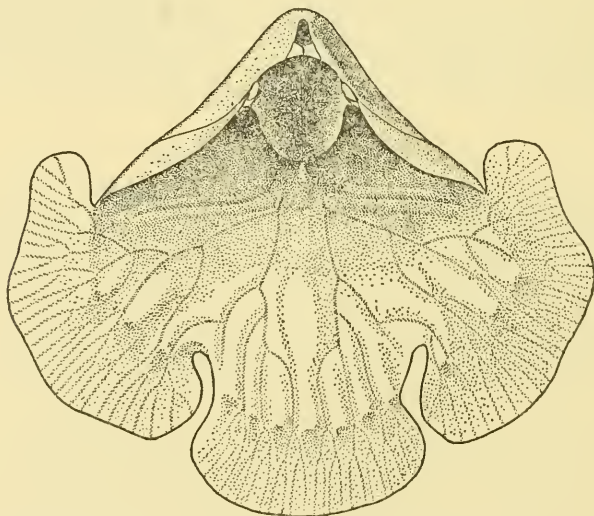


FIG. 2.—Idealized interior of pedicle valve of *Stenoscisma*, showing transverse grooves at anterior edge of median septum, pallial marks on valve floor and on stolidium, and posterolateral margins where edges of brachial valve overlap.

they undergo clear phylogenetic trends that would be of major taxonomic value to earlier genera whose patterns are unknown.

SHELL STRUCTURE

Serial sections prepared for study of internal structures reveal no unusual lamination of the shell. The shell of all stenoscismataceans is impunctate, and consists of an outer primary layer of calcite, and an inner secondary layer. No periostracum is visible. Silicified shells show none of the original lamination, and some calcareous shells have been replaced by calcite that also has destroyed the former structure. Cross-sections of the shell are illustrated in plate 6, figs. 4, 4a; plate 8, figs. 1b, 2a; plate 12, fig. 1d; and plate 17, fig. 5a.

LIFE HABITS

PEDUNCULAR ATTACHMENT

Early Stenoscismatacea had the pedicle foramen open and presumably functional, but both families show progressive diminution of the foramen through time. The earliest genus, Devonian *Atribonium*, has the delthyrium constricted by a pair of small deltidial plates in the normal rhynchonelloid manner, but the foramen is invariably open. Where deltidial plates tend to close the delthyrium, the foramen pierces the apex of the beak of the pedicle valve. Presumably, all species of this genus lived attached throughout life by a functional pedicle.

The earliest Stenoscismatidae, Late Devonian and Early Mississippian species of *Coledium*, also have the foramen open and presumably functional, but later species have the foramen closed by tight apposition of the two beaks. Diminution of the foramen of *Coledium* is accompanied by development of a rudimentary stolidium. This coordinate development continued in *Stenoscisma*, where the stolidium reached its greatest development; Late Permian species have the foramen completely closed by tight curvature of the beak of the pedicle valve onto the umbonal region of the brachial valve. These species apparently broke free of their juvenile peduncular attachment to live on the substrate, possibly supported there by the stolidium.

The two genera of the subfamily Torynechinae, Pennsylvanian and Permian *Septacamera* and Permian *Torynechus*, have the stolidium essentially absent. It is reduced to a mere ridge in *Torynechus* and apparently completely absent from *Septacamera*. The beak is nearly straight to suberect in both of these genera, and the delthyrium is sufficiently exposed to provide an open pedicle foramen. These two genera probably reverted to the earlier habit of the superfamily and lived attached by the pedicle throughout life.

Among the Atriboniidae the trend toward diminution of the pedicle foramen is similar to that in the Stenoscismatidae but no stolidium developed concurrently. The costate genera *Sedenticellula* of the Mississippian and *Camraphorinella* of the Permian apparently lived attached by the pedicle. The smooth and highly arched Pennsylvanian genus *Psilocamara* also typically has an open foramen, although it is greatly constricted by deltidial plates and curvature of the pedicle beak. The open foramen suggests that the genus lived attached by the pedicle, although the shape of the shell, with its deeply convex pedicle valve and highly vaulted fold indicate possible capability of survival living free on the substrate.

The sulcate genus *Camarophorina* includes individuals with the pedicle beak tightly pressed against the brachial valve, and others with the beak suberect and the foramen small but open. Perhaps both the attached and the free modes of life were available to species of this genus, although those with the foramen closed must have lived unattached.

Camerisma ranges from the Mississippian into the Permian without a known individual whose pedicle foramen is open in the slightest degree. This smooth form, with its high vaulted fold, necessarily must have lived free on the substrate, either in the sediment or in vegetation. Ivanova (1949, p. 109) discussed the morphology and inferred living habits of the exceptionally strongly trilobate species *C. pentameroides* (Tschernyshev), which she assigned to *Stenosisma*. Other species exhibit the same adaptations to life on the bottom sediment, namely the deepened and thickened umbonal region of the pedicle valve which provided a posterior center of gravity, and sufficient height to keep the anterior of the shell above the sediment while the posterior lay partly buried. In addition, Ivanova pointed out the broad overlap of the posterolateral edges of the valves which provided a seal that enabled the valve to gape at the anterior and remain effectively closed at the posterior. This overlap is found in all genera whose pedicle foramen is closed. The highly arched fold also helped to place part of the gape above the sea floor, beyond the reach of most sediment.

The Permian genus *Cyrolexis* is characterized by tight apposition of the beaks that provides no opening for a pedicle. The globular shell probably could not remain stationary, balanced on its pedicle valve like *Camerisma*. Therefore both valves are somewhat thickened and deepened at the posterior, and the fold is not high. The shell could rest on either valve with the posterior center of gravity keeping the anterior gape above the substrate. The valves overlap strongly at the sides to provide a seal against sediment as in other free living genera, although the overlap extends proportionately farther to the anterior in *Cyrolexis*.

ORIENTATION

Attached shells probably rotated on their pedicles, changing their orientation at different times (Rudwick, 1962). Shells that attached to upper surfaces of the substrate probably kept the pedicle valve uppermost for more of the time, and those attached to under surfaces probably hung more often with the brachial valve up.

Free-living forms could have assumed any orientation. Those that fell into tangles of Bryozoa or vegetation could have settled in any attitude. Those that settled on the sediment of the sea floor probably were rolled or flipped by currents or other animals. However, the stolidium

of *Stenosisma* probably assured that the shell settled beak foremost; the heavy posterior of *Camerisma* and *Cyrolexis* probably also helped maintain that attitude. The great width and high vaulted fold of species such as *Camerisma pentameroides* or *C. prava* probably helped the shell settle with the pedicle valve down.

The orientation illustrated by Ivanova (1949, fig. 30) with the pedicle valve down and the commissure slanted upward, would have been advantageous for spirolophous forms whose incurrents were anterolateral and median, and excurrents mostly median as illustrated by Rudwick (1962, p. 599). Frequent changes in location and position probably were necessary to keep the shells in unfouled environments (Rudwick, 1962, p. 608).

SUMMARY

Early species in both families of the Stenoscismatacea lived attached by the pedicle throughout life. Later species of Stenoscismatinae lived attached as juveniles but broke free to live on the substrate as adults. Species in the Torynechinae, however, adopted the former habit and remained attached throughout life.

Individuals of some species of the Atriboniidae seem to have lived free on the substrate for much of their lives, but juvenile specimens of *Camerisma* are unknown so their early habits remain undetermined. Although the smallest known specimens of *Cyrolexis* have no pedicle foramen and must have lived free, these are not young juveniles. Therefore, an unattached habit is not clearly demonstrated for the early growth stages.

PHYLOGENY OF SUPERFAMILY STENOSCISMATACEA

The superfamily Stenoscismatacea ranges from the earliest Middle Devonian through the Permian (fig. 3). The progenitor of the group is not known, but evidence in the earliest genus, *Atribonium*, points to a rhynchonelloid ancestry. The ancestor probably was a small septate rhynchonelloid with well-developed dental plates converging toward the floor of the pedicle valve, such as the camarotoechiid genus *Hircinisca* illustrated by Havlicek (1961, p. 66, pls. 4, 7).

No descendants of the Stenoscismatacea are known; apparently the group became extinct at the end of the Permian. By Cretaceous time other rhynchonelloids were mimicking some of the external characters of *Stenoscisma* and *Torynechus* (see pl. 7, figs. 1, 1a), but the defining internal features of the superfamily appear not to have been repeated.

FAMILY ATRIBONIIDAE

The earliest genus is *Atribonium* n. gen. which is characterized by its relatively flat and short camarophorium, blunt anterior shell margin, little or no overlap of posterolateral valve margins, and delthyrium with deltidial plates and consistently open pedicle foramen. This genus is structurally capable of having given rise to the early stenoscismatid genus *Coledium* n. gen., and to all the later atriboniids. The family Atriboniidae extends into the Permian of Timor, the Salt Range of Pakistan, far eastern Siberia, and the northern Caucasus.

Subfamily Atriboniinae.—The Mississippian genus *Sedenticellula* Cooper probably derived from *Atribonium* by addition of costae, compression of the shell, thus lowering the angle of meeting of the anterior edges of the valves (as in juveniles of *Atribonium*), and continuation of the nepionic sessile spondylium of *Atribonium* into a later ontogenetic stage. Internal features of the brachial valve maintained their *Atribonium*-like aspect, with an undivided hinge plate and a well-developed intercamarophorial plate.

The smooth genus *Camerisma* n. gen., with its narrowly arched fold, resembles *Atribonium* in the internal structures of both valves. The structures are stronger, with more reinforcement by secondary shell material, but the spondylium is elevated and the intercamarophorial plate robust.

Subfamily Psilocamarinae.—Mississippian representatives of this subfamily are unknown; the earliest genus is *Psilocamara* Cooper, a smooth Pennsylvanian shell with a high, arched fold that probably derived from the similarly smooth and arched *Camerisma* of the Atri-

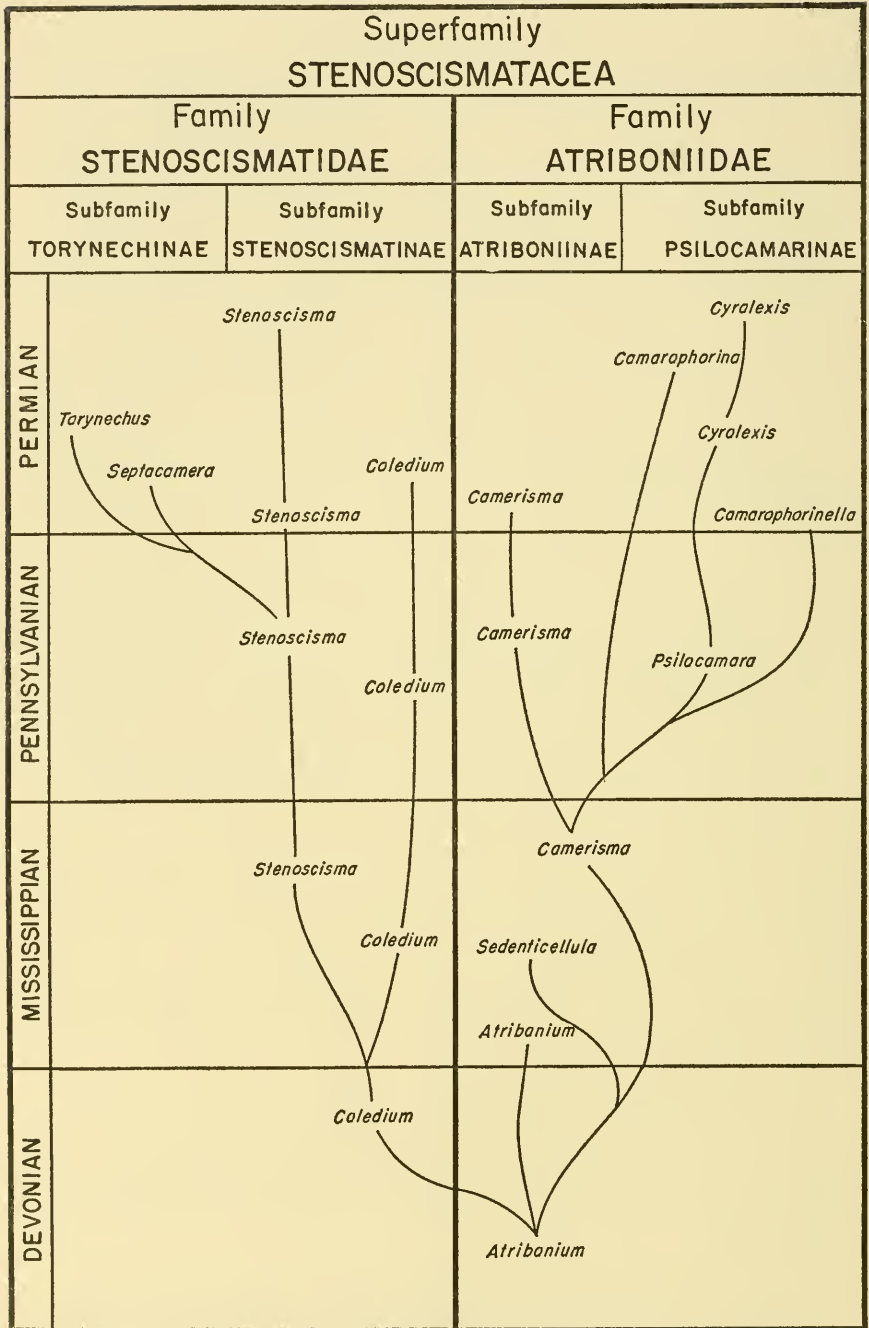


FIG. 3.—Phylogeny of the Stenoscismatacea.

boniinae. The Psilocamarinae are characterized by modifications of the hinge plate and intercamarophorial plate. In *Psilocamara* and sulcate *Camarophorina* the hinge plate is undivided, but the intercamarophorial plate is entirely absent. The trend toward costation became re-established weakly in Permian *Cyrolexis* n. gen., whose hinge plate is complete or perhaps shallowly recessed at the anterior, but whose intercamarophorial plate is very short and thin, or absent.

The hinge plate of *Camarophorinella* Licharev is deeply divided, the intercamarophorial plate entirely absent, and the edges of the posterior part of the camarophorium attach directly to the sides of the hinge plate. Externally, the genus bears little resemblance to others of the Psilocamarinae, its shape and costation most nearly resembling *Sedenticellula* of the Atriboniinae.

The edges of the posterior part of the camarophorium meet the hinge plate also in the sulcate and typically smooth genus *Camarophorina*. If Lower Carboniferous shells from England prove to belong to this genus, it will be the earliest known member of the Psilocamarinae.

FAMILY STENOSCISMATIDAE

This family probably originated from *Atribonium* during the Devonian. The earliest genus with a stolidium is *Coledium* n. gen., although Devonian and Early Mississippian species of that genus lack that structure. Late Paleozoic members of the family can be divided into two subfamilies on the basis of retention or atrophy of the stolidium, and rhynchonelliform or uncinuliform shape.

Subfamily Stenoscismatinae.—The stolidium and a normal rhynchonelliform shape characterize the two genera of this subfamily. *Coledium* extends from the Late Devonian into the Permian, and *Stenoscisma* Conrad began in the Late Mississippian and continued through the Permian. The stolidium is best developed in this genus. Species of *Stenoscisma* whose beaks are relatively straight have the delthyrium constricted by deltidial plates that appear typically rhynchonelloid. Many later species have the pedicle beak tightly curved over the brachial beak, thus constricting or closing the delthyrium. Costation is highly variable among the Stenoscismatinae, but internal structures are entirely normal for the superfamily, with spondylium, camarophorium, hinge plate, and intercamarophorial plate consistently and proportionately developed in all species.

Subfamily Torynechinae.—The two genera of this subfamily are externally uncinuliform and strongly costate; inner structures are normal for the superfamily according to present knowledge. *Septacamera* Stepanov of the Late Pennsylvanian and Early Permian may

have "lateral buttress plates" to the spondylium (Stepanov, 1937), but internal structures of the Permian genus *Torynechus* Cooper and Grant are exactly like those of *Stenosisma*.

Torynechus probably descended from *Stenosisma* by reduction of the stolidium to a marginal ridge, thickening to an uncinuliform shape, and by development of finer, more numerous costae. *Septacamera* lacks any trace of the stolidium, and is assigned to the Torynechinae mainly on the basis of an external shape like *Torynechus* and costation that recalls some species of *Stenosisma*.

CLASSIFICATION

HISTORY

The genus *Camerophoria* originally was described as, “. . . a shell approximating to *Pentamerus* in some points of its internal structure” (King, 1844). In 1850 King assigned it to the family Hypothyridae along with *Pentamerus* and several other genera. Davidson (1858, p. 23, 90) assigned it to the Rhynchonellidae, and since then opinion has been divided on the proper place for *Camerophoria* (now *Stenoscisma*) and its relatives.

Hall and Clarke (1894, p. 214) said that “*Camerophoria* is a genus combining a modified pentameroid interior with a rhynchonelloid exterior.” Hall (1867) classified it in the Rhynchonellidae, but at the time the family included *Pentamerus* as well. Waagen (1883, p. 412, 435) established the Camerophoriinae as a subfamily of the Rhynchonellidae, equal in rank to the subfamily Pentamerinae. Schuchert (1896, in Zittel and Eastman) elevated the Pentameracea to equal rank with the superfamily Rhynchonellacea, subdividing it into families, with *Camerophoria* included with the Pentameridae. Subsequently, many authors accepted this usage; Girty (1909), Weller (1914), Broili (1916), Grabau (1931 a and b, 1934), and Easton (1962) are important works in which “*Camerophoria*” is classed with the Pentameridae.

Kozłowski (1929, p. 132) recognized the Pentameracea as consonant with the Rhynchonellacea, following Schuchert (1897) but placed the Camerophoriidae with the latter. Schuchert and Cooper (1932) excluded *Camerophoria*-like forms from their monograph of the order Pentameroidea, and most subsequent authors have agreed with them and with Kozłowski that these forms belong in the Rhynchonelloidea (e.g., Cooper, 1944; Stehli, 1954; Rzhonsnitskaya, 1958, 1959; Licharev, 1960; Shaw, 1962).

Shrock and Twenhofel (1953) introduced the superfamilial name Stenoscismacea for the group after it had become generally accepted that *Camerophoria* must be abandoned as an objective junior synonym of *Stenoscisma*. This superfamily name was corrected by Muir-Wood (1955) to Stenoscismatacea, and the group was classed with the Rhynchonelloidea. The International Code of Zoological Nomenclature (1961, article 40) requires retention of family-group names that are based on junior synonyms, unless this synonymy was discovered before 1961, the family-group name changed, and the change generally accepted. As Schmidt (1964, p. 132) has pointed out, the family-group

names based on *Stenoscismatinae* Oehlert (1887) were in general use prior to 1961, and should be retained in the interest of stability. She has requested the International Commission on Zoological Nomenclature to put this name on the Official List of Family-Group Names in Zoology. The Rules require, however, that the pertinent date in this case is the first recognition of the family-group, and this is the date of Waagen's (1883) establishment of the *Camarophoriinae*.

EVIDENCE

Early comparison of internal structures of stenoscismatids with those of pentamerids led to classification of the two groups together. The apparent similarities are striking. The high camarophorium in the dorsal valve of the *Stenoscismatacea* is nearly identical in shape to the high ventral spondylium of the *Pentameracea*, and the longitudinal profile of the ventral spondylium of the *Stenoscismatacea* resembles that of the elongate dorsal cruralium of some pentameroids (Schuchert and Cooper, 1932, pl. 26, figs. 31, 35, 40).

Upon analysis, however, the internal structures of the two groups are seen to be unrelated; the similar-appearing structures are in opposite valves. The high spondylium of the pentameroids necessarily must have seated the diductor muscles, and muscle scars are visible there (Schuchert and Cooper, 1932, p. 164), whereas the high structure of the *Stenoscismatacea* is in the opposite valve, and probably bore the adductor muscles on its inner surface.

The brachial processes of the pentameroids are fused to the septal plates, but in the *Stenoscismatacea* they extend anteriorly from the edge of a rhynchonelloid hinge plate and are free for most of their length. These processes are considered the same or analogous to the crura of the *Rhynchonelloidea*, and constitute a strong argument for inclusion of the *Stenoscismatacea* with that suborder (e.g., Muir-Wood, 1955).

The most advanced, and in the U.S. National Museum collection the best preserved, genus of the *Stenoscismatacea* is *Stenoscisma*. Many species of this genus have well-developed deltidial plates to constrict the delthyrium and outline the pedicle foramen. Small deltidial plates are visible on well-preserved specimens of *Torynechus* and *Atribonium* as well. Deltidial plates are characteristic of most rhynchonelloids, but are entirely absent from *Pentameroidea* (Schuchert and Cooper, 1932, p. 163).

Permian representatives of *Stenoscisma* have an elaborate system of bifurcating pallial markings that were well illustrated by King (1850, pl. 8). These resemble the bifurcating pallial systems of some rhynchonelloids and orthoids (Cooper, 1944; Williams, 1956), be-

ginning as two main vascular trunks, dividing rather symmetrically, and becoming finer toward the shell margins. In the Pentameroidea, on the other hand, the pallial sinuses are weakly impressed and their pattern for the whole group is not known certainly. Williams (1956) described the pattern of some pentameroids as lemniscate, with several main trunks, in contrast to the rhynchonelloid pattern seen in the Stenoscismatacea.

The preponderance of evidence favors the currently accepted opinion that the Stenoscismatacea are properly classified with the Rhynchonelloidea rather than with the Pentameroidea. However, they are sufficiently different from most other rhynchonelloids to warrant status as a separate superfamily within that suborder.

MEASUREMENTS

Dimensions of length, width, and thickness are included with descriptions of all new species, and some previously described species that are abundantly represented in the U.S. National Museum collections, or are important to the phylogeny of the superfamily. These measurements are presented to illustrate the range in size of species and the proportions of the individual specimens. Where abundant well-preserved specimens of species of the new genera *Atribonium* and *Coledium* were available, the numerous measurements are summarized on scatter diagrams, to show patterns of growth.

KEY TO THE STENOSCISMATACEA

- Rhynchonelloids with spondylium and
 camarophorium Stenoscismatacea
- A. Stenoscismatacea with stolidium or uncinuliform
 outline Stenoscismatidae
- I. Rhynchonelliform Stenoscismatidae with
 stolidium, beaks smooth Stenoscismatinae
1. Stolidium on adults of all species, costae
 commonly strong *Stenoscisma*
2. Stolidium on adults of few species, costae
 commonly weak or absent *Coledium**
- II. Uncinuliform Stenoscismatidae without stolidium,
 beaks costate Torynechinae
1. Costae fine, numerous, remnant of
 stolidium at anterior margin *Torynechus*

* Small *Coledium* that lacks a stolidium can be distinguished from *Atribonium* by the sharp angle of meeting of the valves of the anterior, and commonly by the weak or absent costae.

- 2. Costae high, strong ; stolidium completely absent *Septacamera*
- B. Stenoscismatacea without stolidium Atriboniidae
 - I. Atriboniidae with intercamarophorial plate . . . Atriboniinae
 - 1. Valves meeting nearly in plane at anterior . . . *Atribonium**
 - 2. Numerous low costae, valves meeting at sharp angle *Sedenticellula*
 - 3. Costae very weak or absent, fold very high *Camerisma*
 - II. Atriboniidae without intercamarophorial plate Psilocamarinae
 - 1. Edges of camarophorium touching hinge plate
 - a. Globular shape, weakly hemicostate *Cyrolexis*
 - b. Numerous fine costae over most of shell *Camarophorinella*
 - 2. Smooth shell
 - a. Uniplicate commissure *Psilocamara*
 - b. Sulcate commissure *Camarophorina*

* Small *Coledium* that lacks a stolidium can be distinguished from *Atribonium* by the sharp angle of meeting of the valves at the anterior, and commonly by the weak or absent costae.

SYSTEMATIC PALEONTOLOGY

Phylum BRACHIOPODA

Class ARTICULATA

Suborder RHYNCHONELLOIDEA Moore, 1952

[*nom. correct.* Muir-Wood, 1955, p. 69 (*ex* Rhynchonellacea Moore, *in* Moore, Lalicker and Fischer, 1952, p. 220)]

Superfamily STENOSCISMATACEA Oehlert, 1887 (1883)

[*nom. correct.* Muir-Wood, 1955, p. 69 (*pro* Stenosismatacea Shrock and Twenhofel, 1953, p. 317; *nom. transl. et correct. ex* Stenoschismatinae Oehlert, 1887, p. 1304)] [= Camerophoriacea Waagen, 1883 (*nom. transl.* Grabau, 1936, p. 70 *ex* Camerophoriinae Waagen, 1883, p. 435)]

Family ATRIBONIIDAE Grant n. fam.

Stenosismatacea without stolidium, ranging from Middle Devonian through Permian without clear evolutionary trends except general increase in size; costae absent, weak, or fine, not strong.

Subfamily ATRIBONIINAE Grant n. subfam.

Atriboniidae with intercamarophorial plate strong, extending anteriorly beyond undivided hinge plate.

Genus ATRIBONIUM Grant n. gen.

(A, Gr., without; tribonion, Gr., cloak)

Shell about average size for family, flatly to strongly biconvex; outline rotund, subtrigonal to subelliptical, normally widest anterior to midlength; anterior margin normally flat or slightly emarginate; anterior commissure uniplicate; fold rather low, broad, crest flat, standing only slightly above flanks, normally with several low plications; sulcus shallow, beginning 5–10 mm. anterior to pedicle beak, trough flattened, depressed only slightly at anterior just behind strong flexure around anterior margin; flanks with costae beginning about 5 mm. anterior to beaks, number on each side about equal to number on fold; posterolateral commissure with only narrow overlap of valves; valve edges slightly protruding around anterior of some species, not extended to form stolidium; growth lines fine, closely spaced, stronger growth laminae rare; radial ornamentation consisting of fine, fibrous shell substance.

Pedicle valve flatly convex transversely, strongly flexed through sulcus, slightly swollen in umbonal region; beak curved, somewhat flattened, acute, with beak ridges distinct although normally short and somewhat blunt; delthyrium small, triangular, sides normally constricted by pair of small, triangular, conjunct or nearly conjunct deltidial plates; foramen small, slit like.

Brachial valve somewhat more convex transversely, strongly curved near anterior margins to produce flattened anterior and flanks; umbonal region transversely convex, longitudinally slightly convex, rather flat, or slightly depressed in some species; brachial beak curved, normally within pedicle valve behind deltidial plates.

Pedicle valve interior with strong dental plates converging slightly toward floor, intersecting floor in apical region of some species, normally abruptly curved to meet one another above floor, fusing to form short median septum duplex; height of septum increasing only slightly toward anterior; dental plates terminating near back, leaving fused portion supported by median septum to form shallow spondylium extending forward about one-third valve length; septum continuing forward to near midlength.

Brachial valve interior with short undivided hinge plate projecting forward slightly along midline; crura slender, extending forward from anterior edge of hinge plate, somewhat tapered anteriorly, continuing forward about one-fourth length of valve; median septum beginning at apex, supporting hinge plate; camarophorium beginning in apex as slight swelling of septum about midway between floor and underside of hinge plate, swelling and becoming wider anteriorly, each side expanding and curving ventrally to produce spoon-shaped camarophorium bisected by intercamarophorial plate supporting hinge plate; intercamarophorial plate thinning and declining anterior to hinge plate, disappearing about 2 mm. anterior to beak; camarophorium capping median septum anterior to termination of intercamarophorial plate, height of septum increasing anteriorly causing camarophorium to curve ventrally, sides of camarophorium becoming thinner and more nearly parallel to valve floor toward anterior, narrowing near termination just short of midlength of shell, about one-third to one-half length of brachial valve.

Type species.—*Atribonium simatum* n. sp.

Diagnosis.—*Atribonium* is characterized by its small size, wedge-shaped to elliptical outline, flat to strongly convex profile with rounded, flattened, or slightly emarginate anterior, high flat-crested fold at the commissure that does not produce a high crest on the valve, short mesial costae that begin far anterior to the beaks, well-developed lateral costae, and lack of a stolidium. Internally the spondylium is com-

pletely elevated in some specimens, partly sessile in others; an intercamarophorial plate is present in the brachial valve; the camarophorium is elevated, intersecting the floor only at its origin in the apex of the beak, and curving ventrally only slightly throughout its length.

Discussion.—No known specimen of *Atribonium* has a stolidium such as that in *Stenoscisma*, but the commissure on some adults protrudes slightly as though anticipating development of that structure later in the history of the superfamily. This modification of the valve edges suggests that *Atribonium* is ancestral to *Stenoscisma*. The sporadically partly sessile spondylium may indicate relationship with the Mississippian *Sedenticellula* in which the spondylium also is sessile in some species. The species of *Atribonium* that are more bulbous than wedge-shaped in profile (e.g., *A. gregeri* (Branson)), with the anterior margin less flattened than is typical, resemble the type species *Sedenticellula hamburgensis* (Weller) in that respect. The bulbous forms also have the costae beginning somewhat farther to the posterior, indicating possible ancestry to the Mississippian form. Juveniles of *Atribonium* have the valves meeting at an acute angle as in *Sedenticellula sacra* n. sp., also indicating a possible link between the two genera.

The intercamarophorial plate of *Atribonium* is duplex, with a narrow band separating the two halves. Each side appears to be derived from the underside of the hinge plate, and to extend to the top of the camarophorium, there to fuse. This conclusion agrees with that of Kozłowski (1929) and Licharev (1936) that the intercamarophorial plate is independent of the median septum of the camarophorium. The camarophorium itself begins as a swelling at the top of the septum in the apical part of the valve, supporting the opinion of the above two authors that the camarophorium formed by modification of the ventral edge of the median septum, not from the hinge plate or the crura.

Growth.—Small juvenile shells of *Atribonium* lack the flattened anterior margin. The valves meet at an acute angle rather than butting directly nearly in one plane as in most adults. Flattening normally begins when the valve has attained a length of 5–7 mm., but some specimens retain their juvenile characteristics to normal adult size. Most adults are 10–15 mm. in length, much of the growth of 10 mm. or larger shells involves increase in volume of the shell by increasing its thickness rather than its length.

The pedicle beak of *Atribonium* is not strongly curved and does not press against the brachial umbo. The foramen, therefore, is not reduced or pinched drastically as in some of the late genera of the superfamily (e.g., Late Permian species of *Stenoscisma*). Presumably, the unconstricted foramen contained a functional pedicle in life, and the

shell attached to some object that kept it suspended above the sea floor.

Assigned species.—The following species are assigned to *Atribonium* (age and occurrence listed for those not discussed further) :

- A. simatum* n. sp. (Type species)
Seminula bisinuata Rowley 1900, Lower Mississippian, Missouri
A. cooperorum n. sp.
Rhynchonella gainesi Nettelroth 1889, Middle Devonian, Kentucky, Indiana
Rhynchonella gainesi cassensis Kindle 1901, Middle Devonian, Indiana
Hypothyris gregeri E. B. Branson 1923
Stenoscisma halli Fagerstrom 1961
S. illinoisensis Cooper 1945, Middle Devonian, Illinois
Pugnax kernahani Whiteaves 1898
Camarophoria nora Belanski 1928, Upper Devonian, Iowa
Camarophoria obesa Clark, of Shaw, 1962, only (not Clark, 1917), Lower Mississippian, Montana
Camarophoria paupera Belanski 1928
C. perplexa Belanski 1928, Upper Devonian, Iowa
A. pingue n. sp.
C. planodorsata Belanski 1928, Upper Devonian, Iowa
C. prolifica Belanski 1928, Upper Devonian, Iowa
C. retziaformis Belanski 1928, Upper Devonian, Iowa
Stenoscisma rhomboidalis Fagerstrom 1961 (not Hall and Clarke)
A. rostratum n. sp.
S. savagei Cooper 1945, Middle Devonian, Illinois
Pugnoides subovata Savage 1921, Middle Devonian, Illinois
Septalaria (?) *subtransuralica* Khodalevitch 1961, Lower Devonian, USSR
A. succiduum n. sp.
Pugnoides swallovi E. B. Branson 1923, Middle Devonian, Missouri
Rhynchonella transuralica Tschernyshev 1893, Lower Devonian, USSR
Stenoscisma uniplicata Shaw 1962, Lower Mississippian, Montana
 (?) *Camarophoria walteri* E. B. Branson 1938, Lower Mississippian, Missouri

ATRIBONIUM SIMATUM Grant n. sp.

Plate 1, figs. 1-12; figures 4, 5, 6

Shell small, flatly biconvex; outline subtrigonal with length and width nearly equal, widest near anterior; commissure uniplicate, fold low, broad, flat, expressed on surface of brachial valve as low flat ridge beginning to stand above flanks about 5 mm. anterior to brachial beak; sulcus shallow, broad, beginning 5-7 mm. anterior to pedicle beak; costae low rounded, simple, beginning 3-5 mm. anterior to beaks, numbering four to seven on fold, one fewer in sulcus, three to six on each flank; anterior margin flattened or slightly emarginate; growth lines fine, closely spaced; growth laminae weak, irregularly and widely spaced.

Pedicle valve flatly convex, slightly swollen just anterior to beak, strongly curved through sulcus, flanks abruptly bent toward commissure; beak sharp, strongly curved to suberect or erect position; beak ridges short, distinct but not sharp; posterolateral slopes slightly compressed; delthyrium small, triangular, constricted by a pair of small deltidial plates leaving small slit-shaped foramen.

Brachial valve more strongly convex in adults, convexity normally fairly even, slight swelling near beak in some individuals; margins abruptly bent toward commissure, producing flat anterior; beak short, blunt, apex inside delthyrium.

Pedicle valve interior with dental plates slightly convergent toward floor near apex, meeting floor in extreme apex of some specimens, normally bending abruptly just above floor to converge and fuse with one another, forming elevated deep spondylium, continuing to floor as median septum duplex supporting spondylium; anterior edges of dental plates concave anteriorly, extending along sides of spondylium only about 1 mm.; floor of spondylium extending anteriorly as shallow trough for about 4 mm.; median septum increasing in height only slightly anteriorly, extending about 5 mm. anterior to pedicle beak, slightly farther than spondylium; muscle and pallial marks not observed.

Brachial valve interior with short median septum in apex, increasing greatly in height toward anterior; crest of septum spread to form narrow, elongate, shallow camarophorium, beginning near floor of valve in apex as slight swelling of crest of septum, becoming well-defined trough less than 1 mm. anterior to beak; median line of trough intersected by low duplex intercamarophorial plate extending from underside of hinge plate, extending forward beyond hinge, there forming median septum in camarophorium with free crest; hinge plate short, anteriorly tapering, apical part slightly swollen to form cardinal process; crura extending anteriorly from anterior edge of hinge plate, long slender, curving ventrally, somewhat shorter than camarophorium or ventral spondylium; muscle and pallial marks not observed.

Holotype.—USNM 141966, plate 1, fig. 7.

Growth.—The graphic pattern of growth for this species is normal for the genus, with points indicating the length-width ratio clustered narrowly along a straight line, and those representing the length-thickness ratio somewhat more widely spread along a curve of gentle acceleration (fig. 6). Young shells are slightly elongate, and mature shells somewhat transverse; only one shell is as thick as it is long. Projection of the length-width trend toward zero or 0.5 on the length-axis indicates a slight change in slope, probably resulting from allometric growth at the smallest post-larval stages. The length-thickness curve can be projected with little or no change in curvature.



FIG. 4.—*Atribonium simatum* n. sp., Newton Creek Limestone, Mich., USNM 141973. Longitudinal section through midline, $\times 5$, showing profiles of camarophorium, hinge plate, and septum of spondylium.

Comparisons.—*Atribonium simatum* is characterized by its sub-trigonal outline, rather flat valves with most of thickness of shell provided by the rather abrupt geniculation of the valves near the anterior, its costate fold and flanks, with normally four but as many as seven on the fold, its flat or slightly emarginate anterior, and sharp beak with distinct beak ridges. It resembles *A. cooperorum* n. sp. from the Bell

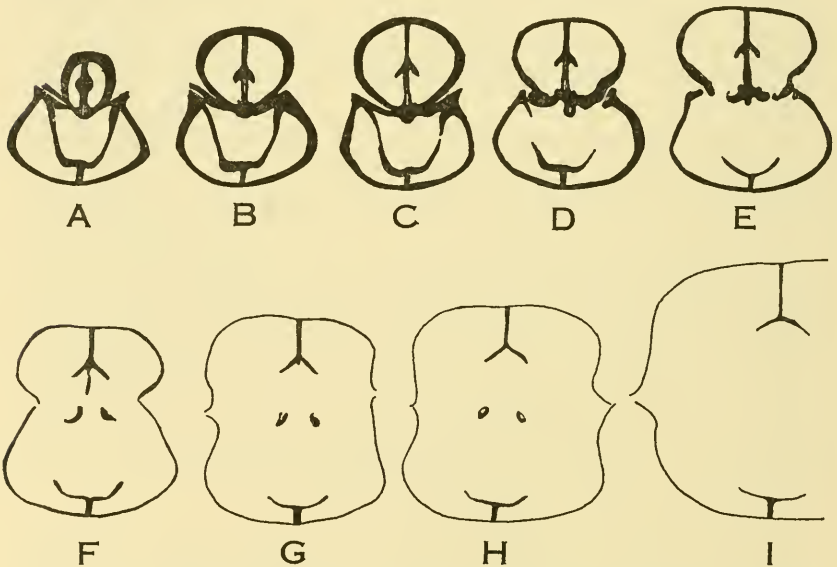


FIG. 5.—*Atribonium simatum* n. sp., Newton Creek Limestone, Mich., transverse sections $\times 6$, USNM 141977, original length: ca. 11.5 mm., all measurements from pedicle valve beak.

A. 0.6 mm.: camarophorium just a swelling on septum, intercamarophorial plate nearly duplex. B. 0.7 mm.: camarophorium wider. C. 0.8 mm.: cardinal process higher. D. 1.0 mm.: maximum height of cardinal process. E. 1.2 mm.: hinge plate detached from walls. F. 1.5 mm.: intercamarophorial plate thin, crural bases apparent. G. 1.6 mm.: intercamarophorial plate gone. H. 1.9 mm.: crura present. I. 2.5 mm.: no crura.

TABLE 1.—*Measurements of Atribonium simatum from Newton Creek Limestone, quarry of Michigan Alkali Co., Alpena, Mich.*

USNM No.	<i>Measurements, in millimeters</i>		
	Length	Width	Thickness
141955	4.3	3.8	1.9
141956	5.0	4.6	2.9
141957	5.6	5.6	3.4
141958	6.6	6.6	3.8
141959	6.9	6.6	3.8
141960	7.7	7.7	6.0
141961	8.0	8.0	4.3
141962	8.9	8.4	6.0
141963	8.9	8.9	6.2
141964	c.9.0	10.8	6.0
141965	10.6	11.3	7.8
141966	10.8	12.5	8.2
141967	11.3	13.2	9.3
141968	11.5	13.0	9.8
141969	11.8	12.6	10.8
141970	12.2	13.8	9.4
141971	12.3	13.1	8.4
141972	13.0	14.9	6.8

Shale in size, but differs in its more trigonal outline with flat or emarginate anterior, more numerous costae on the fold, greater thickness, weaker costae, and less prominent fold. It differs from *A. pingue* n. sp. from the Four Mile Dam Formation in its normally lesser thickness, lower convexity, emarginate or flattened anterior, and subtrigonal rather than subpentagonal outline. It also is similar to *A. succiduum* n. sp. from the Potter Farm Formation, differing in its larger size, more numerous costae on the fold and flanks, sharper beak ridges, and proportionately shorter median septa.

Atribonium simatum is wider and less convex than *A. halli* (Fagerstrom) and *A. rhomboidale* (of Fagerstrom); its fold is lower, and costae more numerous and weaker, and its anterior is flattened. It is narrower and more weakly costate than *A. savagei* (Cooper) from the Grand Tower Limestone of Illinois, its anterior margin is flatter (or emarginate) and the shell outline subtrigonal, the profile lower and less convex. *A. simatum* differs from *A. illinoisensis* (Cooper), also from the Grand Tower Limestone, in its flatter anterior, subtrigonal outline, lower fold, and more numerous costae on fold and flanks.

Species of *Atribonium* that least resemble *A. simatum* are *A. gregeri* (Branson), *A. kernahani* (Whiteaves) and *A. pauperum* (Belanski). *A. simatum* is not bulbous like *A. gregeri*, and it lacks the exaggerated costae of the other two species.

Occurrence and abundance.—Newton Creek Limestone, quarry of

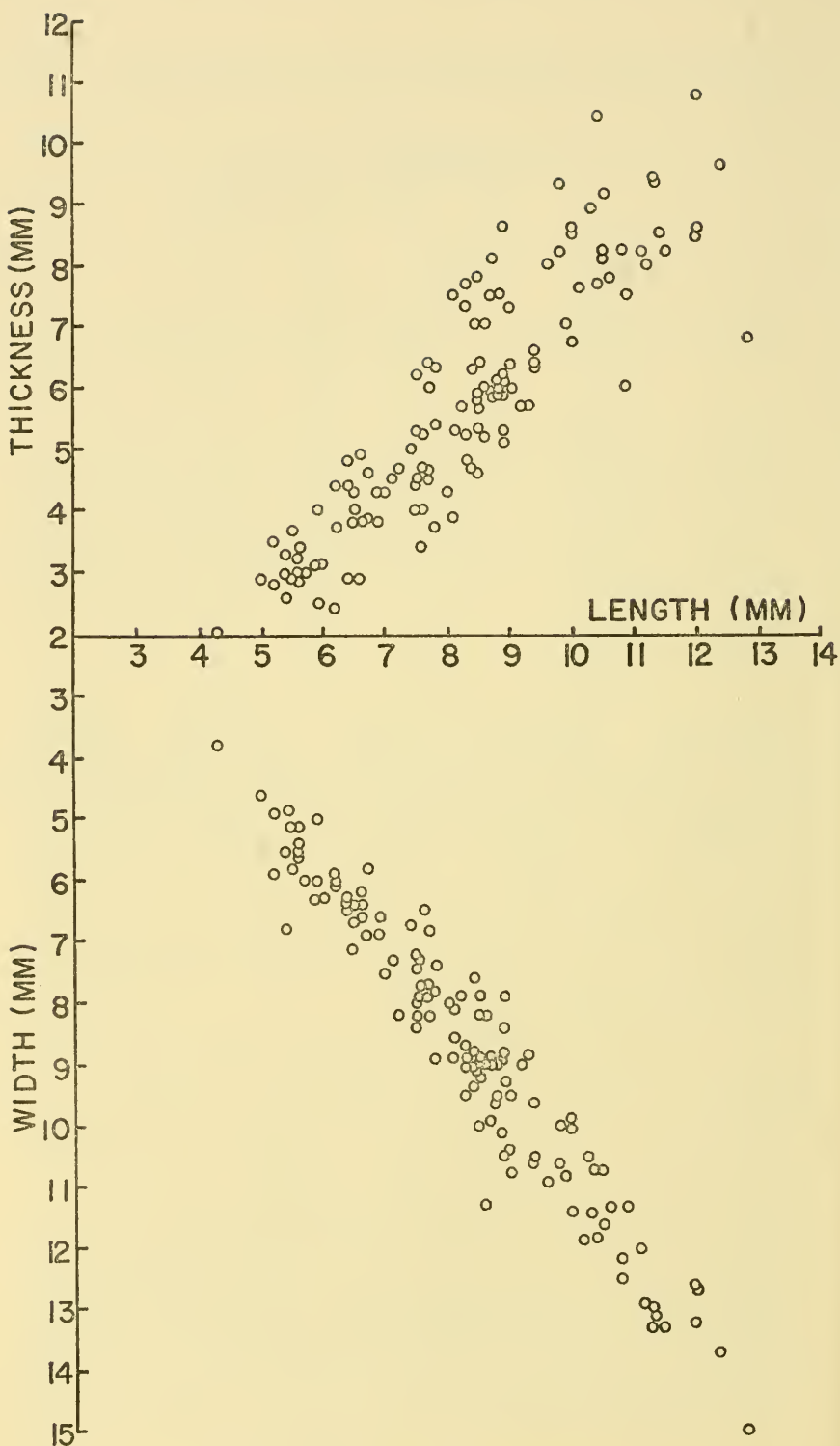


FIG. 6.—(See opposite page for legend.)

Michigan Alkali Co., Alpena, Mich. (151 specimens USNM 141974–5, 141980–82); Dock Street Clay of Grabau (1902) of Alpena Limestone, Thunder Bay Quarry, Alpena, Mich. (1 specimen USNM 141984); Newton Creek east side of French Road, ½ mile south of NW. corner, sec. 16, T-32-N, R-8-E, Alpena County, Mich. (1 specimen USNM 141979: float); Alpena Limestone, 0.15 mi. south of NW. corner, sec. 11, T-31-N, R-8-E, on Long Lake Road, Alpena County, Mich. (1 specimen USNM 141983); lower 10 feet of Ferron Point Formation, at Rockport Quarry, Rockport, Mich. (1 specimen USNM 141978).

Age.—Middle Devonian.

ATRIBONIUM COOPERORUM Grant n. sp.

Plate 2, figs. 3–3c; figure 7

Shell small, flatly biconvex; outlines subtrigonal to subpentagonal, length and width nearly equal, greatest width near midlength; commissure uniplicate; fold high, rather broad, with gently arched or flattened crest, forming prominent fold on brachial valve beginning 4–8 mm. anterior to beak; sulcus extended as tongue at anterior to fill arch of fold, producing broad shallow trough in pedicle valve beginning 4–8 mm. anterior to beak, costae moderately strong, with bluntly angular crests, beginning 4–6 mm. anterior to beaks, numbering four to six on fold (normally four), one fewer in sulcus, four to six on each flank (normally six); anterior margin gently rounded or slightly flattened, not emarginate, valves meeting at less than straight angle at anterior commissure; growth lines fine, closely spaced; growth laminae weak, irregularly spaced, rarely observed.

Pedicle valve flatly convex, with greatest convexity just anterior to beak, abruptly flexed toward commissure at anterior flanks, more evenly and gently curved along midline through sulcus; beak sharp, strongly curved, suberect to erect; beak ridges short, sharp; posterolateral slopes slightly concave in outline but not flattened; delthyrium small, constricted by pair of small, acutely triangular, conjunct or disjunct deltidial plates, leaving small slotlike foramen penetrating apex of beak in some specimens.

Brachial valve more strongly convex transversely, less convex longitudinally, slightly swollen near back, fold prominent at anterior, abruptly bent toward commissure at anterior flanks, more gently bent at anterior of fold; beak short, rounded, apex within delthyrium, obscured by deltidial plates.

Pedicle valve interior with dental plates converging to form spondylium, in configuration normal for genus; spondylium normally sessile in apex of beak, remaining sessile as much as 1.5 mm. along floor; anterior extent of spondylium not ascertained; median septum elevating anterior part of spondylium extending along floor about half length of shell, as much as 6 mm. in largest specimens.

Brachial valve interior with elevated camarophorium; expansion of crest beginning against beak of valve, septum extending anteriorly slightly beyond midlength, considerably beyond midlength of valve.

Holotype.—USNM 141822, plate 2, fig. 3b.

Comparisons.—*Atribonium cooperorum* is characterized by its flat convexity, evenly curved anterior margin, rather prominent fold, strong costae at anterior, and sharp pedicle beak with sharp beak

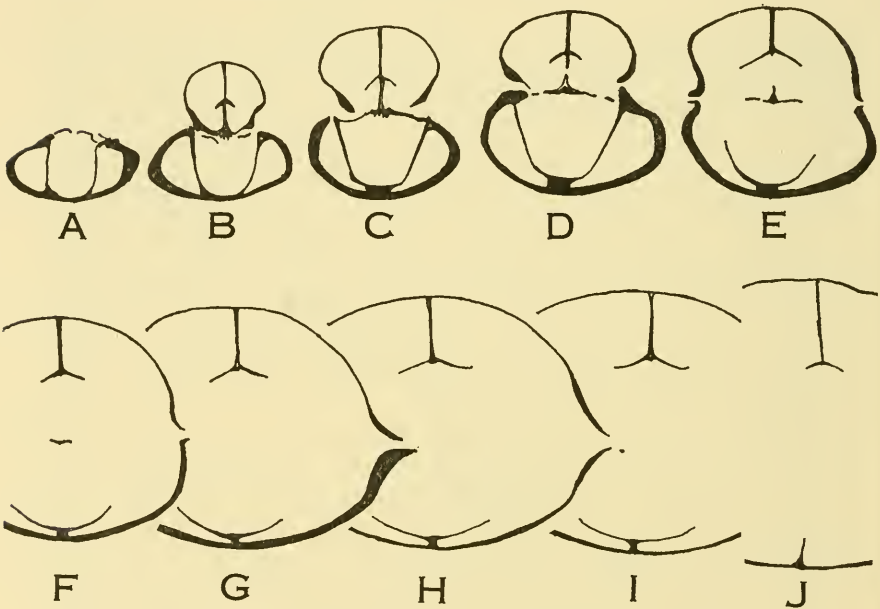


FIG. 7.—*Atribonium cooperorum* n. sp., Bell Shale, Rogers City, Mich.; transverse sections $\times 6$, USNM 141825, original length 9.1 mm., all measurements from pedicle valve beak.

A. 0.3 mm.: spondylium sessile. B. 0.5 mm.: camarophorium and cardinal process visible, spondylium still sessile. C. 0.8 mm.: spondylium elevated. D. 1.1 mm.: hinge plate detached from walls, intercamarophorial plate separated. E. 1.4 mm.: dental plates detached. F. 1.8 mm.: hinge plate small, intercamarophorial plate absent. G. 2.1 mm.: hinge plate absent. H. 2.5 mm.: camarophorium wide. I. 2.9 mm.: camarophorium wider. J. 4.2 mm.: only septum remains of spondylium, camarophorium narrow, high; camarophorium extends to 4.5 mm. from beak.

TABLE 2.—*Measurements of Atribonium cooperorum from the Bell Shale, quarry of Michigan Limestone and Chemical Co., Calcite, east of Rogers City, Presque Isle County, Mich.*

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
141816	6.4	6.1	3.9
141817	6.9	6.5	4.6
141818	7.8	7.8	5.3
141819	7.9	7.9	6.6
141820	8.3	8.7	5.2
141821	9.3	10.1	7.0
141822	9.3	10.2	6.5
141823	10.0	10.0	7.1
141824	10.5	10.4	7.0

ridges. It most nearly resembles *A. simatum* n. sp. from the lower part of Alpena Limestone, differing from that species in its more pentagonal than trigonal outline, rounded or nearly flattened but not actually flat or emarginate anterior surface, its fewer costae on the fold, and its more prominent fold. It is thinner than *A. pingue* n. sp. from the Four Mile Dam Formation, and also has stronger, more numerous costae on fold and flanks, has a more strongly curved pedicle beak and more prominent fold, attains larger size, and is less convex. The height of the fold recalls that of *A. rhomboidale* (of Fagerstrom) and *A. halli* (Fagerstrom), but *A. cooperorum* has lower, narrower, and more numerous costae on fold and flanks, and a much wider, less elongate outline.

Occurrence and abundance.—USNM loc. 31c, Bell Shale, in quarry of Michigan Limestone and Chemical Co. at Calcite, east of Rogers City, Presque Isle County, Mich. (44 specimens USNM 141826, 141834, 141835); USNM loc. 31h, Bell Shale in same quarry, NE. side of railroad track, in shale dump (11 specimens USNM 141827); USNM loc. 31, Bell Shale in sink, same quarry, sec. 36, T-34-N, R-6-E, (3 specimens USNM 141828); USNM loc. 38e, lower part of Ferron Point Formation, in quarry at Rockport, northeast corner, Alpena County, Mich. (1 specimen USNM 141829, aff. *A. cooperorum*); Ferron Point Formation, uppermost beds in quarry at Rockport, Mich. (3 specimens USNM 141830, aff. *A. cooperorum*); Ferron Point Formation (bed D), south end Black Lake, NW. $\frac{1}{4}$, SW. $\frac{1}{4}$, sec. 7, T-35-N-R-2-E, Presque Isle County, Mich. (1 specimen USNM 141831, aff. *A. cooperorum*); lower part of Ferron Point, sink in Rogers City Limestone, NW. $\frac{1}{4}$, SW. $\frac{1}{4}$, sec. 21, T-35-N-R-6-E, Adams Point, Presque Isle County, Mich. (2 specimens USNM 141832, 141833, between *A. cooperorum* and *A. simatum*).

Age.—Early Middle Devonian.

ATRIBONIUM GREGERI (Branson)

Plate 3, figs. 1-1E; figures 8, 9

Hypothyris gregeri BRANSON, E. B., 1923, Missouri Bur. Mines & Geol., vol. 17, 2d ser., p. 91, pl. 17, figs. 5-7, 11-14.

Camarophoria gregeri (Branson) STAINBROOK, M. A., 1942, Journ. Paleont., vol. 16, No. 5, p. 615, pl. 88, figs. 16-21; text fig. 6.

Supplementary description.—**Shell** large for genus, strongly biconvex; globose; outline subcircular to subelliptical, width less than length in small specimens, more than length in large specimens, greatest width slightly anterior to midlength; commissure uniplicate, with broad, high, flat-crested fold at anterior, expressed only as slight elevation of median part of valve; sulcus shallow, scarcely depressed below flanks, broad, flat, extending anteriorly as broad tongue into deep fold; costae low, rounded, most simple, some bifurcating, beginning about 5 mm. anterior to beaks, numbering four to seven on fold, one fewer in sulcus, three to five on each flank; anterior margin of small shells flattened, of larger shells evenly convex; growth lines fine, closely and regularly spaced; growth laminae only slightly stronger, irregularly and more widely spaced.

Pedicle valve moderately convex transversely, more strongly convex longitudinally through sulcus; beak short, sharp, nearly straight; beak ridges distinct but blunt; posterolateral slopes slightly flattened, pinching in toward commissure in some specimens; delthyrium small triangular, nearly filled by small, triangular, conjunct deltidial plates, leaving minute foramen.

Brachial valve more strongly convex in both directions, slightly flattened along crest of fold; beak rather sharp, apex in pedicle valve hidden by deltidial plates.

Pedicle valve interior with dental plates converging, meeting one another to form spondylium; spondylium attached to floor of valve in apex, becoming elevated anteriorly on low median septum duplex; spondylium extending anteriorly about one-fourth length of valve, septum extending slightly farther.

Brachial valve interior with camarophorium supported by high median septum, extending anteriorly about half length of shell, beyond midlength of brachial valve; camarophorium beginning against floor of valve slightly anterior to apex of beak, joined to hinge plate by low intercamarophorial plate; hinge plate undivided, with slight swelling at posterior forming cardinal process; crura extending anteriorly from edge of hinge plate, above camarophorium, extending slightly farther anterior than camarophorium.

Lectotype (here designated).—*Hypothyris gregeri* Branson (1923, pl. 17, figs. 11-14) Callaway Limestone, Callaway County, Mo.

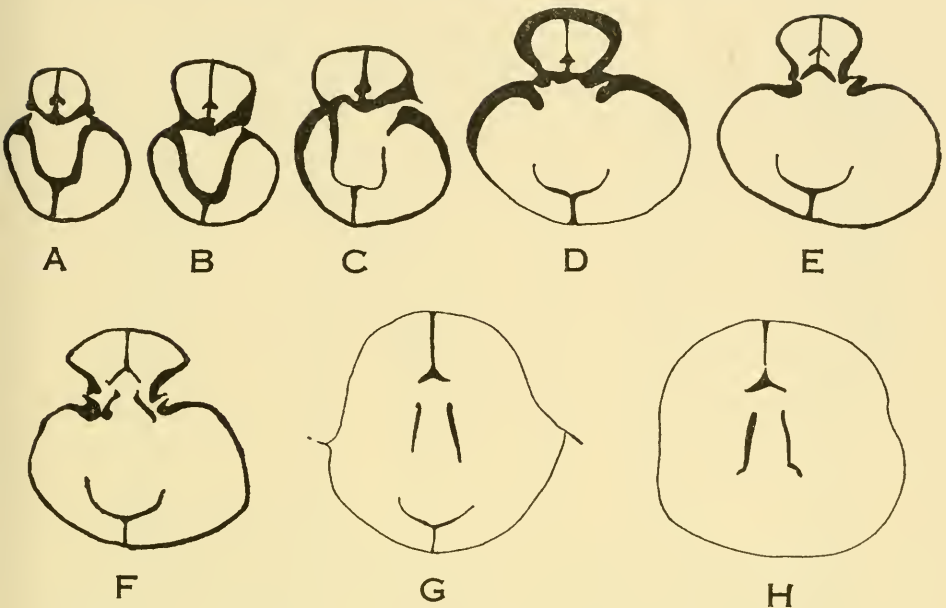


FIG. 8.—*Atribonium gregeri* (Branson), Cedar Valley Limestone, Iowa, transverse sections, $\times 6$, USNM 141857 cut perpendicular to surface of brachial valve to show true height of camarophorium (hence long crura in fig. G, H) original length: 9.9 mm., all measurements from pedicle valve beak.

A. 0.05 mm.: camarophorium thick. B. 0.1 mm.: low cardinal process. C. 0.2 mm. D. 0.6 mm.: dental plates detached from walls. E. 0.8 mm.: hinge plate detached from walls. F. 1.1 mm.: intercamarophorial plate gone, crural bases apparent. G. 1.3 mm.: cut at angle to camarophorium, apparently thickening spoon and showing crura. H. 1.5 mm.: spondylium gone. Crura disappear at 2.0 mm., camarophorium at 3.1 mm.

Growth.—This globose species exhibits a pattern of growth somewhat different from that of other species of *Atribonium*. Points representing the length-width ratio (fig. 9) cluster narrowly along a straight line, which is normal for the genus. However, points representing the length-thickness ratio cluster along a curve of gradual deceleration, where other species normally cluster near curves of acceleration (figs. 6, 10). *A. gregeri* is globose at an early stage, when the shell is only 6 or 7 mm. long. Subsequently the rate of increase in thickness declines slightly, compared with the rate of increase in length. Projection of this curve toward low values on the length-axis necessitates a reverse flexure, indicating that short shells probably were very flat as in other species of the genus. Projection of the length-width line also necessitates a slight change in declivity in the low values, but this is normal.

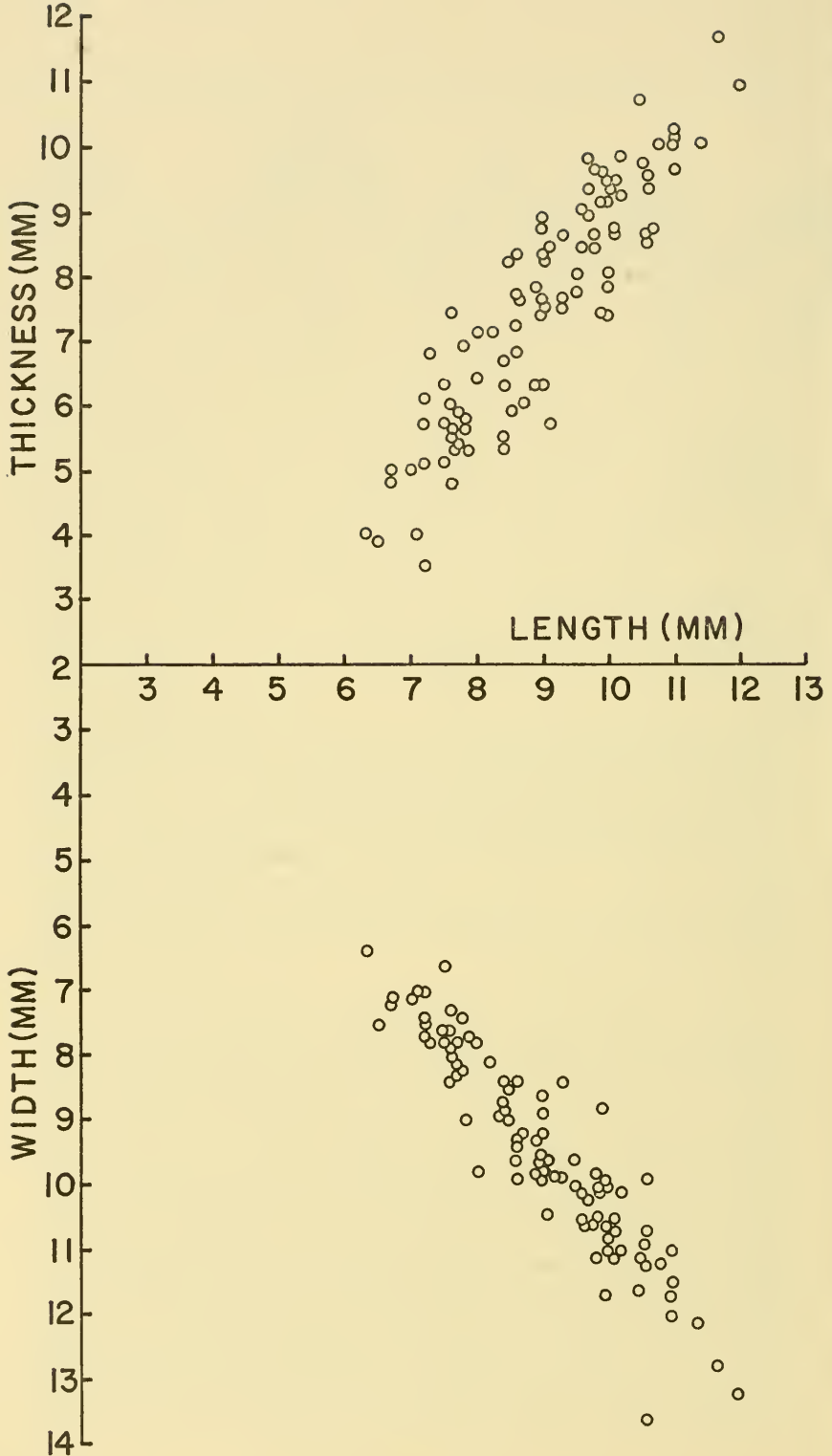


FIG. 9.—(See opposite page for legend.)

TABLE 3.—*Measurements of Atribonium gregeri*

USNM No.	<i>Measurements, in millimeters</i>			Formation	State
	Length	Width	Thickness		
141836	6.3	6.4	4.0	Callaway	Mo.
141837	6.7	7.8	5.4	Callaway	Mo.
141838	7.1	7.0	4.0	Cedar Valley	Ill.
141839	7.2	7.4	6.1	Callaway	Mo.
141840	7.6	7.6	5.6	Callaway	Mo.
141841	7.9	7.7	5.3	Cedar Valley	Iowa
141842	8.0	7.8	7.1	Callaway	Mo.
141843	8.6	8.4	7.2	Cedar Valley	Ill.
141844	c.9.0	8.9	6.3	Cedar Valley	Ill.
141845	9.3	9.9	7.6	Cedar Valley	Iowa
141846	9.5	9.6	7.7	Cedar Valley	Iowa
141847	9.8	10.6	8.6	Cedar Valley	Ill.
141848	10.1	11.1	8.6	Cedar Valley	Ill.
141849	c.11	12.0	9.6	Cedar Valley	Ill.
141850	11.0	11.0	10.2	Callaway	Mo.
141851	12.0	13.3	10.9	Callaway	Mo.

Comparisons.—*Atribonium gregeri* is characterized by its rather large size for the genus, and its globose shape. Adults of this species are easily distinguished from all other known species of the genus by their globose shape and lack of the flattened anterior that characterizes all other species. Juveniles retain the flattened anterior, although not as flat as in other species; they can be distinguished by their more convex valves and rather gentle curvature toward the commissure at the anterior.

Discussion.—This globose species retains the flattened anterior surface that characterizes the genus *Atribonium* only in its juvenile stages. As the shell grew, the increase in thickness was accomplished by increasing the convexity of the valves, rather than by adding shell material nearly perpendicular to the plane of commissure as in most species of the genus. However, the normal atriboniid juveniles, and the high flat uniplication of the anterior commissure and the numerous weak costae identify it as a species of *Atribonium*, and distinguish it from similarly globose but much more strongly costate species of *Coledium*. Furthermore, despite the convexity of the anterior of *A. gregeri*, the valves meet nearly in a plane, rather than at a relatively sharp angle as in *Coledium*.

Stainbrook (1942, text fig. 6) presented drawings of cross-sections of *A. gregeri* showing the spondylium braced against floor of the valve by two short lateral plates in addition to the median septum. My serial

FIG. 9.—Scatter diagrams of the dimensions of *Atribonium gregeri* from all localities listed for the species.

sections reveal no such lateral plates. Some specimens of this and other species of stenoscismataceans have short fractures in the beak region, some arranged nearly symmetrically, equidistant from the median septum. A cross-section normally reveals these as fractures, not plates, because they appear only as thin dark lines. Perhaps such lateral fractures account for the auxiliary plates in Stainbrook's drawings.

Occurrence and abundance.—Upper part of the Callaway Formation, 1.5 mile SE. of Danville, Montgomery County, Mo. (53 specimens USNM 141852); upper part of the Callaway Formation, branch of Whippoorwill Creek, about 5 miles S. of New Florence, Mo. (43 specimens USNM 141853); upper part of Callaway, in stream bed, NE. $\frac{1}{4}$ sec. 13, T-46-N, R-6-W, 2 miles N. of Danville, Mo. (13 specimens USNM 141854); upper part of Callaway, on Missouri Highway 19, one mile N. of Big Spring, Mo. (4 specimens USNM 141858); Cedar Valley Limestone (*Cranaena iowensis* zone), Mid-river, Johnson County, Iowa (1 specimen USNM 141861); Cedar Valley (*C. iowensis* zone) Lost Creek, 2 miles S. of old State Quarry, on W. side of Cedar River, Iowa (1 specimen USNM 141862); Cedar Valley, SW. $\frac{1}{4}$ SE. $\frac{1}{4}$, 15, T-77-N, R-2-E, Buffalos Twp., Scott County, Iowa, on Dodges Creek (33 specimens USNM 141859); Cedar Valley, NE. $\frac{1}{4}$ NE. $\frac{1}{4}$, sec. 26, T-17-N, R-2-E, Andalusia, Ill. (8 specimens USNM 141860).

Age.—Late Middle Devonian, in the Callaway Limestone and the correlative part of the Cedar Valley Limestone.

ATRIBONIUM HALLI (Fagerstrom)

Stenoscisma halli FAGERSTROM, J. A., 1961, Journ. Paleont. vol. 35, No. 1, p. 29, pl. 9, figs. 48-51, (not *Camarophoria rhomboidalis* HALL AND CLARKE, 1894; HALL, 1894).

Stenoscisma rhomboidalis (Hall and Clarke) FAGERSTROM, J. A., 1961, Journ. Paleont. vol. 35, No. 1, p. 29, pl. 9, figs. 45-47, (not *Camarophoria rhomboidalis* HALL AND CLARKE, 1894; HALL, 1894).

Discussion.—The little specimens from Formosa, Ontario, which Fagerstrom (1961) equated with *Camarophoria rhomboidalis* Hall and Clarke have the generic characters of *Atribonium*. Their sub-trigonal outline, short and weak costae, and especially their flattened anterior surfaces are characteristic features. They differ from all other known species of the genus in having few (two or three) costae on the fold, and normally the same or a greater number on each flank. These specimens differ from Hall and Clarke's Indiana species (here assigned to the genus *Coledium* n. gen.) in their smaller size, lower convexity, trigonal rather than ovate outline, weaker costae that begin farther anterior, and especially in their geniculation of each valve to produce the characteristic flattened anterior of *Atribonium*.

The range of variation between specimens that Fagerstrom assigned to *S. rhomboidalis* and *S. halli* is well within the limits for other species of *Atribonium*, therefore, they are treated here as a single species.

TABLE 4.—*Measurements of Atribonium halli*

USNM No.	Measurements, in millimeters			Fagerstrom's	
	Length	Width	Thickness	Plate	Figure
549475	c.5.5	5.6	3.5		
549476	6.4	6.2	4.4		
549477	7.6	7.8	4.8	9	48-41

Occurrence.—Localities 6 and 43 of Fagerstrom (1961), in Formosa Reef of Detroit River Group in southwestern Ontario.

Age.—Early Middle Devonian (Onondaga).

ATRIBONIUM KERNAHANI (Whiteaves)

Plate 3, fig. 4

Pugnax kernahani WHITEAVES, J. F., 1898, Contr. to Canadian Paleont., vol. 1, pt. 5, No. 7, p. 387-388, text fig. 3.

Camarophoria kernahani (Whiteaves) STUMM, E. C., 1942, Journ. Paleont., vol. 16, No. 5, p. 556, pl. 84, figs. 25-27.

Supplementary description.—**Shell** small for genus, outline sub-trigonal to subpentagonal, profile wedge-shaped; commissure unipli-cate; fold very high, narrow at anterior, standing above flanks only beyond 3-4 mm. from brachial beak; sulcus deep at anterior, depressed below high and sharp flanks; costae distinct only at anterior, there having sharply rounded crests, beginning 3-5 mm. anterior to beaks, numbering two on fold, one in sulcus, two or three on each flank; growth lines fine, closely and evenly spaced, visible primarily on flattened anterior surface; growth laminae stronger, widely and irregularly spaced.

Pedicle valve flatly convex, with slight swelling in umbonal region, recurvature of anterior flanks on adults, strong longitudinal convexity through sulcus; beak proportionately long, sharp, nearly straight to suberect; beak ridges sharp, outlining flattened and compressed areas on each side of beak; delthyrium small, triangular, partly closed by pair of conjunct deltidial plates, leaving small elongate oval foramen in apical part; foramen not piercing apex of beak.

Brachial valve more strongly convex, producing most of wedge-shaped profile; beak short, somewhat attenuate, apex in pedicle valve; posterior lateral slopes somewhat pinched, meeting edge of pedicle valve without overlap.

Pedicle valve interior with dental plates meeting to form spondyl-

ium: sessile in posterior for about 1 mm., elevated on low median septum duplex for most of length; spondylium extending anteriorly about half length of valve.

Brachial valve interior with flat, undivided hinge plate; camarophorium separate from hinge plate, connected to it by intercamarophorial plate, elevated on high median septum, extending anteriorly slightly beyond spondylium; septum extending along floor slightly less than half length of valve.

TABLE 5.—*Measurements of Atribonium kernahani*

USNM No.	<i>Measurements, in millimeters</i>			Unit	State or Province
	Length	Width	Thickness		
141864	4.7	4.4	3.0	Hungry Hollow	Ont.
141865	4.9	5.5	5.0	Hungry Hollow	Ont.
141866	5.0	4.8	4.6	Hungry Hollow	Ont.
141867	5.0	5.3	4.4	Hungry Hollow	Ont.
141868	5.4	5.7	5.1	Hungry Hollow	Ont.
141869	5.6	6.5	5.0	Hungry Hollow	Ont.
141870	5.7	6.0	4.7	Hungry Hollow	Ont.
141871	5.9	5.9	5.3	Hungry Hollow	Ont.
141872	6.0	6.2	4.9	Hungry Hollow	Ont.
141873	6.3	5.0	4.5	Hungry Hollow	Ont.
141874	6.3	6.6	5.3	Hungry Hollow	Ont.
141875	6.3	6.5	4.9	Centerfield Limestone Member of Ludlowville Shale	N.Y.
141876	6.5	6.9	6.4	Hungry Hollow	Ont.
141877	6.7	7.5	6.0	Hungry Hollow	Ont.
141878	6.8	6.3	5.7	Centerfield Limestone Member of Ludlowville Shale	N.Y.
141879	6.9	7.2	6.5	Hungry Hollow	Ont.
141880	c.7.0	7.5	7.5	Centerfield Limestone Member of Ludlowville Shale	N.Y.
141881	7.0	7.5	6.3	Centerfield Limestone Member of Ludlowville Shale	N.Y.

Comparisons.—*Atribonium kernahani* is characterized by its small size, strongly wedge-shaped profile, high narrow fold, sharp and slightly attenuate beak, and normally recurved anterior flanks on the pedicle valve. Its profile is most like that of *A. gainesi* (Nettelroth) and *A. succiduum* n. sp., but it differs in its smaller size, flatter anterior surface, and its fewer costae. In addition, many specimens of *A. succiduum* are less wedge-shaped, and less abruptly flattened at the anterior. The small size and sharp wedge shape distinguish *A. kerna-*

hani from *A. simatum* n. sp., *A. pingue* n. sp., and *A. cooperorum* n. sp.; it is easily distinguished from the large and globose *A. gregeri* (Branson). *A. rostratum* n. sp. has a similarly sharp beak, but is larger and less wedge-shaped than *A. kernahani*, and has more costae on folds and flanks. *A. halli* (Fagerstrom) also has few costae, but is larger and less strongly wedge-shaped than *A. kernahani*. The latter is much less strongly costate than *A. pauperum* (Belanski) and also differs in its more wedge-shaped profile and more rounded anterior surface.

Occurrence and abundance.—Hungry Hollow Formation, Tile Yard at Thedford, Ontario (45 specimens USNM 26503, 141882-5); Hungry Hollow Formation, 2.5 miles E. of Arkona, Ontario (16 specimens USNM 141886, 141891); Hungry Hollow Formation, 4.1 miles N. of Arkona, Ontario (2 specimens USNM 141887); lower part of Centerfield Limestone Member of Ludlowville Shale, $\frac{1}{4}$ mile E. of milepost 357, south side of railroad tracks, 2.5 miles west of East Bethany, N.Y. (7 specimens USNM 141888); Centerfield Member, on Shaffer Creek, 1 mile north of Centerfield, N.Y. (1 specimen: aff. *A. kernahani* USNM 141889); Prout Formation of Stauffer (1907); tributary to Pipe Creek, 1.25 miles E. of Bloomingville, on ridge road, Ohio (1 specimen: aff. *A. kernahani* USNM 99815); lower part of Sellersburg Limestone, Gheens Quarry, on Silver Creek, about 5 miles N. of Jeffersonville, Ind. (1 specimen USNM 141890).

Age.—Late Middle Devonian.

ATRIBONIUM PAUPERUM (Belanski)

Plate 3, fig. 3

Camarophoria paupera BELANSKI, C. H., 1928, Univ. Iowa Studies in Nat. Hist., vol. 12, No. 7, p. 27, pl. 4, figs. 6-14.

Shell small for genus, flatly biconvex; outline transversely subtriangular, greatest width slightly anterior to midlength; commissure strongly plicated; fold beginning about 2 mm. anterior to brachial beak, normally formed of two strong subsidiary plications, fold high at anterior but not standing high above flanks of valve; sulcus deep, strongly bounded laterally, with one median subsidiary fold; lateral folding strong, angular, deeply serrating commissure, numbering two on each flank, each slightly acutely pointed at anterior margin; anterior surface of shell flattened, about perpendicular to dorsal and ventral valve surfaces; growth lines weak, primarily visible on flattened anterior surface.

Pedicle valve flatly convex, greatest swelling just anterior to beak, slightly recurved just behind margins where plications rise to sharp points; beak short, sharp, suberect; beak ridges moderately sharp,

short; delthyrium small, trigonal, constricted by pair of conjunct deltidial plates, leaving small elongate elliptical foramen only slightly penetrating apex of beak; posterolateral edges of valve slightly overlapped by narrow flange of brachial valve.

Brachial valve slightly flatter, also recurved on crests of plications; beak bluntly pointed, apex within pedicle valve beneath deltidial plates.

Pedicle valve interior with dental plates forming deep spondylium, meeting floor in apex of valve for 1 mm. or less, then combining to form low median septum duplex, elevating spondylium slightly for remainder of length; spondylium continuing anterior to near mid-length, septum extending somewhat beyond midlength.

Brachial valve interior with short concave hinge plate, depressed slightly to meet top of intercamarophorial plate; camarophorium beginning near apex of valve as median septum with narrow lateral protuberances, widening anteriorly, entirely separate from hinge plate except for connection through intercamarophorial plate, curving ventrally on increasingly high septum, trough nearly flat in posterior, becoming shallowly concave toward anterior, extending beyond mid-length of valve, continuing beyond anterior edge of supporting septum; crura shorter than camarophorium.

Holotype.—Belanski, 1928, pl. 4, figs. 10–14, No. 10 in Belanski Coll.; illustrated specimen: USNM 71027.

Occurrence.—Shell Rock Limestone of Thomas (1924) at Nora Springs, Iowa.

Age.—Early Late Devonian.

TABLE 6.—*Measurements of Belanski paratype specimens of Atribonium pauperum from the Shell Rock Limestone of Thomas (1924) Nora Springs, Iowa*

USNM No.	<i>Measurements, in millimeters</i>		
	Length	Width	Thickness
71027	5.5	6.6	4.8
Do.	5.7	6.2	5.0
Do.	6.0	7.0	5.4
Do.	6.3	7.3	5.1

Comparisons.—*Atribonium pauperum* is characterized by its strong and sharp plications. They are too deep to be termed costae; they greatly fold both valves as well as the commissure. No other species of *Atribonium* is as strongly folded.

Discussion.—This species is described and illustrated to show the extent of variation within the genus. Despite its extreme costation or plication, it retains the external characters of short beak with small, open foramen, only slightly overlapping posterolateral valve edges, and

flattened anterior surface nearly perpendicular to dorsal and ventral surfaces. Internal features, the spondylium and camarophorium, are typical for Devonian species in the Stenoscismatacea. The camarophorium is shallow, and only gently curved longitudinally.

ATRIBONIUM PINGUE Grant n. sp.

Plate 2, figs. 1-1c; figure 10

Shell large for genus, strongly biconvex; outline subtrigonal to sub-pentagonal, widest slightly anterior to midlength; profile wedge-shaped but curved, becoming very thick at anterior of adults; commissure uniplicate; fold high, flat crested, normally beginning more than 5 mm. anterior to brachial beak, producing rather high elevation of valve; sulcus broad, shallow, also beginning more than 5 mm. anterior to beak; costae distinct, rounded, simple, beginning 5-8 mm. anterior to beaks, numbering four or five on fold, one fewer in sulcus, normally three on each flank; anterior margin convex in outline, convex but somewhat flatter in profile; growth lines fine, closely spaced; growth laminae stronger, irregularly spaced.

Pedicle valve moderately strongly convex, with greatest swelling anterior to beak, slight prominence of anterolateral margins, elevating costa on each side of sulcus of some specimens; geniculation at anterior sharp in few specimens, gentler in most; beak short, suberect; beak ridges sharp, short; delthyrium constricted by pair of conjunct deltidial plates; foramen slotlike, not observed to pierce apex of beak.

Brachial valve more strongly convex, especially so transversely; beak somewhat attenuate, apex hidden beneath deltidial plates; anterior geniculation of valve normally rather gentle.

Pedicle valve interior with spondylium sessile for about 1 mm. in apex of beak, elevated anteriorly on low median septum, extending forward one-third to one-half length of valve.

Brachial valve interior with camarophorium extending anteriorly about the same proportionate distance.

Holotype.—USNM 141919, plate 2, fig. 1c.

Growth.—The pattern of growth of this species seems typical for the genus. Points representing the length-width ratio cluster narrowly along a straight line, whereas those representing the length-thickness ratio spread more widely along a curve of gentle acceleration (fig. 10). This latter curve could be projected toward the length-axis and intersect it just above zero with little change in curvature. The line of length-width however, must bend somewhat to flatten its curvature in order to intersect the length-axis in the same region, indicating some allometry in increase in width at early shell stages. Small juveniles probably were elongate and very thin.

TABLE 7.—*Measurements of Atribonium pingue from the Four Mile Dam Formation near Four Mile Dam, Alpena County, Mich.*

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
141892	4.5	4.2	2.9
141893	5.1	4.3	3.2
141894	5.3	4.9	2.7
141895	5.5	4.9	3.9
141896	5.6	5.4	4.4
141897	6.0	5.2	2.8
141898	6.0	5.7	3.2
141899	6.4	5.8	4.3
141900	6.3	6.2	5.5
141901	6.3	6.0	4.0
141902	6.6	6.5	4.2
141903	7.1	6.5	4.6
141904	7.3	7.2	4.8
141905	7.4	6.7	3.3
141906	7.6	9.1	6.6
141907	7.9	8.0	5.8
141908	8.2	7.4	4.3
141909	8.2	8.9	6.8
141910	8.5	8.2	4.8
141911	8.9	9.8	6.9
141912	9.0	8.4	7.2
141913	9.3	8.9	4.8
141914	9.5	9.7	5.9
141915	9.7	9.6	8.7
141916	9.9	10.4	4.8
141917	10.4	10.3	6.9
141918	10.6	10.5	7.0
141919	12.5	13.0	10.0

Comparisons.—*Atribonium pingue* is characterized by its large size, comparatively great convexity, normally rather gently curved anterior geniculation, outwardly convex anterior surface, and its rounded costae that begin far forward. Some specimens of this species attain rather large size before beginning the right-angle growth at the anterior that produces the great thickness and the wedge shape of most specimens (longest known specimen maintaining juvenile form: 10 mm.). Only two known species of *Atribonium* attain a maximum size as great as that of *A. pingue*; these are *A. simatum* n. sp. and *A. gregeri* (Branson). The latter is very convex, normally globose, and has a low fold. *A. pingue* differs from *A. simatum* in its fewer and weaker costae, higher fold, greater thickness of adults, and proportionately somewhat narrower outline.

FIG. 10.—Scatter diagrams of dimensions of *Atribonium pingue* from Four Mile Dam, Mich.

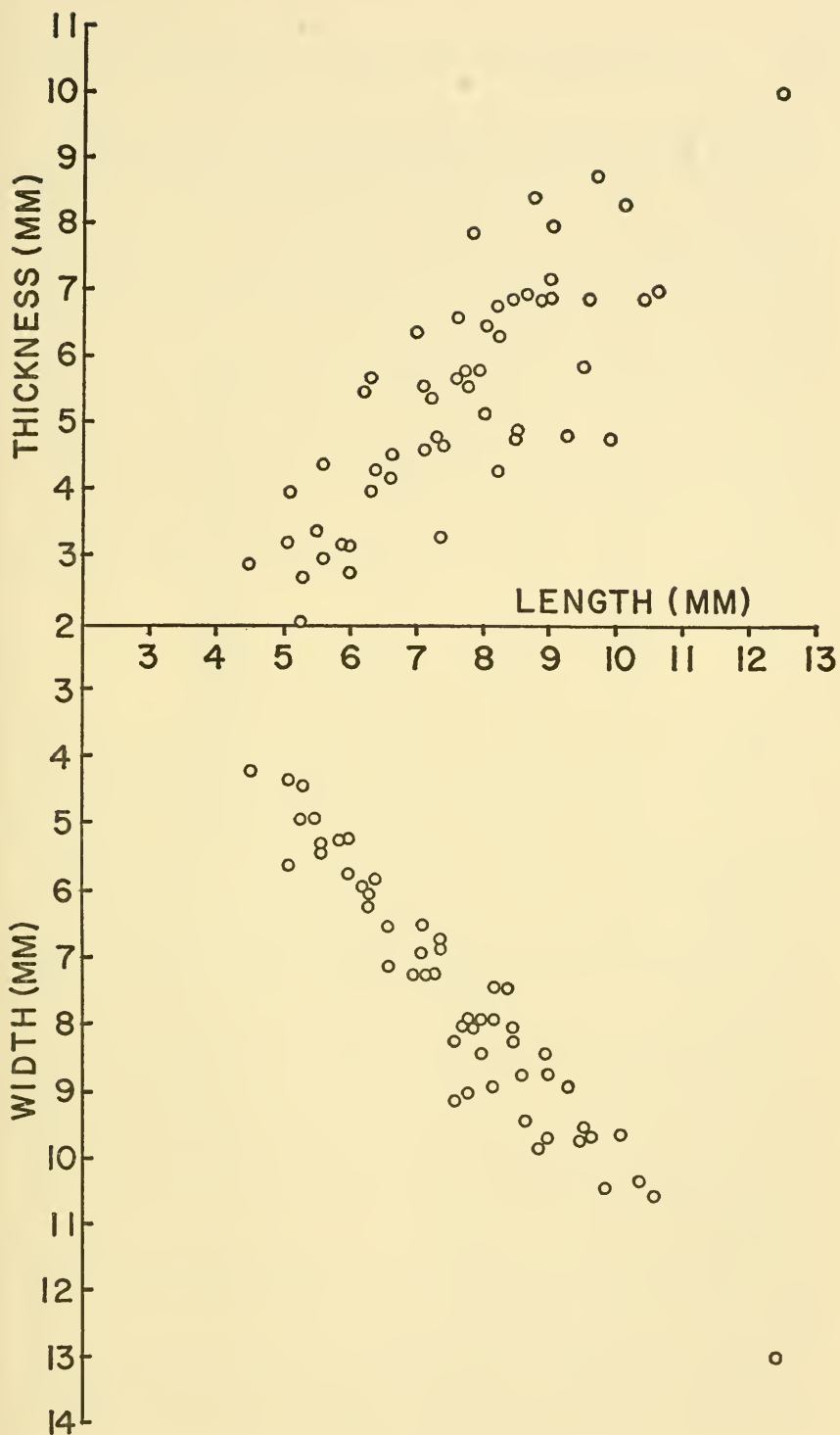


FIG. 10.—(See opposite page for legend.)

Occurrence and abundance.—"Upper part of Alpena Limestone" (now Four Mile Dam) at Four Mile Dam in Thunder Bay River, sec. 7, T-31-N, R-8-E, Alpena County, Mich. (44 specimens USNM 141920-22); upper part of Alpena at Four Mile Dam (3 specimens USNM 141929); Four Mile Dam Formation, at Four Mile Dam, S. $\frac{1}{2}$, sec. 7, T-31-N, R-8-E, 3 miles NW. of Alpena, Mich. (2 specimens USNM 141923); upper blue shale of Gravel Point Formation of Cooper and Warthin (1942) in Bell Quarry, NW. $\frac{1}{4}$ NW. $\frac{1}{4}$, sec. 9, T-34-N, R-6-W, 2.3 miles E. of Bay Shore, Mich. (16 specimens USNM 141924-6); just under upper blue shale of Gravel Point Formation, on shore of Lake Michigan opposite Pennsylvania Railroad station, Bay View, Mich. (6 specimens: aff. *A. pingue* USNM 141927, 141930); upper blue shale of Gravel Point Formation, Quarry of Charlevoix Rock Products Co., SE. $\frac{1}{4}$, sec. 28, T-34-N, R-8-W, Charlevoix County, Mich. (2 specimens: aff. *A. pingue* USNM 142928).

Age.—Middle Devonian.

ATRIBONIUM ROSTRATUM Grant n. sp.

Plate 3, figs. 2-2a

Shell small, wedge-shaped, greatest width and thickness located near anterior; commissure uniplicate; fold broad, flat, beginning about 5 mm. anterior to brachial beak, producing definite flat elevation of brachial valve; sulcus shallow, greatest depression located near anterior geniculation of shell; costae low, rounded to bluntly pointed, beginnings 3-5 mm. anterior to beaks, numbering three to six, normally four on fold, one fewer in sulcus, two or three weaker ones on each flank; anterior margin flattened, slightly convex outward; growth lines fine, most obvious on flattened anterior region; growth laminae slightly stronger, widely and irregularly spaced.

Pedicle valve flatly convex, with slight swelling anterior to beak, strong geniculation near anterior margin, bending abruptly toward commissure; beak long, suberect, apex sharp, standing well away from brachial beak, providing ample space for delthyrium and small, conjunct deltidial plates; foramen narrow, cutting apex of beak; beak ridges sharp, proportionately long.

Brachial valve more strongly convex transversely, flatly convex but rather steeply sloping upward toward anterior, there abruptly geniculated toward commissure; beak extending into pedicle valve, apex hidden beneath deltidial plates.

Pedicle valve interior with spondylium sessile for about 1 mm. in apex of beak, elevated on median septum farther anterior; septum extending forward about half length of valve.

Brachial valve interior with camarophorium beginning against shell floor, separated from hinge plate by intercamarophorial plate; median septum extending anteriorly beyond midlength of valve.

Holotype.—USNM 141950, plate 3, fig. 2a.

TABLE 8.—*Measurements of Atribonium rostratum from the Thunder Bay Limestone at Partridge Point, Mich.*

USNM No.	<i>Measurements, in millimeters</i>		
	Length	Width	Thickness
141932	5.9	6.0	4.1
141933	6.7	6.7	5.1
141934	6.8	6.4	5.0
141935	6.9	6.7	4.9
141936	7.0	6.7	4.6
141937	7.1	6.9	4.0
141938	7.4	7.9	6.7
141939	7.5	7.1	4.2
141940	7.5	7.8	5.3
141941	7.6	7.9	4.9
141942	7.9	8.2	6.2
141943	8.2	8.2	4.8
141944	8.5	9.4	7.0
141945	8.7	8.4	6.4
141946	8.9	10.2	4.9
141947	9.1	9.3	7.5
141948	10.0	10.6	6.6

Comparisons.—*Atribonium rostratum* is characterized by its small size, long pedicle beak with perforated apex, subtrigonal outline and profile, and its few lateral costae. The beak is similar to that of *A. succiduum* n. sp. from the Potter Farm Formation, but *A. rostratum* has sharper costae and a convex rather than slightly concave anterior margin. It is smaller than *A. simatum* n. sp. from the Alpena Limestone, is not as thick, has fewer costae on fold and flanks, and has a proportionately shorter beak. It is larger and not as thick at the anterior as *A. kernahani* (Whiteaves); smaller and not as globose as *A. gregeri* (Branson); thicker and more costae than *A. halli* (Fagerstrom). It is smaller, narrower, and has fewer costae than *A. savagei* (Cooper) or *A. illinoisensis* (Cooper) from the Grand Tower Limestone of Illinois.

Occurrence and abundance.—Thunder Bay Limestone, on Partridge Point, south of Alpena, Mich. (44 specimens USNM 141951); Thunder Bay Limestone, on Partridge Point, south of Alpena, Mich. (8 specimens USNM 141954); Thunder Bay Limestone at Partridge Point, Mich. (6 specimens USNM 141953).

Age.—Late Middle Devonian.

ATRIBONIUM SUCCIDUUM Grant n. sp.

Plate 2, figs. 2-2b

Shell small for genus; outline subtrigonal to subpentagonal, widest anterior to midlength; profile moderately biconvex to wedge-shaped, greatest thickness at anterior; commissure uniplicate, with moderately high fold extending dorsally about two-thirds height of anterior surface; fold elevating brachial valve only at anterior, normally more than 5 mm. anterior to brachial beak; sulcus shallow, beginning about 5 mm. anterior to pedicle beak; costae low, rounded, beginning about 3 or 4 mm. anterior to beaks, numbering three or four, rarely five on fold, one fewer in sulcus, two or three on each flank anterior margin flattened, gently convex to gently concave; growth lines fine, weak, closely spaced; growth laminae stronger, irregularly and widely spaced.

Pedicle valve flatly convex, with greatest convexity just anterior to beak, strong geniculation at anterior, beak long, sharp, suberect; beak ridges blunt but distinct; delthyrium small, constricted by pair of conjunct deltidial plates; pedicle foramen elongate, oval, normally penetrating apex of beak.

Brachial valve more strongly convex transversely, flatly convex longitudinally, strongly geniculate at anterior; apex of beak beneath deltidial plates in pedicle valve.

Pedicle valve interior with spondylium sessile in posterior, elevated on low median septum toward anterior, septum extending slightly anterior to midlength of valve.

Brachial valve interior with camarophorium beginning against valve floor in apex, separated from hinge plate by intercamarophorial plate; median septum extending forward nearly three-fourths length of valve.

Holotype.—USNM 141996, plate 2, fig. 2a.

Comparisons.—*Atribonium succiduum* is characterized by its small size, few and weak costae, conjunct deltidial plates, and proportionately long median septum in each valve. It most nearly resembles *A. rostratum* n. sp. from the Thunder Bay Limestone in its relatively long pedicle beak, but differs in its smaller size, less trigonal outline, weaker and fewer costae, and concave anterior surface in some specimens. It is smaller and has fewer and weaker costae than *A. simatum* n. sp. or *A. cooperorum* n. sp.; it is larger and proportionately not as thick at the anterior as *A. kernahani* (Whiteaves); smaller and much narrower than *A. savagei* (Cooper) or *A. illinoisensis* (Cooper). In addition, *A. succiduum* is so much smaller and less globose than *A. gregeri* (Branson) and less strongly folded than *A. pauperum* (Belanski) that detailed comparisons are unnecessary. It has more numerous costae and is much thicker at the anterior than *A. halli* (Fagerstrom).

TABLE 9.—*Measurements of Atribonium succiduum, Potter Farm Formation, Mich.*

USNM No.	<i>Measurements, in millimeters</i>			Locality
	Length	Width	Thickness	
141985	5.3	5.7	3.5	Alpena
141986	5.4	5.4	3.4	Alpena
141987	5.6	5.9	2.9	Alpena
141988	5.9	5.3	2.6	Alpena
141989	6.2	6.5	4.0	Alpena (37a)
141990	6.4	6.8	4.2	Alpena
141991	6.7	6.8	4.9	Alpena
141992	7.1	7.6	5.6	Alpena
141993	7.5	7.2	5.1	Alpena
141994	7.5	7.7	6.6	Alpena
141995	7.8	7.9	5.7	Alpena
141996	7.9	8.3	6.0	Alpena
141997	7.9	7.9	6.7	Alpena
141998	8.1	8.8	7.4	Alpena
141999	8.6	9.2	5.6	nr. Four Mile Dam
142000	9.8	11.0	8.2	nr. Four Mile Dam

Occurrence and abundance.—Potter Farm Formation, pit in NW. corner of Alpena Cemetery, NW. $\frac{1}{4}$ SW. $\frac{1}{4}$, sec. 21, T-31-N, R-8-E, Alpena County, Mich. USNM loc. 37a (89 specimens USNM 142001–142003); Potter Farm Formation, $\frac{1}{4}$ mile south of Four Mile Dam, NW. $\frac{1}{4}$, sec. 18, T-31-N, R-8-E, Alpena County, Mich. (3 specimens USNM 142004); Potter Farm Formation, 0.25 mile south of bend in road at Four Mile Dam, SE. corner NE. $\frac{1}{4}$ NW. $\frac{1}{4}$, sec. 18, T-31-N, R-8-E, Alpena County, Mich. (2 specimens USNM 142006); Potter Farm Formation, at Potter Farm, Alpena, Mich. (1 specimen USNM 142005).

Age.—Late Middle Devonian.

Genus CAMERISMA Grant n. gen.

(Camera, L., vaulted chamber; erisma, L., prop)

Laevicamera GRABAU, A. W., 1936, Paleont. Sinica, ser. B, vol. 8, fasc. 4, p. 87.

Levicamera Grabau, SARYCHEVA, T. G., and SOKOLSKAYA, A. N., 1952,

Trudy Paleont. Inst. Mosc., vol. 38, p. 171 (as subgenus of *Camarophoria*).

NOT *Levicamera* GRABAU, A. W., 1934, Paleont. Sinica, ser. B, vol. 8, fasc. 3, p. 18 (= *Psilocamera* Cooper 1956a).

Shell wall thick; profile strongly biconvex; outline subovate to sub-pentagonal; commissure strongly uniplicate; fold high, arched, producing blunt-crested ridge along midline of brachial valve; sulcus shallow, median line with narrow trough or flattening, extending around anterior as broad tongue; costae weak or absent, confined to anterior of fold and sulcus, normally barely perceptible, there number-

ing up to five on fold, one fewer in sulcus (normally an odd number: median crest counted as costa); valve edges butting around anterior margin, strongly overlapping at posterior in some species; stolidium entirely absent; growth lines weak, closely spaced; growth laminae slightly stronger.

Pedicle valve moderately strongly convex, slightly swollen in umbonal region; beak thick, bluntly pointed, strongly curved against brachial umbo, closing delthyrium and foramen; beak ridges absent.

Brachial valve more strongly convex transversely, moderately convex longitudinally along crest of fold; beak not swollen, apex within pedicle valve.

Pedicle valve interior with thick dental plates uniting at midline to form deep spondylium, elevated on low median septum duplex, extending anteriorly about one-third length of valve; spondylium wall becoming thinner toward anterior.

Brachial valve interior with well-developed cardinal process at posterior apex of hinge plate; crura extending anteriorly from edge of hinge plate; camarophorium elevated for entire length, formed by spreading of upper edges of thick median septum duplex (each wing of camarophorium formed of one plate); intercamarophorial plate thick, duplex, extending from midline of posterior part of camarophorium to underside of hinge plate, continuing anteriorly for short distance beyond hinge plate; median septum extending anteriorly about one-third length of shell, camarophorium extending somewhat farther.

Type species.—*Camerisma prava* Grant n. sp.

Additional species assigned to CAMERISMA.—

Camerisma girtyi n. sp.

Camerisma sagmaria n. sp.

? *Pentamerus sella* Kutorga 1844

Camarophoria sella (Kutorga) of Licharev & Einor, 1939 (non Kutorga)

? *Camarophoria pentameroides* Tschernyshev 1902; Ivanova, 1949; Sarycheva and Sokolskaya, 1952.

The two questioned species are assigned tentatively to *Camerisma* on the basis of diagnoses and illustrations by Tschernyshev. Presence of the intercamarophorial plate has not been established beyond doubt. See discussion, below.

Grabau (1936) identified specimens from the Mapping Limestone of Kweichow, China, with *Camarophoria sella* and *C. pentameroides*. Neither of his two species appear to be similar to the Eastern European or Alaskan species, but both might belong to *Camerisma*. Further study of the Asian species is necessary before their proper place in the Stenoscismatacea can be determined.

Comparisons.—*Camerisma* is characterized by its smooth or nearly smooth shell, high vaulted fold, tightly curved pedicle beak, thick shell

walls and internal structures, and prominent intercamarophorial plate. Its larger size and presence of the intercamarophorial plate distinguish it from the externally similar Pennsylvanian genus *Psilocamara* Cooper. The high Gothic arch-shaped fold distinguishes it from smooth or weakly costate species of *Coledium* n. gen., as does its more tightly curved pedicle beak and thicker shell walls. Its weak or absent costae, high vaulted fold, presence of an intercamarophorial plate and less strongly globose shape distinguish it from *Cyrolexis* n. gen. which also has thick walls. It differs from the smooth genus *Camarophorina* Licharev in its uniplicate rather than sulcate commissure, its high-vaulted fold, and presence of an intercamarophorial plate. *Camerisma* is not closely similar to other genera of the Stenoscismatacea.

Discussion.—Species of this genus seem to be essentially noncostate, although two species have a few weak costae confined to the fold and sulcus of some individuals. The smooth exterior and high Gothic arch-like fold were diagnostic features of *Psilocamara* Cooper (1956a). Now it is determined that the intercamarophorial plate is consistently absent from Pennsylvanian *Psilocamara*, a significant generic distinction from the externally similar Permian forms in which the plate is present. Therefore, the group in which the plate is present, and the fold *Pugnax*-like, needs a new generic category. These species are designated *Camerisma*.

Range.—Mississippian to Lower Permian.

The only species known definitely to belong to *Camerisma* are the two from Alaska and *C. sagmarium* n. sp. from the Lower Permian (Artinskian) of Yugoslavia. Schellwien (1900) reported this species as *Camarophoria sella* (Kutorga) from the Trogkofelschichten of the Karawanken Range near Neumarkt, Yugoslavia, the locality from which the type specimens of *C. sagmarium* are derived. This horizon now is interpreted as Artinskian by Gignoux (1955).

Camarophoria sella is reported from the Upper Carboniferous (Gschelian, C₃) in Darvaz, U.S.S.R. (Tschernyshev, 1914), and from the Lower Permian in the Ural and Timan regions (Tschernyshev, 1902).

Tschernyshev (1902) reported *Camarophoria pentameroides* Tschernyshev from the Lower Permian ("*Schwagerina* horizon") in the Ural region, and Sarycheva and Sokolskaya (1952) report it from the mid-Moscovian (Podolskian) to the Gschelian.

Grabau (1936) reported both *C. sella* and *C. pentameroides* from the Mapping Limestone of Kweichow, China. His specimens differ in several respects from either of these species, but nevertheless, they may belong properly to *Camerisma*. The Asian specimens are from beds that are Uralian, according to Grabau's analysis of the fauna,

therefore, their occurrence does not extend the known range of the genus.

CAMERISMA PRAVA Grant n. sp.

Plate 8, figs. 1-1b; figure 11

Shell about average size for genus, strongly biconvex; outline transversely subelliptical or rhomboid, typically asymmetrical, distorted; commissure strongly uniplicate at anterior; fold high, sharp-crested, in form of Gothic arch, crest curving left or right toward anterior; sulcus moderately deep, median trough sharp, curving left or right to match fold; costae entirely absent; posterolateral edge of pedicle valve with narrow flange overlapped by edge of brachial valve; edges of valve elsewhere meeting at obtuse or right angle, without protruding, without trace of stolidium; concentric growth lines fine, closely spaced; growth laminae only slightly stronger, strongest and most frequent near margins.

Pedicle valve strongly convex longitudinally through sulcus; umbonal region slightly swollen; beak short, thick, erect to recurved against brachial umbo, therefore foramen not observed.

Brachial valve flatly convex longitudinally along crest of fold, strongly convex transversely; beak bluntly pointed, apex hidden within pedicle valve.

Pedicle valve interior with dental plates forming spondylium elevated on low median septum, not sessile in apex; septum becoming gradually higher anteriorly, remaining rather low, extending anteriorly about one-third length of valve.

Brachial valve interior with short, undivided hinge plate in posterior, apex of plate slightly swollen to form cardinal knob for attachment of diductor muscles; camarophorium beginning in apex as thickening of crest of median septum, becoming definitely spoon-shaped anteriorly; height of septum increasing anteriorly, curving camarophorium ventrally; strong intercamarophorial plate connecting midline of camarophorium to underside of hinge plate; crura extending anteriorly from hinge plate, curving ventrally like camarophorium.

Holotype.—USNM 172074, plate 8, fig. 1.

Comparisons.—*Camerisma prava* is characterized by its wide outline,

TABLE 10.—Measurements of *Camerisma prava* from the Mississippian of Alaska

USNM No.	Measurements, in millimeters			USGS loc.
	Length	Width	Thickness	
142072	15.0	16.0	9.5	3779
142073	15.3	16.9	10.2	3779
142074	c.17.0	23.8	18.9	3779

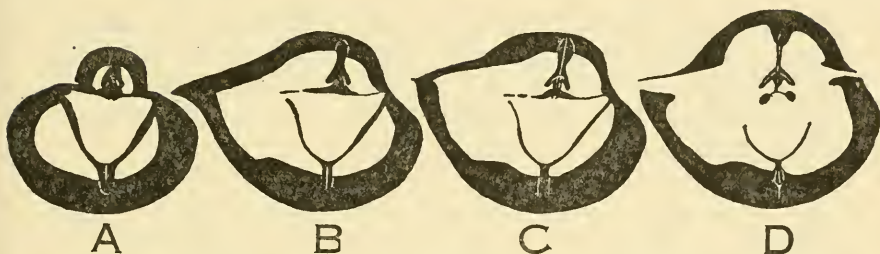


FIG. 11.—*Camerisma prava* n. sp., Mississippian, Ladrões Islands, Alaska; transverse sections $\times 4$, USNM 142072, original length 15.0 mm., measurements from pedicle valve beak.

A. 2.0 mm.: cardinal process low. B. 2.6 mm. C. 2.7 mm.: camarophorium, intercamarophorial plate, and septum of spondylium all duplex, with wedged insertion of septa into shell. D. 3.0 mm.: hinge plate thin, crura visible, camarophorium slightly thickened at base of septum.

complete lack of costae, sharp fold and sulcus, and asymmetry. It is smaller than the other Mississippian species from Alaska, *C. girtyi* n. sp., and is wider, has a higher, narrower, sharper fold, and is strongly asymmetrical. It differs from the species *C. sagmaria* n. sp. from the Permian of Yugoslavia, in its much larger size, wider and asymmetrical outline, sharper fold, and lack of any trace of costae.

C. prava resembles *C. ? sella* (Kutorga) in its broad outline, sharp-crested fold, and similar size. It differs from Permian species in its longer, thick pedicle beak, somewhat lower fold and in its pronounced asymmetry. Similarity of the two species, despite their age difference, argues for inclusion of *C. ? sella* in the genus *Camerisma*.

Occurrence and abundance.—Unnamed Upper Mississippian limestone of Condon (1961), Craig Quadrangle, Southeastern Alaska, all specimens collected by G. H. Girty in 1918: U.S.G.S. loc 3779, white massive limestone at south end of island No. 205 in Ladrões Islands, three specimens (USNM 142072–74).

CAMERISMA GIRTYI Grant n. sp.

Plate 8, figs. 3–3a; figure 12

Shell somewhat large for genus, adults strongly biconvex; outline subtrigonal to subelliptical, transverse in young specimens, elongate in adults, juveniles widest near midlength, adults widest farther anterior; commissure uniplicate; fold moderately high, becoming very high in largest specimens, with bluntly pointed crest, in shape of Gothic arch, standing only slightly above flanks; sulcus rather shallow, with sharp median trough; costae absent from flanks, one weak costa on each side of fold, with corresponding shallow troughs on each side of sulcus,

costae beginning about 7 mm. anterior to beak, along with fold and sulcus; concentric growth lines fine, growth laminae weak, only slightly more prominent than growth lines; edges of valves meeting in acute angle in flat juveniles, obtuse angle in convex adults, not protruding, without forming trace of stolidium.

Pedicle valve strongly convex (in adults) beak thick, rather long, erect to strongly incurved, pressed against brachial umbo of large adults; beak ridges short, rounded; foramen small, constricted by curvature of beak, apparently completely closed in large adults.

Brachial valve strongly convex, beak somewhat attenuate, apex within pedicle valve.

Pedicle valve interior with dental plates uniting above floor to form shallow spondylium, elevated on low median septum duplex in apex, septum becoming rather high anteriorly, leaving spondylium shallow, extending anteriorly about one-third length of valve.

Brachial valve interior with undivided hinge plate, swollen in apex to form cardinal process with shallow longitudinal striae for muscle attachment; camarophorium with thick trough, supported on thick median septum duplex extending anteriorly about one-fourth length of valve; intercamarophorial plate bracing camarophorium to hinge plate.

Holotype.—USNM 142071, plate 8, fig. 3a.

Comparisons.—*Camerisma girtyi* is characterized by its large size, bulbous convexity, high fold with bluntly pointed crest, strongly curved pedicle beak, and weak costae, one on each side of the fold. It is larger and narrower than the other known Mississippian species from Alaska, *C. prava* n. sp., and differs further in its greater convexity

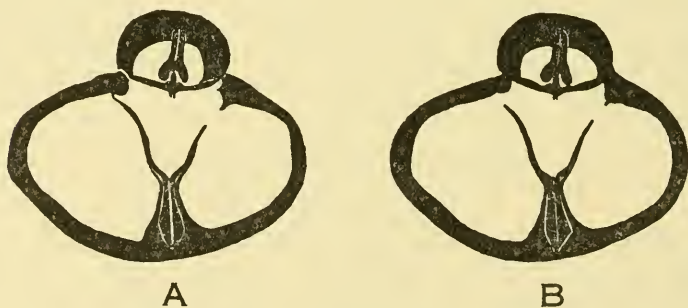


FIG. 12.—*Camerisma girtyi* n. sp., Mississippian, Ladrone Ids., Alaska, transverse sections $\times 4$, USNM 142070, original length about 19.0 mm.

A. About 3 mm. from pedicle valve beak: cardinal process low and narrow, intercamarophorial plate independent of camarophorium, septa both duplex, with wedged insertions into valve floors, ventral septum and lower part of spondylium secondarily thickened. B. Slightly farther anterior, dental plates lower.

TABLE 11.—*Measurements of Camerisma girtyi from the Mississippian of Alaska*

USNM No.	<i>Measurements, in millimeters</i>			USGS loc.
	Length	Width	Thickness	
142069	16.7	22.0	12.8	3684
142070	c.19.0	c.23.0	17.5	3684
142071	20.0	20.0	19.0	3708

and in its bilateral symmetry. It is larger than the Permian species *C. sagmaria* n. sp. and has fewer costae. It is somewhat smaller than *C. ? pentameroides* (Tschernyshev) from the Permian of Russia, and its fold is higher and slightly sharper at the crest. However, Mississippian *C. prava* and Permian *C. ? pentameroides* are so similar that from external appearances it is difficult to doubt that they are congeneric. *C. girtyi* is narrower, more globose, and has a broader, more gently arched fold and shallower sulcus than *C. ? sella* (Kutorga) from the Russian Permian.

Discussion.—This species is based on three well-preserved specimens which are described, despite the small number, because they add importantly to the concept of the rare genus *Camerisma*, and because it is not likely that additional specimens will be collected soon.

Occurrence and abundance.—Unnamed Upper Mississippian limestone of Condon (1961), Craig Quadrangle, Southeastern Alaska, all specimens collected by G. H. Girty in 1918: U.S.G.S. loc. 3708, south shore of island No. 85 in Ladrone Islands, one specimen (USNM 142071); U.S.G.S. loc. 3684, massive white limestone at north point of island No. 250 in Ladrone Islands, two specimens (USNM 142069-70).

CAMERISMA SAGMARIA Grant n. sp.

Plate 8, figs. 2-2a; figure 13

Camerophoria sella (Kutorga) SCHELLWEIN, E., 1900, Abhand. Geol. Reichsanstalt, Wien, vol. 16, pt. 1, p. 99, pl. 15, figs. 1-4.

Shell about medium size, strongly biconvex; outline transversely subpentagonal; anterior commissure strongly uniplicate, with high vaulted fold in shape of Gothic arch, not standing strongly above flanks, but greatly increasing convexity of valve; sulcus shallow, broad, narrowing anteriorly to form tongue extending into arch of fold; costae low, rounded, confined to fold and sulcus, beginning about 5 mm. anterior to beaks, numbering up to five on fold, one fewer in sulcus, increasing anteriorly by bifurcation (median costa formed by crest of fold, not bifurcating); concentric ornament weak, consisting of fine growth lines and widely spaced laminae.

Pedical valve thick in umbonal region; beak curved, apparently

pressed tightly against brachial umbo; slight constriction of postero-lateral slopes.

Brachial valve more strongly convex transversely and longitudinally; beak slightly attenuate, apex within pedicle valve.

Pedicle valve interior with thick dental plates forming deep spondylium; dental plates becoming thinner anteriorly; spondylium elevated on comparatively high median septum duplex, extending anteriorly about one-third length of valve.

Brachial valve interior with strong hinge plate, fimbriate knoblike cardinal process at apex, crura extending from anterior edge; camarophorium formed by spreading of upper edges of high median septum duplex, apparently in contact with hinge plate at posterior, extending anteriorly about one-third length of valve, reaching slightly farther anterior than spondylium; intercamarophorial plate thick, duplex, propping underside of hinge plate from median line of camarophorium, extending anteriorly farther than edge of hinge plate; muscle and palial marks not observed.

Types.—Holotype: USNM 127876; Paratype: USNM 63169.

Occurrence.—Troglkofel beds at Teufelsschlucht, near Neumarkt, Yugoslavia (Permian; Artinskian according to Gignoux, 1955, p. 228).

Comparisons.—*Camerisma sagmaria* is characterized by its relatively small size, fold that is high at the anterior commissure but not set off from the flanks by a break in lateral slopes, and its weak (barely perceptible on some specimens) costae that split symmetrically. It is

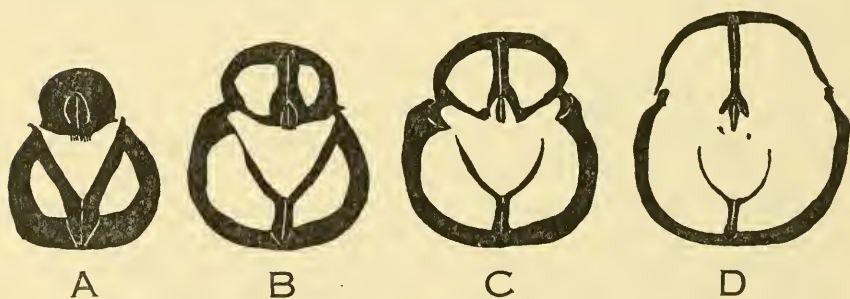


FIG. 13.—*Camerisma sagmaria* n. sp., Troglkofelschichten, Neumarkt, Yugoslavia, transverse sections $\times 5$, original length ca. 10 mm., USNM 63169, measurements from pedicle valve beak.

A. 0.5 mm.: thick shell shows wedged insertion of spondylium into valve floor; cardinal process fimbriate. B. 1.5 mm.: edges of camarophorium meet hinge plate, intercamarophorial plate thick. C. 2.1 mm.: intercamarophorial plate distinct. D. 2.5 mm.: crura show anterior to hinge plate.

TABLE 12.—Measurements of specimens of *Camerisma sagmaria* from Neumarkit

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
63169	c.10.0	c.10.0	7.3
63169	10.3	11.4	10.0
127876	11.8	12.9	10.3

much smaller than *C. ? pentameroides* (Tschernyshev), is more elliptical and less transverse in outline, has a less strongly convex pedicle valve, and a more narrowly arched fold. It differs from *C. ? sella* (Kutorga) in its less distinctly demarcated fold, much longer pedicle beak, and slightly more distinct costae, especially on the pedicle valve (*C. ? sella* has one costa on each flank, weak or absent costae on fold), and its less transverse outline. Kutorga (1844, pl. 9) enlarged the drawing without so indicating (in fact, stating that there was no enlargement) but Tschernyshev (1902, pl. 23) provided photographs of the same specimen, showing its size near that of *C. sagmaria*.

It is smaller and proportionately much narrower than *C. prava* n. sp. and its fold is broader and not as sharp; in addition, it shows no tendency to asymmetry. It is much smaller than *C. girtyi* n. sp., proportionately narrower, and has more numerous, although equally weak, costae.

Cooper (1956b) placed *Camarophoria sella* (Kutorga) in the genus *Psilocamara* Cooper, on the basis of its smooth shell and high arched fold. He noted absence of the intercamarophorial plate in *Psilocamara*, but left open the question of its consistent absence in *P. renfroarum*, the type species, and of its possible generic significance. Sectioning of additional specimens of *P. renfroarum* indicates that the intercamarophorial plate is truly absent; however, it is unmistakably present, high, thick, and long in *Camerisa sagmaria*. This species was identified by Tschernyshev (1902, p. 509) as *Camarophoria sella*, therefore, the probability is strong that it is congeneric with *C. sella*. The thick shell seems to be a consistent feature of this genus, in contrast to the thinner shell of *Psilocamara*, so the evidence supports the inference that the intercamarophorial plate is present in *C. ? sella* and *C. ? pentameroides*, similar to *C. sagmaria* and in contrast to *P. renfroarum*. Further differences between *C. sagmaria* and *P. renfroarum* are in the much larger size of the former, wider outline, proportionately lower and broader fold, and presence of weak costae on the fold.

Discussion.—This species shows most clearly the construction of the camarophorium, spondylium, and intercamarophorial plate. All three structures are duplex, each formed of two plates. The spondylium

clearly is a uniting of two dental plates that join to form a septum duplex. The camarophorium is formed by spreading of the upper edges of the two plates that combined make up the dorsal median septum. Or it might be stated that the septum forms by uniting of the two single plates that make up the trough of the camarophorium. The intercamarophorial plate also is duplex, and serial sections of this species show that it is entirely separate from the camarophorium, with its base inserted into the camarophorium much as the septa of the spondylium and camarophorium are inserted into the valve floors.

Genus SEDENTICELLULA Cooper 1942

Sedenticellula COOPER, G. A., 1942, Journ. Wash. Acad. Sci., vol. 32, No. 8, p. 231.

Shell small rhynchonelliform, biconvex; outline elongate to transversely subelliptical, tear-drop to bean-shaped; commissure weakly uniplicate, with low fold slightly depressed medially in some species, normally rather wide, beginning at least 5 mm. anterior to brachial beak; posterolateral edges of valves butting, not overlapping, gently curved or protruding; stolidium absent. Costae low, narrow, beginning at beaks or as much as 5 mm. anterior to beaks, simple or increasing anteriorly by intercalation and bifurcation, on flanks as well as fold and sulcus, producing slightly serrate commissure. Growth lines weak, irregularly spaced, somewhat more frequent near margins.

Pedicle valve flatly convex, swollen in beak region; beak short, bluntly pointed, nearly straight to erect, beak ridges distinct, outlining flattened area resembling interareas; delthyrium small, triangular, normally nearly filled by brachial beak, deltidial plates not observed; foramen small.

Brachial valve more strongly convex, maximum convexity near beak and laterally toward flanks, crest of fold nearly flat; beak bluntly pointed, not prominent, apex covered by beak of pedicle valve.

Pedicle valve interior with strong, outwardly bowed dental plates, converging, nearly meeting, on floor of apex, floor between plates thickened in some species, forming sessile spondylium, plates meeting anteriorly in other species: spondylium sessile in juveniles and at posterior of adults, raised at anterior end in adults.

Brachial valve interior with undivided hinge plate in apex; short crura extending forward from anterior edge of hinge plate; median septum low in apex, height increasing anteriorly, extending forward about 5 mm. along floor of adult valve; camarophorium shallowly concave, narrow in apex of valve, expanding narrowly toward anterior; thick, low, intercamarophorial plate bisecting posterior half of camaro-

phorium braced against hinge plate in extreme apex, gradually lowering toward anterior.

Type species.—*Camarophoria hamburgensis* Weller, 1910, Bull. Geol. Soc. America, vol. 21, p. 500, fig. 2, (by original designation of Cooper, 1942).

Comparisons.—*Sedenticellula* is characterized by its normally flat shell with low fold and shallow sulcus, its numerous fine costae that begin at or near the beaks, and may increase in number anteriorly by intercalation and bifurcation. Internally, it is distinguished by its spondylium that remains sessile for 1 or 2 millimeters from the pedicle beak, somewhat farther anterior than in other genera.

The other stenoscismatacean genus that most nearly resembles *Sedenticellula* externally is *Camarophorinella* Licharev, which also has a low fold and numerous low costae that begin far posterior and may bifurcate. *Sedenticellula* differs in its lower fold, weaker costae, and especially in its undivided hinge plate and strong intercamarophorial plate. *Torynechus* Cooper and Grant also has bifurcating costae, but it is clearly distinguished from *Sedenticellula* by its uncinuliform exterior. No other genus of the superfamily resembles *Sedenticellula* strongly.

Range.—*Sedenticellula* has been found only in the Mississippian (Kinderhook), in Illinois and Texas.

SEDENTICELLULA HAMBURGENSIS (Weller)

Plate 4, figs. 1–2b; figure 14

Camarophoria hamburgensis WELLER, S., 1910, Bull. Geol. Soc. America, vol. 21, p. 500, fig. 2; WELLER, S., 1914, Illinois State Geol. Survey Monogr. 1, p. 170, fig. 2, pl. 23, figs. 52–60; COOPER, G. A. 1942, Journ. Wash. Acad. Sci., vol. 32, No. 8, p. 231.

NOT *Sedenticellula* aff. *S. hamburgensis* (Weller) CLOUD, P. E., Jr. and BARNES, V. E., 1948, Univ. Texas Pub. 4621, pl. 44, figs. 12–16 (*S. sacra* n. sp.).

Shell small for genus, flatly to strongly biconvex; outline slightly elongate subovate to slightly transverse subelliptical; commissure uniplicate: low fold beginning slightly anterior to pedicle beak. Costae distinct, beginning at or slightly anterior to beaks, crests and troughs about equal in width, rounded or bluntly V-shaped, normally simple, without bifurcation or intercalation, numbering five to seven on fold and sulcus, four to six on each side. Growth lines fine, closely spaced, producing weak, chevron-shaped ornamentation; slightly stronger growth laminae at irregular intervals.

Pedicle valve flatly convex, outline subovate; beak blunt, prominent but not attenuate, suberect; beak ridges sharp, outlining flattened posterolateral area; delthyrium broadly triangular, nearly filled by beak

of brachial valve; deltidial plates not observed; foramen small, sub-circular, perforating apex of beak.

Brachial valve more strongly convex, outline subcircular; beak short, blunt, apex within pedicle valve.

Pedicle valve interior with one small hinge tooth on each side; dental plates bowed outwardly, reaching valve floor, extending forward one-third to one-half length of valve, nearly meeting one another on posterior floor, there slightly thickened to form sessile spondylium, bases of plates converging anteriorly, meeting at anterior edge of spondylium of some specimens but not joined to form septum. Muscle and pallial marks not observed.

Brachial valve interior with undivided hinge plate extending forward about 1 mm.; crura extending forward from anterior edge of plate; median septum strong, rather low, height increasing anteriorly, extending about one-third valve length; camarophorium narrow, flatly concave, widening toward anterior, posterior half with short intercamarophorial plate braced to underside of hinge plate in apex, then declining anteriorly.

Lectotype (here designated).—Weller, 1914, plate 23, fig. 57 (Walker Mus., Univ. Chicago, No. 13937).

Comparisons.—*Sedenticellula hamburgensis* is characterized by its small size, rotund outline, simple costae, flattened posterolateral areas on the pedicle valve outlined by sharp beak ridges, and its completely sessile spondylium. These features distinguish it from the only other known species, *S. sacra* n. sp.

Occurrence and abundance.—Hamburg Oolite of Weller (1906), shore of Mississippi River $\frac{1}{2}$ mile north of Hamburg, Ill. (8 specimens USNM 89886); Hamburg Oolite, Irish Hollow, just east of Hamburg, Calhoun County, Ill. (23 specimens USNM 142021); plas-

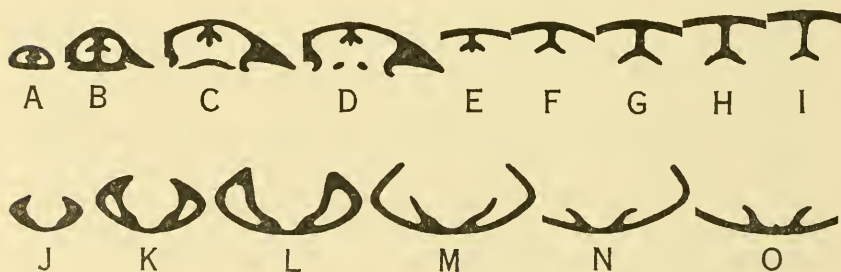


FIG. 14.—*Sedenticellula hamburgensis* (Weller), Kinderhook, Hamburg, Ill.; sections by Weller (1914, p. 170, fig. 2, B, D, F-H, J-S) $\times 3\frac{3}{4}$; A-I, brachial valve; J-O, pedicle valve showing sessile spondylium.

TABLE 13.—*Measurements of Sedenticellula hamburgensis from the Hamburg Oolite of Weller (1906) of Illinois*

USNM No.	<i>Measurements, in millimeters</i>		
	Length	Width	Thickness
142007	3.0	3.0	1.2
142008	3.8	4.0	1.6
142009	3.9	4.0	1.6
142010	4.0	4.4	1.8
142011	5.0	5.4	1.9
142012	5.4	5.6	2.0
142013	5.9	5.6	2.6
142014	6.0	5.9	2.8
142015	6.4	6.6	3.0
142016	6.6	6.7	3.4
142017	7.1	8.0	3.1
142018	8.0	8.0	3.7
142019	c.9.5	10.7	—
142020	10.5	11.4	—
68188	11.4	12.7	—

tic molds of three brachial valves illustrated by Weller, 1914, pl. 23, figs. 56–58, Walker Museum No. 13937 (USNM 68188).

Age.—Early Mississippian.

SEDECICELLULA SACRA Grant n. sp.

Plate 5, figs. 1–9

Sedenticellula aff. *S. hamburgensis* (Weller) CLOUD, P. E., Jr., and BARNES, V. E., 1948, Univ. Texas Pub. 4621, pl. 44, 12–16.

Shell large for genus, moderately strongly biconvex; outline sub-elliptical to rounded subpentagonal, elongate or transverse in juveniles, transverse in adults; anterior commissure with broad, low gentle fold forming arc or flattened arc; fold not standing abruptly higher than flanks of shell; sulcus shallow, slightly depressed below flanks, expressed mainly as tongue at anterior filling fold; valves butting or meeting with narrow flange on posterolateral slopes, meeting acutely along anterior sides, near right angle at anterior; costae fine, low, rounded, beginning at or within 3 mm. of beaks, number increasing toward anterior by intercalation and bifurcation, totaling as many as 45 around margins of valve, producing only slight crenulation of commissure; concentric growth lines or other fine ornamentation absent; growth laminae weak, widely spaced, rarely observed; fibrous shell structure producing appearance of fine radial ornamentation.

Pedicle valve flatly convex, somewhat swollen in umbonal region, flat toward flanks, gently convex through sulcus; beak short, sharp,

suberect to erect; beak ridges blunt, short; delthyrium small, wider than long, constricted but not filled by pair of very small, disjunct deltidial plates; foramen not clearly observed, apparently open but small.

Brachial valve more strongly and evenly convex transversely and longitudinally; beak blunt, apex within pedicle valve.

Pedicle valve interior with short spondylium duplex, about one-fourth length of adult valve, normally sessile in apex of valve, with sides converging anteriorly to form median septum elevating anterior part of spondylium; muscle and other marks not observed.

Brachial valve interior with camarophorium on high median septum, joined to underside of hinge plate by short intercamarophorial plate; septum slightly shorter than septum of pedicle valve, crest of camarophorium extending farther anterior than trace of septum along floor; crura extending anteriorly from edge of hinge plate, curving to follow crest of camarophorium.

Holotype.—USNM 142040, plate 5, fig. 9.

TABLE 14.—*Measurements of Sedenticellula sacra, from Chappel Limestone, Tex.*

USNM No.	<i>Measurements, in millimeters</i>			Locality
	Length	Width	Thickness	
142023	5.0	5.4	2.8	TF-406
142024	5.4	5.2	2.5	TF-406
142025	5.7	6.0	3.0	TF-406
142026	6.0	6.2	2.9	TF-406
142027	6.2	6.4	3.9	TF-406
142028	6.4	7.0	2.6	TF-406
142029	c.6.8	7.4	3.9	TF-406
142030	7.0	7.7	3.3	TF-406
142031	7.5	8.0	3.4	TF-406
142032	7.8	8.1	3.9	TF-406
142033	7.8	8.7	3.5	TF-406
142034	8.4	c.11.0	4.2	TF-406
142035	8.7	9.5	5.9	TF-406
142036	8.9	8.6	4.7	TF-406
142037	11.6	16.2	8.1	16T-2-27A
142038	12.3	14.9	8.0	16T-2-27A
142039	13.0	14.9	8.2	16T-2-27A
142040	14.0	18.3	9.9	16T-2-27A

Comparisons.—*Sedenticellula sacra* is characterized by its large adult size, transversely subelliptical to subpentagonal outline, numerous fine costae that begin near the beaks and bifurcate and intercalate anteriorly. It is much larger and more transverse than the type species, *S. hamburgensis* (Weller), its costae are stronger and more numerous, beak ridges less acute, beak shorter and more strongly curved, and the

spondylium is sessile for less of its length. The rather low convexity, costate umbones, bifurcating costae, low fold, and lack of fine concentric ornamentation distinguish this species from species of *Coledium* with which it occurs in the Chappel Limestone.

Occurrence and abundance.—Chappel Limestone, 0.55 mile N. 39 W. of High Lonesome Windmill, 8 miles SE. of Brady, Bald Ridge area, McCulloch County, Tex. (locality TF-406 of Cloud and Barnes, 1948) (98 specimens USNM 142041); Chappel Limestone, 3,800 feet NE. of Elm Pool, Johnsons City area, Blanco County, Tex. (locality 16T-2-27A of Cloud and Barnes, 1948) (5 specimens USNM 142042); Chappel Limestone, 600 feet SW. of mouth of Joe Davis Hollow, San Saba River, southeast McCulloch County, Tex. (9 specimens USNM 142043).

Age.—Early Mississippian (Kinderhook).

Subfamily PSILOCAMARINAE Grant n. subfam.

Atriboniidae with intercamarophorial plate absent or rudimentary, hinge plate divided or short.

Genus PSILOCAMARA Cooper 1956

Levicamera GRABAU, A. W., 1934, Paleont. Sinica, ser. B, vol. 8, fasc. 3, p. 18.
Psilocamara COOPER, G. A., 1956a, Journ. Paleontology, vol. 30, No. 3, p. 523.
 NOT *Laevicamera* GRABAU, A. W., 1936, Paleont. Sinica, ser. B, vol. 8, fasc. 4, p. 87 (= *Camerisma* n. gen.).

NOT *Levicamera* Grabau, SARYCHEVA, T. G. and SOKOLSKAYA, A. N., 1952, Trudy Paleont. Inst. Moscow, vol. 38, p. 171 (= *Camerisma* n. gen.).

Shell small for family, strongly biconvex, subglobose to subpyramidal; outline subtrigonal to subpentagonal; anterior commissure strongly uniplicate; fold high, ogival, crest blunt to sharp, some sloping without break toward flanks, normally smooth; sulcus shallow, with weak median groove corresponding to crest of fold, anterior extended as tongue, curved around margin; flanks smooth, without costation; valve edges butting around most of commissure, brachial valve slightly overlapping posterolateral edge of pedicle valve; valve edges nowhere flexed or extended to form stolidium; growth lines fine, closely spaced; fine radial ornament absent.

Pedicle valve moderately strongly convex transversely, strongly convex longitudinally; umbonal region somewhat swollen, flanks relatively flat; beak short, blunt, straight to suberect; beak ridges gently rounded, barely discernible; delthyrium small, triangular, constricted at sides by small, triangular, disjunct deltidial plates, leaving elongate, slitlike foramen, partly filled by beak of brachial valve; posterolateral

edges of valve flattened to form narrow lateral pseudointerarea as bearing for overlap of edge of brachial valve (some species without overlap).

Brachial valve strongly convex transversely, moderately convex longitudinally; beak short, rounded, slightly attenuate in some, apex normally within pedicle valve.

Pedicle valve interior with one small hinge tooth on each side of anterior edge of delthyrium, each parallel to valve edge; dental plates large, curved toward floor of valve, meeting above floor, there joining to form low, thick median septum, thus producing deep, scoop-shaped spondylium duplex; septum becoming thinner and slightly higher anteriorly, extending forward about one-third length of valve.

Brachial valve interior with short undivided hinge plate; crura extending from anterior edge of hinge plate, curved gently dorsally for most of length, slightly more strongly curved near anterior ends; median septum beginning at beak, under hinge plate, ventral edge expanded to form spoon-shaped camarophorium, not attached to hinge plate, and without intercamarophorial plate, height increasing anteriorly, camarophorium extending slightly farther anteriorly than septum, length of septum only about one-fourth length of valve on floor, remaining as median keel along underside of camarophorium.

Type species.—*Psilocamara renfroarum* Cooper, 1956a, Journ. Paleontology, vol. 30, No. 3, p. 524, pl. 61B, figs. 20–32, text-fig. 1B, Nos. 4–15 (by original designation).

Range.—The known range of the genus at present is confined to that of the type species; Middle Pennsylvanian (Des Moines) of Texas and Missouri. If *Levicamera athyriformis* Grabau is found to belong to *Psilocamara*, the range of the genus will extend into the Lower Permian in Nantan and Yunnan, China.

Comparisons.—*Psilocamara* is characterized by its normally smooth shell with a single high fold in the anterior margin that takes up nearly the entire brachial valve and thus produces no flexure between it and the flanks. Internally it is characterized by a septum in the pedicle valve so low in the beak area that the spondylium is sessile in many specimens, and by a camarophorium in the brachial valve that lacks an intercamarophorial plate and is completely independent of the hinge plate. The partly sessile spondylium is similar to that in species of *Atribonium* n. gen. and *Sedenticellula* Cooper, but *Psilocamara* is easily distinguished by its noncostate shell with high fold. Lack of an intercamarophorial plate is a characteristic of *Camarophorinella* Licharev, but *Psilocamara* has the edges of the camarophorium free of the hinge plate, and its shell is essentially smooth.

Camarophorina Licharev is similarly smooth, but differs from *Psilo-*

camara in its sulcate rather than uniplicate commissure. Among lower Paleozoic forms, *Psilocamara* most nearly resembles *Atribonium* which normally is only weakly costate. *Psilocamara* differs from that Devonian form in its smoother shell with high arched rather than broad and flat-crested fold and, internally, in its partly sessile spondylium and lack of an intercamarophorial plate.

Psilocamara is similar externally to *Camerisma* n. gen., but differs in its thinner shell walls and, most importantly, in its lack of an intercamarophorial plate between the camarophorium and the underside of the hinge plate in the brachial valve. The relationships of these two genera are discussed further under *Camerisma* (q.v.).

Discussion.—As presently restricted to species lacking an intercamarophorial plate, *Psilocamara* contains only its type species, *P. renfroarum* Cooper. Possibly *Levicamera athyriformis* Grabeau belongs to this genus, but inasmuch as only the pedicle valve of that species is known, presence of an intercamarophorial plate cannot be determined.

Ustritski (1961, p. 48) placed *Psilocamara* in the synonymy of *Levicamera* Grabau, stating that Cooper had violated the rule of priority in establishing it. However, the Code of Zoological Nomenclature requires unambiguous designation of the type species as a necessary condition to establishment of a genus after 1930. Cooper (1956a) argued correctly that Grabau (1934) had not met the necessary requirements, basing *Levicamera* on a *nomen nudum*, and that the name was not available. Ustritski himself disregarded the rules of nomenclature by attempting to change the type species of *Levicamera* to *Camarophoria pentameroides* Tschernyshev (a species now tentatively included with *Camerisma* n. gen.). His unorthodox interpretation of the rules is illustrated further by his use of the name *Camarophoria* King, 1844, for *Stenoscisma* Conrad, 1839, despite clear priority of the latter (Dall, 1877; Cooper, 1942).

PSILOCAMARA RENFROARUM Cooper

Plate 9, fig. 1-1d; figure 15

Psilocamara renfroarum COOPER, 1956a, Journ. Paleontology, vol. 30, No. 3, p. 524, pl. 61B, figs. 20-32, text fig. 1B, Nos. 4-15.

Shell small for genus, subglobose; outline subpentagonal to subelliptical, length normally greater than width, greatest width anterior to midlength; anterior commissure strongly uniplicate; fold high, ogival, with crest gently rounded to slightly carinate, gently curved to flanks without break in slope; sulcus short, shallow, nearly flat, extending as broad tongue around anterior margin, some specimens with barely perceptible median groove corresponding to crest of fold; other

radial plication or ornamentation absent. Valve edges butting except at posterolateral slopes, there brachial valve edge slightly overlapping narrow flange on pedicle valve; concentric growth lines weak, closely spaced, some forming low laminae at wide intervals.

Pedicle valve slightly swollen in umbonal region, strongly convex longitudinally through sulcus, flanks relatively flat; beak slightly attenuate, suberect to erect, pressed against brachial umbo in some specimens; beak ridges short, gently rounded; delthyrium small, triangular, sides constricted by small, triangular, disjunct deltidial plates; foramen small, elongate, normally open but filled by brachial beak in some specimens.

Brachial valve strongly convex transversely, flatly convex along crest of fold; beak blunt, apex within pedicle valve.

Pedicle valve interior with large dental plates converging toward floor, meeting to form scoop-shaped spondylium, normally sessile near beak, elevated on short septum duplex toward anterior, extending forward about one-third length of valve.

Brachial valve interior with short, undivided hinge plate giving rise to pair of long, slender, ventrally curved crura; median septum beginning at beak, extending forward about 1 mm. along floor, anterior edge curved forward thus extending length of septum above floor; top of septum expanded on each side to form camarophorium, originating on floor of valve in extreme apex, rising high above floor toward anterior, extending forward slightly farther than spondylium, not connected to hinge plate, intercamarophorial plate absent.

Holotype.—Cooper, 1956a, p. 524, plate 61, figs. 20–25, USNM 124412a; this paper, plate 9, fig. 1.



FIG. 15.—*Psilocamara renfroarum* Cooper, Capps Limestone Member of Mineral Wells Formation, Tex., transverse sections of 3 specimens.

A. Section near beak, \times ca.4.5, USNM 124412g; Cooper, 1956a, Text-fig. 1B, No. 4: intercamarophorial plate absent.

B–E. Transverse sections \times $\frac{3}{4}$ ca.4, one specimen from Cooper, 1956a, Text-fig. 1, part B: B. 0.3 mm. from beak, Cooper's fig. 7. C. 0.65 mm. from beak, Cooper's fig. 9. D. 0.77 mm. from beak, Cooper's fig. 10, intercamarophorial plate clearly absent. E. 1.0 mm., Cooper's fig. 11. F. 1.2 mm., Cooper's fig. 13.

G. Section \times 5, about 1.00 mm. from beak, USNM 142047, intercamarophorial plate absent.

Measurements.—Dimensions of the holotype and six paratypes are given by Cooper (1956a, p. 524). The average length is about 6 mm., width about 5 mm., and thickness about 4 mm.

Comparisons.—*Psilocamara renfroarum* is characterized by its small size, relatively narrow outline, entirely noncostate surface, and its fold that is high at the commissure but does not stand greatly above flanks along its length. Normally it is about half as wide as *Camerisma* (?) *sella* (Kutorga) and also differs in its more gently rounded crest of the fold, weaker median trough in the sulcus, and complete lack of costation. It is about one-sixth the size of *C.* (?) *pentameroides* (Tschernyshev), and its fold is much lower and has no break in slope toward the flanks. *P.* (?) *athyriiformis* (Grabau) is about the same size as *C.* (?) *sella*, much larger than *P. renfroarum*, but its assignment to *Psilocamara* is uncertain.

Occurrence.—Pennsylvanian (Des Moines) in Texas and Missouri (localities listed in Cooper, 1956a), about 110 specimens in collection.

Genus CAMAROPHORINA Licharev 1934

Camarophorina LICHAREV, B., 1934, Doklady Akad. Nauk, Leningrad, vol. 1, No. 4, p. 211, 213.

NOT *Camerophorina* SCHMIDT, H., 1941, Senkenb. Naturfor. Gesell., Abhand. 459, p. 43 (in Rhynchonellacea).

Shell small, rhynchonelliform, biconvex; outline elongate to transverse, subelliptical to subpentagonal; commissure strongly sulcate; fold on pedicle valve beginning 5–10 mm. anterior to beak, not strongly elevated above flanks except at anterior, normally very weakly costate, with costae beginning at beak or near anterior; sulcus on brachial valve short, beginning about 10 mm. anterior to beak, rather shallow but steeply flexed longitudinally to extend as tongue into arch of fold; posterolateral edges of valves butting at commissure without overlap; stolidium absent; flanks smooth or very weakly costate; growth laminae weak, irregularly spaced, more frequent toward anterior; growth lines fine, closely spaced, producing barely visible concentric ornamentation over entire shell surface.

Pedicle valve somewhat swollen in umbonal region, rather flatly convex longitudinally along crest of fold, strongly convex transversely and from beak to anterolateral flanks; beak strongly curved, erect or suberect, sharply pointed; beak ridges rather sharp to poorly defined; delthyrium small, triangular, partly or entirely filled by brachial beak; deltidial plates not observed, probably absent.

Brachial valve strongly convex longitudinally through sulcus, gently convex transversely, midregion somewhat swollen; apex of beak largely or completely concealed by pedicle beak.

Pedicle valve interior with dental plates strongly curved toward midline, meeting above floor to form spondylium duplex and high median septum duplex; height of septum increasing anteriorly.

Brachial valve interior with short hinge plate; low cardinal boss at apex, finely fimbriate for insertion of diductor muscles; camarophorium low and thick at posterior, curving ventrally toward anterior on increasingly high median septum duplex, edges touching hinge plate at posterior; intercamarophorial plate absent.

Type species.—*Camarophoria antisella* Broili, F., 1916, Die Permischen Brachiopoden von Timor, in Wanner, J., ed., Paleont. von Timor, No. 12, p. 58, pl. 126 (12), figs. 1–3, 5 (by designation of Licharev, 1934).

Comparisons.—*Camarophorina* is characterized by its smooth shell with the commissure sulcate rather than uniplicate. Internally, the spondylium is elevated on a rather high median septum (as in *Psilocamara*); the camarophorium is thick in the posterior region, with the edges touching the underside of the hinge plate as in *Camarophorinella* Licharev, and the intercamarophorial plate is absent. It is the only sulcate genus known in the Stenoscismatacea. In addition, it differs from *Psilocamara* in its larger size, flat-crested fold, and camarophorium that touches the hinge plate. It differs further from *Camarophorinella* in its lack of costae.

The tightly curved ventral beak on some individuals recalls *Camerisma*, *Cyrolexis*, and Late Permian species of *Stenoscisma*. The sulcate commissure of *Camarophorina* distinguishes it easily from those genera. In addition, the absence of an intercamarophorial plate differentiates it from *Stenoscisma* and *Camerisma*, and absence of costae separates it from *Cyrolexis* and *Stenoscisma*.

Species assigned to CAMAROPHORINA.—*Camarophoria antisella* Broili (1916) from the Permian of Timor is the only species that can be assigned with certainty to the genus. *Rhynchonella hanieli* Broili (1916) from the same locality also may belong to *Camarophorina* on the basis of its smooth and sulcate exterior, but its internal features are unknown. *Rhynchonella wettonensis* Davidson from the Lower Carboniferous limestone of Staffordshire, England, also might be assigned doubtfully, as it is sulcate and specimens in the U.S. National Museum seem to show edges of what may be a camarophorium near the apex of the brachial valve. This assignment is so uncertain, however, that the range of the genus ought not to be extended confidently to the Mississippian on the basis of that species.

Range.—Permian of Timor; possibly originating in the Carboniferous of England.

CAMAROPHORINA ANTISELLA (Broili)

Plate 7, fig. 2; figure 16

Camarophoria antisella BROILI, F., 1916, Perm. Brach. von Timor, p. 58, pl. 126 (12), fig. 1-3, 5; LICHAREV, B., 1934, Doklady Akad. Nauk, Leningrad, vol. 1, No. 4, p. 211, 213.

Shell moderately strongly biconvex; outline rounded subpentagonal to subelliptical, widest near or anterior to midlength; anterior commissure strongly sulcate, lateral commissure smooth; pedicle valve fold flat-crested, standing only slightly above flanks, crest slightly depressed in some specimens, producing hint of costation; brachial valve sulcus depressed only near anterior of valve, curving to fill fold at anterior, floor slightly convex or flat, with very low, short, rounded costa on midline at anterior of shells with slightly depressed crest of fold; shell otherwise lacking radial structures or ornamentation; concentric growth lines fine, closely and evenly spaced; growth laminae somewhat stronger, irregularly and more widely spaced, most frequent near margins.

Pedicle valve with greatest convexity about one-third distance anterior to beak, transversely rather evenly convex posterior to fold, more steeply sloping lateral to fold; beak short, sharp, strongly curved, suberect or erect; delthyrium small, open, triangular, apparently without deltidial plates, opening nearly directly dorsally; beak ridges blunt, short.

Brachial valve somewhat less strongly convex, greatest swelling in umbonal region, strongest convexity longitudinally through sulcus; beak blunt, with apex in pedicle valve, somewhat constricting delthyrium.

Pedicle valve interior with broad spondylium elevated on high median septum duplex; septum becoming thin and slightly higher toward anterior edge, extending about one-fifth length of valve.

Brachial valve interior with short thin hinge plate in apex; cardinal boss low, fimbriate for muscle insertion; camarophorium thick in posterior, edges touching hinge plate, posterior part elevated on thick median septum duplex; septum becoming thinner and much higher anteriorly, extending about one-third length of shell, intercamarophorial plate absent.

Lectotype (here designated).—*Camarophoria antisella* Broili, F., 1916, Die Permischen Brachiopoden von Timor, J. Wanner, ed., No. 12, pl. 58, pl. 126 (12), fig. 1 (deposited in Wanner Exped. coll., Univ. Museum, Bonn).

Comparisons.—*Camarophorina antisella* is characterized by its small

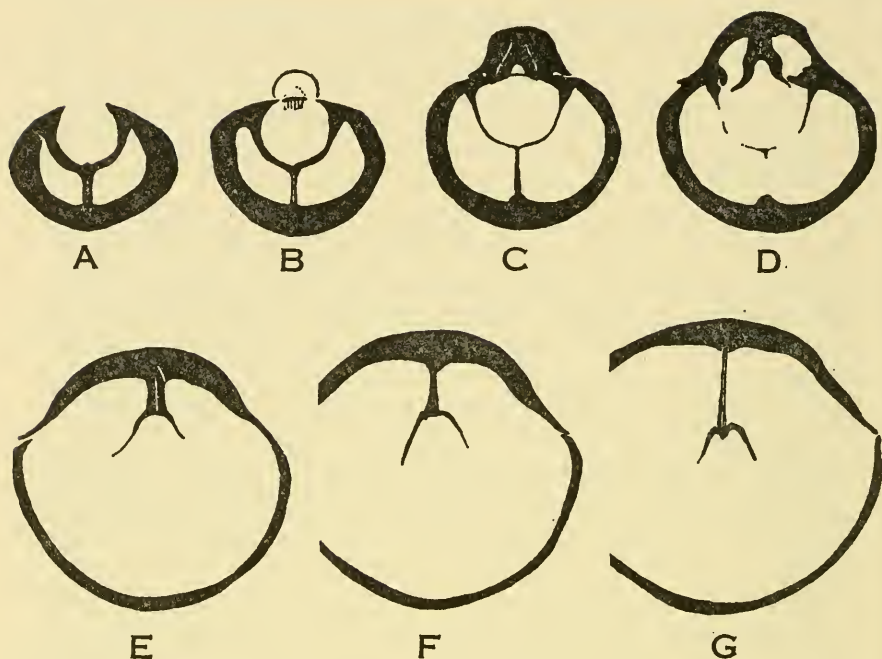


FIG. 16.—*Camarophorina antisella* (Broili), Permian at Basleo, Timor; transverse sections $\times 5$, USNM 142044, original length 11.0 mm., measurements from pedicle valve beak.

A. 0.8 mm.: spondylium elevated, camarophorium not shown, but visible through clear shell. B. 1.2 mm.: hinge plate and cardinal process visible, camarophorium thick, without intercamarophorial plate. C. 1.6 mm.: intercamarophorial plate definitely absent. D. 1.8 mm.: plates and septum of spondylium very thin. E. 2.6 mm.: spondylium absent, duplex septum of camarophorium apparent. F. 3.0 mm.: trough of camarophorium deep. G. 3.4 mm.: trough of high camarophorium slightly distorted, pushed onto septum. Camarophorium ends 3.9 mm. from beak.

TABLE 15.—*Measurements of Camarophorina antisella from the Permian at Basleo, Timor*

USNM No.	<i>Measurements, in millimeters</i>		
	Length	Width	Thickness
142044	10.4	11.9	8.6
142045	11.0	11.9	8.4
142046	11.8	12.8	8.0
95046	12.0	12.6	9.0
92213	12.7	13.3	8.7

size, subglobose shape, short beak, smooth exterior, and high fold at the anterior. *Rhynchonella hanieli* Broili (1916) also may belong to *Camarophorina*, although its internal characters are not sufficiently known to place it certainly in that genus. It differs from *C. antisella* in its somewhat larger size, broader outline, flatter profile, and lower, broader fold and sulcus, and slightly stronger growth laminae. Broili (1916, p. 63) considered the two species to be generically distinct, their similar sulcation illustrating convergent evolution.

Camarophorina antisella differs from *C. (?) wettonensis* (Davidson) from the Carboniferous of Britain in its smaller and more globose form, less flattened crest of the fold on the pedicle valve, and in its total lack of costae. *C. (?) wettonensis* has numerous weak costae on the fold, in the sulcus, and on the flanks of both valves.

Genus CAMAROPHORINELLA Licharev 1936

Shell subtrigonal, subpentagonal or subelliptical, biconvex; commissure uniplicate; fold low, broad at anterior, standing only slightly above flanks; sulcus shallow, producing only short tongue at anterior; costae low, rounded, numerous, beginning at or near beaks, number increasing anteriorly by bifurcation or intercalation; valves meeting acutely at anterior; stolidium absent; growth laminae distinct, widely spaced.

Pedicle valve moderately convex; beak short, sharp; curvature of beak, form of delthyrium and foramen, and possibility of presence of deltidial plates not observed.

Brachial valve more strongly convex; beak short, probably curved into delthyrium of pedicle valve.

Pedicle valve interior with large dental plates converging toward floor, meeting just above floor to form large, boat-shaped spondylium; median septum formed by juncture of dental plates on midline, low and thick at posterior, becoming slightly higher and much thinner anteriorly; height of dental plates decreasing anteriorly, hence spondylium reduced to shallow concave platform at anterior end. Muscle marks not observed.

Brachial valve interior with small, irregularly fimbriate cardinal process at apex. Hinge plate divided anterior to process; camarophorium on median septum, posterior edges attached to underside of hinge plate; intercamarophorial plate absent; camarophorium extending anteriorly beyond hinge plate, curving ventrally, height of septum increasing anteriorly; crura extending anteriorly from forward edges of hinge plate, continuing near edges of camarophorium. Muscle marks not observed.

Discussion.—*Camarophorinella* was established by description and illustration of the internal features of its type species (Licharev, 1936). Its exterior form was illustrated by Licharev in 1960, who questioned its inclusion in the Camarophoriidae (Stenosclimatidae).

The camarophorium of this genus is different from that of most other genera of the Stenosclimatacea in that the edges of its trough are directly attached to the sides of the divided hinge plate, whereas in most other genera the hinge plate is undivided and is joined to the midline of the camarophorium by the intercamarophorial plate, weakly connected laterally (*Cyrolexis* and *Camarophorina*) or (as in *Psilocamara*) the camarophorium and hinge plate are entirely unconnected. Licharev's serial sections (1936, text-fig. 4) show that the camarophorium is characteristic for the superfamily in all respects except its distal rather than mesial attachment to the hinge plate. Therefore, *Camarophorinella* here is included with the superfamily Stenosclimatacea. Divided or undivided hinge plates are variations that appear in many groups of rhynchonellids, and normally are not accorded more than generic importance. The manner of attachment of the camarophorium probably reflects merely the incompatibility of an intercamarophorial plate and a divided hinge plate. The edges of the camarophorium in all genera of the superfamily are very near the underside of the hinge plate, and in Permian genera they nearly are in contact. The slight extension of the edges to meet the hinge plate seems a likely structural modification to compensate for absence of the bracing effect of the intercamarophorial plate.

Type species.—*Camarophoria* (*Camarophorinella*) *caucasica* Licharev, B., 1936, Am. Journ. Sci., ser 5, vol. 32, No. 187, p. 63, text fig. 4, (original designation); exterior first illustrated by Licharev, B., 1960, Osnovi Paleont., Moscow, p. 250, pl. 49, fig. 1.

Additional species of CAMAROPHORINELLA.—Licharev (1936, p. 64, text fig. 5) established *Camarophorinella pauciconvexa* as the second species of *Camarophorinella*. He did not illustrate its exterior, but presented a series of 10 serial sections to show its internal structures. He mentioned that he knew of no weakly costate or smooth species of *Camarophorinella*, implying that *C. pauciconvexa* is strongly costate. To my knowledge, this is all that has been written about the form of this species. Like the type species, it is from the Permian of the North Caucasus.

Range.—The genus is represented by only two species: *C. caucasica* Licharev and *C. pauciconvexa* Licharev. Both are from the Upper Permian of the northern Caucasus. According to Licharev's (1960) usage, Upper Permian includes the Kazanian and Tatarian.

CAMAROPHORINELLA CAUCASICA Licharev

Plate 4, fig. 5; figure 17

Camarophoria (*Camarophorinella*) *caucasica* LICHAREV, B., 1936, Am. Journ. Sci., ser. 5, vol. 32, No. 187, p. 63, text fig. 4.

Camarophorinella caucasica Licharev, LICHAREV, B., 1960, Osnovi Paleont., Moscow, p. 250, text fig. 292 (not 294), pl. 49, fig. 1.

Shell small, transversely subtrigonal to subelliptical, moderately strongly biconvex; greatest width near or anterior to midlength; fold low, broad, flat-crested, beginning about 5 mm. anterior to brachial beak, standing only slightly above flanks, height increasing anteriorly; sulcus shallow beginning just anterior to pedicle beak; costae low, rounded, number increasing anteriorly by intercalation or bifurcation, numbering about 4–6 on fold (depending on length of shell), one fewer in sulcus, about 6 or 7 on each flank; growth laminae widely spaced, weak but distinct, other concentric ornamentation not observed.

Pedicle valve moderately and evenly convex longitudinally and transversely; beak short, obtusely pointed.

Brachial valve slightly more strongly convex; beak slightly swollen, not protruding.

Pedicle valve interior with large spondylium supported by low, thick median septum in posterior, plates of spondylium and septum becoming thinner anteriorly, septum slightly more elevated toward anterior.

Brachial valve interior with divided hinge plate supported by sides of trough of camarophorium in posterior; camarophorium extending anteriorly well beyond hinge plate, height of median septum increasing anteriorly, elevating camarophorium.

Discussion.—The above descriptions are based on illustrations in

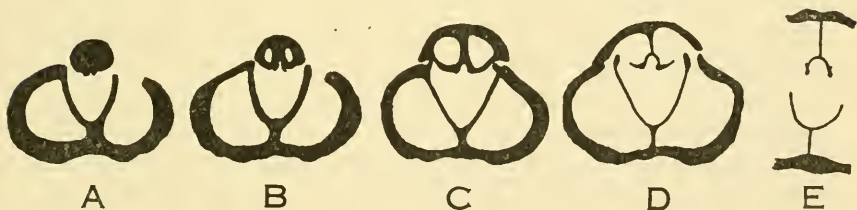


FIG. 17.—*Camarophorinella caucasica* Licharev, Permian, North Caucasus transverse sections \times ca.3, from Licharev, 1936 text-fig. 4.

A. Cardinal process visible, Licharev's fig. b. B. Hinge plate divided, joined to edges of camarophorium, Licharev's fig. c. C. Licharev's fig. d. D. Hinge plate reduced, camarophorium and spondylium detached from shell proximally, Licharev's fig. e. E. Camarophorium and spondylium thin, Licharev's fig. g.

the two available references dealing with the genus *Camarophorinella* and its type species (see synonymy). Licharev (1936, p. 63) announced his intention to describe the species fully in the fourth part of his monograph of the Permian brachiopods of the North Caucasus, but he made no further reference to the species until publication of the "Osнови" in 1960. (Since the above was written, specimens were sent to the U.S. National Museum by Licharev. They agree with the above description from the literature. Broken beaks reveal spondylium and camarophorium, confirming placement in the Psilocamarinae.)

If species of *Camarophorinella* vary as species of other genera of the Stenosismatacea, then specific characters probably are in the convexity of the valves, differences in shell outline, height of the fold, and number and place of origin of costae. Internal features probably remain relatively invariable within the genus (see Licharev, 1936, text-fig. 5).

Genus CYROLEXIS Grant n. gen.

(Kyro, Gr., attain; lexis, Gr., lot, destiny)

Shell thick, strongly biconvex, ellipsoidal; outline subtrigonal to subelliptical, normally somewhat elongate, greatest width anterior to mid-length; anterior commissure uniplicate, fold high, flat-crested, occupying about one-third shell width, forming only short and low elevation of brachial valve at extreme anterior; sulcus shallow, broad, beginning far anterior, primarily expressed as tongue extending into fold at anterior commissure; valves butting, meeting at slightly obtuse angle at anterior and anterior sides, overlapping strongly on posterolateral slopes, nowhere extended to form stolidium; costae weak to moderately strong, present on fold and flanks, beginning several millimeters anterior to beaks, crests rounded at origin, sharper toward anterior; growth lines fine, closely spaced; growth laminae only slightly stronger, widely and irregularly spaced, other concentric or radial ornamentation absent.

Pedicle valve moderately to strongly convex, slightly swollen in umbonal region; beak short, strongly curved, normally erect or slightly recurved, pressed rather closely onto brachial umbo; beak ridges blunt but distinct, outlining large flat posterolateral surfaces for overlap by brachial valve; delthyrium normally filled by brachial umbo, deltidial plates apparently absent.

Brachial valve somewhat more strongly convex, umbonal region swollen; beak short, blunt, normally covered by pedicle beak; posterolateral edges of valve very thin, overlapping broad smooth areas of pedicle valve.

Pedicle valve interior with one small hinge tooth at each side of

hinge; dental plates large, thin, reaching to floor in apex but converging to form sessile spondylium, joining to form low septum duplex just anterior to apex, elevated slightly by septum toward anterior, spondylium extending anteriorly between one-fifth and one-fourth length of shell, septum continuing slightly farther; muscle marks and other internal features not observed.

Brachial valve interior with undivided hinge plate, slightly swollen in apex to form cardinal process; camarophorium beginning in apex, supported by high median septum duplex, lateral edges of spoon directly butting against underside of hinge plate on one or both sides; intercamarophorial plate short and weak, or absent; hinge plate short; camarophorium curving slightly ventrally and greatly widening, length more than one-third length of shell, nearly half length of valve; anterior edge of septum concave, length of septum on floor slightly greater than length of camarophorium; crura extending from anterior edge of hinge plate, somewhat shorter than camarophorium; muscle marks and other internal features unknown.

Type species.—*Cyrolexis haquei* n. sp., named for A.F.M.M. Haque, Geological Survey of Pakistan.

Additional species.—*Terebratula superstes* Verneuil (1845), long included in *Camerophoria* or *Stenoscisma*, is strikingly similar externally to *C. haquei*. Specimens from near Novgorodsk in the U.S.S.R. (just north of Korea) illustrated by Licharev (1913, pl. 1; 1960, pl. 48) have all the external features of the genus. Verneuil's drawings (1845, pl. 5a-e) are slightly different, and his description mentions the external generic characters of closely curved pedicle beak, weak plication, low and short fold, shallow sulcus, and entirely closed pedicle foramen. The major differences from *C. haquei* are its larger size, narrower outline, somewhat lower fold, and the lack of costae on the flanks.

Specimens of *C. superstes* from the Moscow region illustrated by Sarycheva and Sokolskaya (1952, p. 171, pl. 48, fig. 267) also are similar to *C. haquei* in profile and outline. However, the valves protrude slightly at the fold and sulcus, indicating either an incipient stolidium, or perhaps a stolidium that was broken from the specimens. Possibly these specimens also belong to *Cyrolexis*; direct study of the specimens is necessary.

According to Tschernyshev (1902, p. 489), the Ural and Siberian stenoscismataceans fall into two distinct groups: those with the stolidium present, and those with it absent. His conclusion was the same as that which I derived from study of representatives of the entire superfamily; namely, that certain groups of stenoscismataceans lack the stolidium, not through incomplete preservation but because the shell was

so constructed that its development was impossible. Although not specifically stated by Tschernyshev, his implication is that presence or absence of the stolidium was genetic. He did not consider it advisable at the time to subdivide "*Camarophoria*" on that basis. However, now it appears that two distinct phyletic stocks are involved, and subdivision is necessary. I believe that of the many species that Tschernyshev (1902, p. 76-101, 488-510) assigned to *Camarophoria*, most of those in his Group IV (p. 77) probably belong to *Cyrolexis*: *C. superstes* (Verneuil), *C. netschajewi* Tschernyshev, and *C. parvula* Tschernyshev. He also included *C. rhomboidea* (Phillips) in Group IV, and named the group for it, although that species is not present in his Ural-Timan fauna. Specimens similar to *C. rhomboidea* (Phillips) in the U.S. National Museum collection (not topotypes) support Tschernyshev's contention that that species lacked the stolidium congenitally. However, they are not similar to *Cyrolexis haquei* nor to the Ural-Timan species of Tschernyshev's Group IV. Instead they most nearly resemble *Coledium bowsheri* (Cooper) and probably are congeneric with it. Species in Tschernyshev's other five species-groups of *Camarophoria* belong to genera other than *Cyrolexis*; most can be assigned to *Stenoscisma*.

Tschernyshev (1902, p. 77) included *Terebratulula globulina* Phillips with the species of *Camarophoria* in Group IV. The specimens that he illustrated appear to be of the type that completely lacks the stolidium, but they more clearly resemble *T. rhomboidea* Phillips than other species of Group IV. Therefore, perhaps they should be linked with that species, probably in the genus *Coledium* n. gen. Specimens of Phillips' species in the U.S. National Museum collection greatly resemble Tschernyshev's illustrations, confirming his identification and supporting my contention that the species belongs more properly with *Coledium* than with *Cyrolexis*.

Species belonging to CYROLEXIS.—

Cyrolexis haquei n. sp. (type species)

Camarophoria waageni Netschajev, 1894 (same as *Camarophoria superstes* (Verneuil) of Waagen, 1883)

Terebratulula superstes Verneuil, 1845

Species probably belonging to CYROLEXIS.—

Camarophorina superstes (Verneuil) of Tschernyshev, 1902

Camarophoria netschajewi Tschernyshev, 1902

Camarophoria parvula Tschernyshev, 1902

Camarophoria superstes (Verneuil) of Licharev, 1913, 1960

Species possibly belonging to CYROLEXIS.—

Dielasma cf. *D. gemmula* de Koninck of Diener, 1915

Camarophoria karpinskii Tschernyshev, 1902

Comparisons.—*Cyrolexis* is characterized by its strongly curved

pedicle beak that normally presses too tightly to the brachial umbo to allow a pedicle opening, the broad overlap of its valves along the posterolateral slopes, the absence of a stolidium, and by its camarophorium whose edges may touch the underside of the hinge plate, without support of a strong intercamarophorial plate. Lack of a stolidium and normal lack of an intercamarophorial plate distinguish it from genera of the Stenoscismatidae, although it resembles those genera in its broadly overlapping posterolateral valve edges and strongly curved pedicle beak that closes the pedicle foramen. It differs from most genera of the Atriboniidae in its strongly curved beak, broadly overlapping valve edges, and weak or absent intercamarophorial plate. *Psilocamara* Cooper lacks the plate entirely, and its camarophorium does not meet the hinge plate; that genus differs further in its complete lack of costation, its open pedicle foramen, and its butting rather than overlapping posterolateral valve edges. *Camarophorinella* Licharev lacks an intercamarophorial plate, but *Cyrolexis* differs from it in its stronger convexity, weaker costation, strongly overlapping posterolateral valve edges, and its undivided hinge plate.¹

Range.—*Cyrolexis* is confined to the Permian, apparently ranging through the entire Permian of Asia. It has been found in the Kazanian of the Siberian Far East, in the Lower and Upper Productus Limestones of the Salt Range, and species probably belonging to it occur in the Lower Permian of the Urals.

CYROLEXIS HAQUEI Grant n. sp.

Plate 6, figs. 1-5; figures 18, 19

Shell strongly biconvex, slightly longer than wide, outline subovate; commissure uniplicate, with rather high fold only slightly elevating median portion of brachial valve for short distance near anterior, fold normally beginning 8-10 mm. anterior to brachial beak; sulcus shallow, beginning about same distance anterior to pedicle beak; costae low, sharp at anterior, normally numbering three or four on fold, one fewer in sulcus, commonly same number on flanks as on fold, beginning 5-10 mm. anterior to beaks.

Pedicle valve moderately strongly and rather evenly convex, greatest swelling in umbonal area; beak erect or slightly recurved, normally tightly pressed against brachial umbo; large flat areas on posterolateral

¹ Numbering of the figures on the top of page 251 in the *Osnovii Paleontologii* (Licharev, 1960) appears to be erroneous: figure 293 purports to be a section of *Stenoscisma margaritovi* (Tschernyshev), but instead is a drawing from Schmidt (1941) of *Camarophorina pachyderma* (Quenstedt). The section of *Camarophorinella caucasica* Licharev is figure 292 rather than 294 (cf. Licharev, 1936, fig. 4).

slopes for overlap by edges of brachial valve, normally exposed by breakage or weathering.

Brachial valve more strongly convex; beak covered by pedicle beak; posterolateral valve-edges thin, commonly broken.

Pedicle valve interior with large, thin-walled spondylium, sessile in extreme apex, elevated on very low septum toward anterior, extending anteriorly about one-fourth length of valve.

Brachial valve interior with large, spoon-shaped camarophorium on high median septum, edges of posterior part of camarophorium touching underside of undivided hinge plate, continuing free into cavity of shell, extending forward about half length of valve, anterior of camarophorium becoming slightly fluted longitudinally, height increasing, length slightly greater than length of median septum, extending considerably farther anteriorly than spondylium of opposite valve; crura short, extending from anterior edge of hinge plate; intercamarophorial plate thick at posterior, very short, becoming thin and terminating in apex of valve, entirely absent from some specimens.

Holotype.—USNM 142061, plate 6, fig. 2.

Comparisons.—*Cyrolexis haquei* is characterized by its rather small size, slightly elongate globose shape, narrow outline, moderately high fold, strongly curved pedicle beak, and normally costate fold and flanks. It differs from *Terebratula superstes* Verneuil in its smaller size, higher fold, narrower outline, and costate flanks. It is much larger than *Camarophoria parvula* Tschernyshev (1902, pl. 46) and is much more strongly convex, strongly folded, and has more and sharper costae. It resembles the Timanian species *C. netschajevi* Tschernyshev in its strong convexity, but differs in its narrower and more elliptical out-

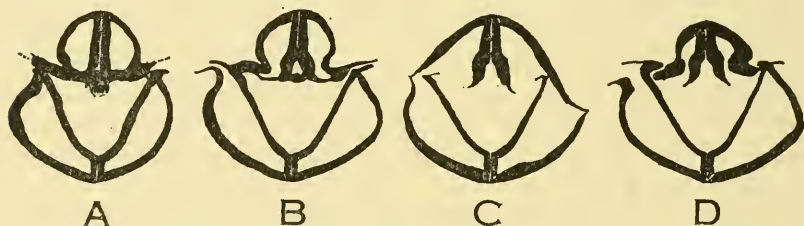


FIG. 18.—*Cyrolexis haquei* n. sp., Lower Productus Limestone, Salt Range, Pakistan; transverse sections $\times 4$, USNM 142066, each valve cut nearly perpendicular to internal structures, the two cuts meeting nearly perpendicular to one another.

A. Near beaks: top of brachial septum not yet spread to form camarophorium, cardinal process fimbriate. B. Farther anterior, no intercamarophorial plate. C. About 0.5 mm. from brachial valve beak and 0.7 mm. from pedicle valve beak. D. Slightly different angle from fig. C, 0.9 mm. from brachial valve beak, 1.5 mm. from pedicle valve beak.

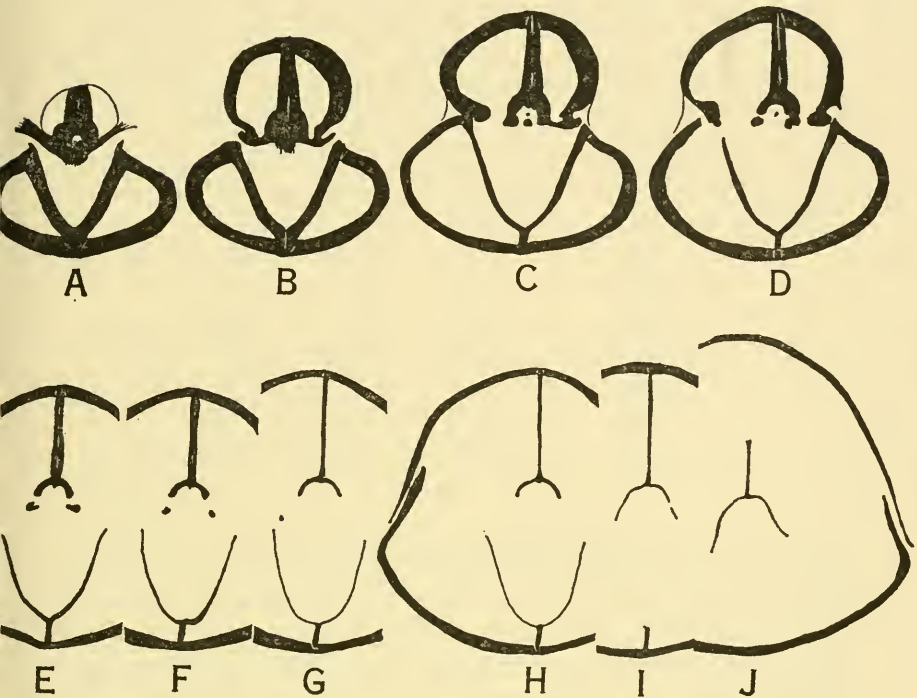


FIG. 19.—*Cyrolexis haquei* n. sp., Lower Productus Limestone, Salt Range; transverse sections $\times 4$, cut perpendicular to commissure, USNM 142065, original length 12.9 mm., distances from pedicle valve beak.

A. 0.9 mm.: no intercamarophorial plate. B. 1.1 mm.: thick filling between hinge plate and camarophorium, edges of camarophorium meet hinge plate, cardinal process high. C. 1.3 mm.: small dot of shell at locus of intercamarophorial plate. D. 1.6 mm.: camarophorium separating from crura. E. 1.8 mm.: crura separate from camarophorium. F. 1.9 mm.: crura thinner, divergent. G. 2.2 mm.: crura separated widely, near edges of spondylium. H. 2.4 mm.: crura gone; wide overlap of valves. I. 2.8 mm.: spondylium nearly gone. J. 3.5 mm.: septum of camarophorium separated from valve floor; wide overlap of valve edges. Camarophorium disappears at 4.5 mm.

line, weaker and fewer costae that begin farther forward, and its shorter and more strongly curved pedicle beak.

Of the species compared above, only *C. superstes* is represented by Russian specimens in the U.S. National Museum collections. These specimens, ten in number, show the generic characters of *Cyrolexis*, and undoubtedly belong to that genus. They have the pedicle beak tightly curved onto the brachial umbonal region completely closing the foramen; the brachial valve strongly overlaps the posterolateral edges of the pedicle valve; costation is weak, and the stolidium is ab-

TABLE 16.—*Measurements of Cyrolexis haquei from the Lower Productus Limestone*

USNM No.	<i>Measurements, in millimeters</i>		
	Length	Width	Thickness
142052	12.0	12.3	10.0
142053	12.2	11.8	10.0
142054	12.3	12.7	c.9.0
142055	12.7	10.5	9.1
142056	12.7	11.9	10.9
142057	13.0	12.6	9.6
142058	13.0	12.4	9.6
142059	c.13.0	11.2	9.8
142060	13.1	12.0	10.2
142061	13.1	11.4	11.6
142062	14.0	12.4	12.3
142063	c.14.5	13.0	12.6
142064	c.15.0	14.2	12.4

sent. Tschernyshev's drawings (p. 96, fig. 31–35) show that the internal structures are nearly identical to those of *C. haquei*. The other species are assigned to *Cyrolexis* only tentatively because no specimens were examined directly. However, Tschernyshev's descriptions are clear and his illustrations are so good that the others may be assigned with little doubt.

C. haquei most nearly resembles *C. waageni* (Netschajev, 1894) from the Upper Productus Limestone of the Salt Range. It differs only slightly from that species, in its less strongly convex pedicle valve with narrower, slightly more attenuate beak, greater number of costae on the fold, normally fewer costae on each flank, and its somewhat more strongly convex brachial valve. Many specimens of *C. haquei* are proportionately wider than is typical for *C. waageni*, but others have the same dimensions as that species. The fold on some specimens of *C. haquei* is lower and broader, although this feature also is variable and not a clear distinction from *C. waageni*.

Netschajev (1894) cited Waagen's (1883) specimens of *C. superstes* (Verneuil) as examples of *Camarophoria waageni*. These are compared above to *C. haquei*. He illustrated (Netschajev, 1894, pl. 5, fig. 10) a specimen from the Russian Permian near Atary which, while probably belonging to a species of *Cyrolexis*, is greatly different from either of the two Salt Range species. It is more strongly and more completely costate, less globose and proportionately longer. The drawings probably are approximate, so Netschajev's specimens may have resembled the Salt Range species more closely than shown.

Occurrence and abundance.—Lower Productus Limestone, Rukhla area, Salt Range, Pakistan (19 specimens USNM 142068).

Age.—Lower Permian.

Family STENOSCISMATIDAE Oehlert, 1887 (1883)

[*nom. transl. et correct.* Muir-Wood, 1955, p. 91, *ex* Stenoschismatinae Oehlert, 1887, p. 1304] [= Camerophoriidae Waagen, 1883 (*nom. transl.* Grabau, 1936, p. 70, *ex* Camerophoriinae Waagen, 1883, p. 435)]

Stenoscismatacea with stolidium incipient, well-developed or degenerate, ranging from Middle Devonian through Permian; early representatives small, smooth, or weakly costate; later representatives larger, more strongly costate.

Subfamily STENOSCISMATINAE Oehlert, 1887 (1883)

[*nom. correct.* Muir-Wood, 1955, p. 91, *ex* Stenoschismatinae Oehlert, 1887, p. 1304] [= Camerophoriinae Waagen, 1883, p. 435]

Stenoschismatidae with stolidium incipient or well-developed; shell rhynchonelliform; costae beginning anterior to beaks.

Genus COLEDIUM Grant n. gen.

(Kolos, Gr., stunted; ledion, Gr., little dress)

Shell small for family, rhynchonelliform, moderately to strongly biconvex; outline subelliptical to subpentagonal, slightly transverse to slightly elongate; commissure uniplicate, with fold expressed primarily at anterior, not standing high above flanks, beginning 5–10 mm. anterior to brachial beak; sulcus similarly shallow, beginning 5–10 mm. anterior to pedicle beak; costae absent, weak, or moderately strong, occupying fold or fold and flanks, beginning about same distance anterior to beaks as fold and sulcus, rarely beginning 1 or 2 mm. anterior to beaks, rarely bifurcating; valves overlapping on posterolateral slopes, butting at anterior and anterolateral margins, there slightly protruding in most species; stolidium narrow, rudimentary, erratically present in some species, absent from others, most common on fold, rare on flanks. Growth lines weak, closely spaced; growth laminae slightly stronger, most frequent near anterior margins, irregularly spaced.

Pedicle valve somewhat swollen in umbonal region, flatly convex toward flanks, more strongly convex longitudinally through sulcus, edges of flanks not reflexed; beak short to moderately long, suberect to erect, tightly pressed to brachial umbo in some species and some individuals; beak ridges normally blunt, rarely sharp; delthyrium triangular, small; deltidial plates absent, or small, normally disjunct; foramen small, slotlike, penetrating apex of beak in some species.

Brachial valve more strongly convex, normally greatly swollen in umbonal region, crest of fold flatly convex transversely and in profile; beak short, bluntly rounded, apex within pedicle valve.

Pedicle valve interior with dental plates converging to form deep, boat-shaped spondylium, commonly meeting above floor of valve to fuse and form low median septum duplex, elevating spondylium above floor, but intersecting floor in apex of valve (within 2 mm. of beak) in some species to produce apically sessile, anteriorly elevated spondylium; median septum extending farther anterior than spondylium, normally slightly less than half length of valve; muscle and pallial markings not observed.

Brachial valve interior with short hinge plate; camarophorium beginning in apex, expanding anteriorly as shallow trough on increasingly high median septum, extending farther to anterior than septum, somewhat beyond midlength of valve and shell; septum extending about one-third length of valve; posterior part of trough of camarophorium united to underside of hinge plate by low intercamarophorial plate; apex of hinge plate swollen to form knoblike, finely fimbriate cardinal process; crura extending from anterior edge of hinge plate, curving ventrally above trough of camarophorium, conforming to its curvature, not observed to extend as far forward as camarophorium; muscle and pallial markings not observed.

Type species.—*Coledium erugatum* n. sp.

Comparisons.—*Coledium* is characterized by its small size (for a stenoscismatid), slight overlap of the posterolateral margins of the valves, angular meeting of the anterior margins of the valves, with slight outpushing of the valve edges in some species and development of a narrow stolidium in others, longitudinally strongly curved camarophorium, and by its normally weak costation, especially on the flanks. It differs from *Atribonium* in its higher fold and deeper sulcus, normally weaker costation, angular meeting of the anterior edges of the valves, overlapping of the posterior edges, strongly curved rather than nearly flat camarophorium, and in presence in some species of a narrow stolidium.

Coledium probably is ancestral to *Stenoscisma*; it resembles that genus by possession of a stolidium. It differs in the inconsistent presence of the stolidium, the narrowness of the stolidium where it is present, the normally narrower outline of the shell, and weak or absent costae. Some Permian species of *Stenoscisma* are abnormally smooth for that genus, but none is as smooth as normal in *Coledium*; furthermore, the Permian species are wider, more triangular (with greatest width farther anterior), and normally possess stronger costae on the flanks.

Coledium probably descended from *Atribonium*, or both genera derived from a common ancestor in the Late Silurian or Early Devonian. The earliest known species of *Coledium* is *C. rhomboidale* (Hall and

Clarke) from the Middle Devonian of Indiana. This species retains some of the characters of *Atribonium*; some individuals have the valves meeting in a gentle curve at the anterior, recalling the flattened anterior of *Atribonium*, and the camarophorium is unusually flat longitudinally for *Coledium*. The last known representatives are *C. crassum* (Hamlet) from the Permian of Timor and *C. globulinum* (Phillips) from the Permian of England.

Species assigned to COLEDIUM.—

Coledium angarium n. sp.

Coledium erugatum n. sp.

Coledium torvum n. sp.

Camarophoria obesa Clark 1917

Stenoscima bowsheri Cooper 1956

Camarophoria cestriensis Snider 1915

Rhynchonella explanata McChesney 1860

Coledium dutroi n. sp.

Coledium evexum n. sp.

Coledium opimum n. sp.

Coledium undulatum n. sp.

Camarophoria rhomboidalis Hall and Clarke 1894 (part)

Camarophoria crassa Hamlet 1928

Terebratula globulina Phillips 1834

Terebratula rhomboidea Phillips 1836

Rhynchonella thera Walcott 1884

Stenoscima saquensis Muir-Wood 1948

"*Terebratula pleurodon* Phillips" (Tournai, Belg. in USNM coll.)

Camarophoria indentata de Koninck 1887

Species probably belonging to COLEDIUM.—Grabau (1931a, p. 87) established four species that he called the "Group of *Camarophoria tingi*"; namely *C. bitingi*, *C. tritingi*, *C. quadritingi*, and *C. pentatingi*. In doing so, he neglected to establish the species *C. "tingi."* Distinctions among these four species are entirely upon the basis of number of costae in the sulcus, which ranges from two to five. In defense of this subdivision Grabau states, "It might be supposed that these were individual variations of a single specific group, one merging into the other, but this fact cannot be substantiated, for in none of our well-preserved specimens is there any indication of such mergence. If, for example, the triplicate group were derived from the biplicate, we should now and then find the latter with an incipient third plication, and we should also expect to find that the triplicate group shows a biplicate character in the younger stage. The same relationship should hold between the triplicate and the quadruplicate, or between this and the biplicate form." Then he describes one specimen with a bifurcated costa, whose significance he discounts, continuing, "So far as the specimens permit us to judge, the plicae appear simultaneously, which

would imply that these various forms diverge at the outset, that they in other words represent a sudden explosion, and therefore represent distinct specific groups."

If the number of costae in the four species of the *C. "tingi"* group is invariable, these are the only known species of stenoscismatacean in which that is true. To suppose that if the biplicate form were conspecific with the tricostate form, some specimens with two and one-half costae must necessarily occur, is biologically naive. More likely, the *C. "tingi"* group is a normal species, containing individuals with two to five costae in the sulcus. Further evidence that they constitute a single species: (1) their occurrence—they all occur together; (2) their numbers—a qualitative normal distribution curve could be constructed from Grabau's statements of abundance. Concerning *C. bitingi* he says, "Less common than the next"; for *C. tritingi* it is, "This species is the most common"; for *C. quadritingi*, "Occurs with the preceding, but less common"; and *C. pentatingi* is "very rare." The first valid species in the group is *C. bitingi* (p. 88); the others belong in its synonymy.

I have not been able to examine specimens of *C. bitingi* (as emended here), but Grabau's descriptions and illustrations (including a sketch, Text-fig. 8, p. 87, of an apical cross-section) show specimens that seem to fit the definition of *Coledium*. They definitely are stenoscismatacean, with ventral spondylium and dorsal camarophorium. Their valves meet at the anterior to form an obtuse angle, but not in a plane or a gentle curve as in species of *Atribonium*. The valve edges protrude slightly, as in some other species of *Coledium* (e.g., *C. angarium* n. sp.; *C. therum* (Walcott)); they have numerous costae on the flanks, but these are very low and weak, similar to costation of *C. undulatum* n. sp. Until it is possible to examine authenticated specimens of *C. bitingi*, the evidence makes it reasonable to group them with other species of *Coledium*.

Range.—The earliest known species of *Coledium* occurs in the Middle Devonian. The genus is most abundant in the Mississippian and, although rare in the Pennsylvanian, it is nevertheless the most common stenoscismatacean in that period. Its range terminates in the Permian of Timor.

COLEDIUM ERUGATUM Grant n. sp.

Plate 10, figs. 2-3; figures 20, 21

Shell average size for genus, moderately to strongly biconvex; outline subpentagonal to subelliptical, length and width nearly equal; commissure uniplicate with high fold at anterior, producing only short and low fold along brachial valve; sulcus shallow, rather broadly

rounded, both fold and sulcus beginning far forward, normally more than 5 mm. anterior to beaks; costae entirely absent from flanks, normally absent from fold (slight hint of costation at extreme anterior of one specimen) producing smooth margins; posterolateral edges of brachial valve overlapping edges of pedicle valve nearly to widest part of shell; valves meeting at acute angle around anterior, produced in some specimens to form narrow stolidium on crest of fold, narrowing on sides of fold: none observed on flanks; growth lines fine, closely spaced; growth laminae slightly stronger, widely and irregularly spaced.

Pedicle valve swollen in umbonal region, flatly convex toward flanks, slightly reflexed (concave) at flanks of some specimens, strongly convex longitudinally through sulcus but without abrupt change in convexity; beak thick, blunt (but with apex sharp), moderately long, normally erect, but not curving tightly against brachial beak; beak ridges blunt, short; delthyrium narrowly trigonal, sides constricted by small, disjunct or barely conjunct deltidial plates, leaving small, slotlike foramen, not penetrating apex of beak.

Brachial valve more strongly convex; umbonal region swollen, profile flat along crest of fold, sloping strongly toward sides; beak blunt, apex within pedicle valve.

Pedicle valve interior with dental plates forming deep spondylium, sessile for about 1 mm. in apex of beak, elevated on median septum duplex for remainder of length; septum extending anteriorly slightly less than half length of valve, spondylium about 1 mm. shorter than septum.

Brachial valve interior with camarophorium beginning in apex, curving slightly ventrally on high median septum, septum extending anteriorly along floor about one-third length of valve; trough extending farther toward anterior, producing concave anterior edge to septum; camarophorial trough shallow, rather broad near midlength; intercamarophorial plate extending from underside of hinge plate to intersect camarophorium, extending anteriorly about half length of camarophorium; hinge plate in apex of valve, posterior part swollen to form small, finely fimbriate cardinal process; crura extending anteriorly from edge of hinge plate, following course of camarophorium, reflecting its ventral curvature.

Holotype.—USNM 142121, pl. 10, fig. 2d.

Comparisons.—*Coledium erugatum* is characterized by its smooth shell without costae on fold or flanks, its high and relatively narrow fold in the anterior commissure, and by presence on some specimens of a narrow stolidium projecting from the crest of the fold. A stolidium is not preserved on the flanks of any specimens, but the valves meet in



FIG. 20.—*Coledium erugatum* n. sp., Moorefield Formation, Okla., USNM 142125. Longitudinal section near midline, $\times 5$, showing profiles of one edge of camarophorium and posterior part of its septum, hinge plate, one edge of spondylium, and part of septum of spondylium.

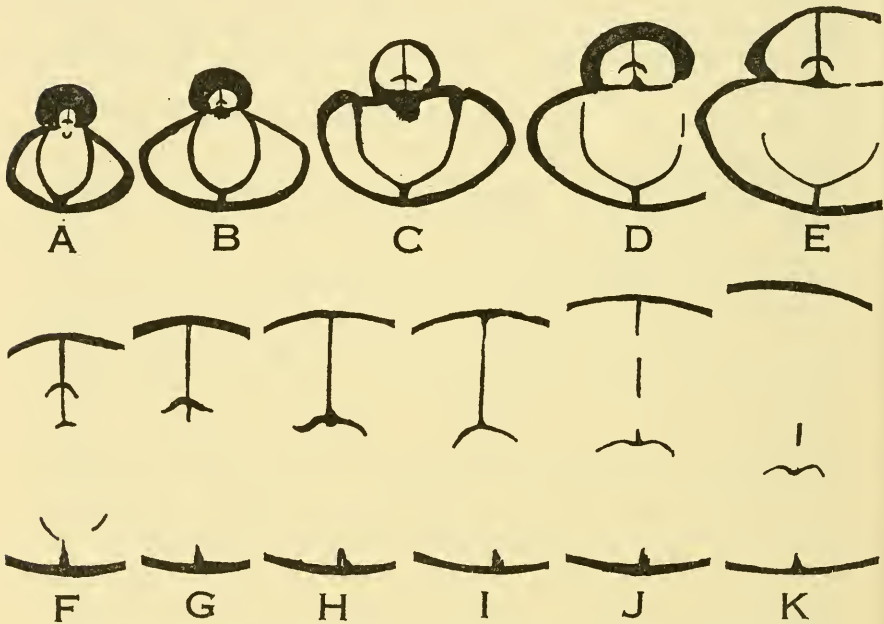


FIG. 21.—*Coledium erugatum* n. sp., Moorefield Formation, Okla., USNM 142127, transverse sections, $\times 6$, length originally 11.4 mm., distances given from pedicle valve beak.

A. 1.2 mm.: hint of cardinal process. B. 1.5 mm.: hinge plate and cardinal process. C. 2.1 mm.: cardinal process large, fimbriate. D. 2.6 mm.: no cardinal process. E. 2.9 mm. F. 3.0 mm.: hinge plate reduced, spondylium low, narrow. G. 3.4 mm.: intercamarophorial plate low, spondylium absent, septum low. H. 4.0 mm.: intercamarophorial plate nearly gone. I. 4.2 mm. J. 4.7 mm.: camarophorium high, wider, flexed; septum thin: section cuts anterior edge. K. 5.5 mm.: camarophorium high, strongly flexed transversely, septum detached from valve floor. All structures absent anterior to 5.7 mm. from beak.

TABLE 17.—*Measurements of Coledium erugatum from the Moorefield Formation of Oklahoma*

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
142114	9.7	8.9	4.9
142115	9.7	8.9	5.9
142116	10.0	9.4	6.7
142117	10.0	10.3	6.9
142118	10.3	10.3	8.0
142119	10.8	11.2	8.1
142120	11.0	12.1	7.4
142121	11.4	11.3	8.0
142122	11.9	10.3	7.3
142123	12.0	12.9	7.3
142124	c.18.0	c.18.0	10.0

such a way that it is possible that they also protruded slightly to form a narrow stolidium. The smooth shell distinguishes this species from *C. explanatum* (McChesney) and *C. cestriensis* (Snider). The high narrow fold also distinguishes it from the latter species. Its smaller size and high, narrow fold distinguish it from *C. dutroi* n. sp., another smooth or nearly smooth species of *Coledium*.

The smooth shell of *C. erugatum* recalls species of *Psilocamara* Cooper, but there is little resemblance other than smoothness. The fold of *C. erugatum* is rounded, without the Gothic-arched crest of *Psilocamara*, *C. erugatum* attains much greater size, has a stolidium on the fold of many specimens, and the valves overlap in the posterior; internally, it has an intercamarophorial plate, a shallower camarophorium, and internal structures are proportionately longer.

Occurrence and abundance.—Upper part of Moorefield Formation, $\frac{1}{4}$ mile north of southeast corner, sec. 20, T-15-N, R-20-E, Hulbert Quadrangle, Okla. (14 specimens USNM 142128); Moorefield Formation, 0.2 mile south of Glendale School, center of east line, sec. 20, T-15-N, R-20-E, Muskogee County, Okla. (7 specimens USNM 142126); Moorefield Formation, NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 21, T-15-N, R-20-E, 0.1 mile south of Glendale School, Muskogee Quadrangle, Okla. (3 specimens USNM 142129); upper part of Moorefield, NW $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 18, T-15-N, R-21-E, 1 mile south of Fort Gibson, Okla. (2 specimens USNM 142130); Moorefield Formation, $\frac{1}{4}$ mile south of Glendale School, SE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 20, T-15-N, R-20-E, on road 1 mile east of Oklahoma Highway 10, south of Bayou Manard, Muskogee Quadrangle, Okla. (2 specimens USNM 142131); Moorefield Formation, NW $\frac{1}{4}$ sec. 18, T-15-N, R-21-E, 1 $\frac{1}{4}$ miles south

of U.S. Highway 62, 7.5 miles east of Fort Gibson, Okla. (1 specimen 142132).

Age.—Late Mississippian (low in Meramec).

COLEDIUM ANGARIUM Grant n. sp.

Plate 12, figs. 2-2b; figure 22

Shell small for genus, moderately to strongly biconvex; outline subtrigonal to subelliptical, slightly elongate to strongly transverse; fold low, broad, gently arched at anterior, standing only slightly above flanks; sulcus similarly shallow; costae low, rounded, beginning about 5-7 mm. anterior to beaks (many shells without costae; average length being about 5-7 mm.), numbering up to four on fold, one fewer in sulcus, normally none on flanks; valve edges slightly protruding at anterior, especially on fold, producing rudiment of stolidium: not continuous for more than 2 mm. along commissure; growth lines very weak, crowded; growth laminae slightly stronger, widely spaced.

Pedicle valve flatly to moderately strongly convex, greatest swelling in umbonal region; beak unusually long, nearly straight to suberect, sharp, with well-defined beak ridges; broad and long flattened area between beak ridges and valve edges; delthyrium small, trigonal, constricted by pair of small deltidial plates (conjunction not observed), leaving small, slit-shaped foramen, not penetrating apex of beak.

Brachial valve more strongly convex, with greatest longitudinal curvature in umbonal region; beak curved into pedicle valve, apex hidden by deltidial plates.

Pedicle valve interior with dental plates meeting just above floor, forming large, boat-shaped spondylium, sessile or nearly so at apex, elevated anteriorly on low median septum duplex; septum extending anteriorly about one-third length of valve.

Brachial valve interior with low cardinal process near apex, at posterior of hinge plate; crura extending from anterior edge of hinge plate; camarophorium connected to underside of hinge plate by thin intercamarophorial plate, supported on high median septum duplex; septum extending anteriorly about one-fourth length of valve, camarophorium extending farther anterior, curving ventrally.

Holotype.—USNM 142085, plate 12, fig. 2b.

Comparisons.—*Coledium angarium* is characterized by its small size, few or absent costae confined to the fold and sulcus, long sharp pedicle beak with distinct beak ridges, and short, sporadic rudiment of a stolidium. *C. therum* (Walcott) also has a rudimentary stolidium on some specimens, but is much larger, little resembling *C. angarium*.

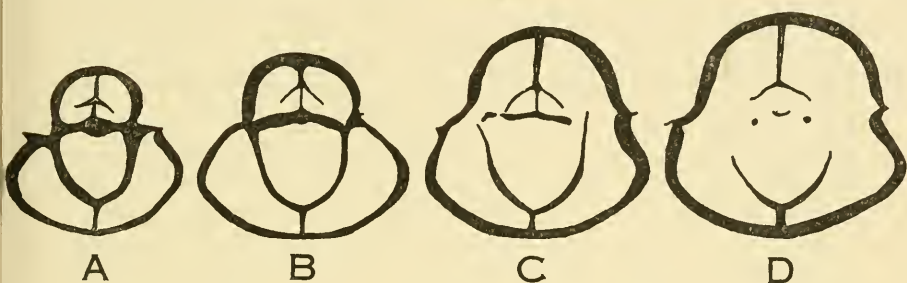


FIG. 22.—*Coledium angarium* n. sp., Barnett Shale, Mason Co., Tex.; transverse sections $\times 5$, USNM 142087, original length 8.9 mm., distances given from pedicle valve beak.

A. 1.3 mm.: camarophorium wide, cardinal process low. B. 1.8 mm.: camarophorium wider. C. 2.0 mm.: dental plates and hinge plate detached from walls. D. 2.2 mm.: hinge plate reduced to thin central part, crura present, intercamarophorial plate absent.

The small size and relatively long sharp beak of *C. angarium* distinguish it from other weakly costate American species such as *C. erugatum* n. sp. and *C. torvum* n. sp. Its small size recalls some European species such as *C. globulinum* (Phillips) (pl. 18, fig. 2) and *C. indentatum* (de Koninck), but its straighter beak and weaker costae distinguish it from them.

Discussion.—This Mississippian species from the Barnett Formation of Texas is described as a further example (with *C. therum* (Walcott)) of an early protrusion of the valve edges to form what presages a stolidium. As shown in the illustrations (pl. 12) the incipient stolidium of this species is very small, undoubtedly not a structure to function in the same manner as the wide stolidium of *Stenoscisma*. However, its presence in the Mississippian shows the genetic

TABLE 18.—Measurements of *Coledium angarium*, Barnett Formation, Tex.

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
142075	6.4	6.4	3.6
142076	7.0	7.5	4.4
142077	7.4	7.0	5.0
142078	c.7.4	7.1	6.0
142079	7.9	8.0	4.5
142080	8.2	8.5	5.4
142081	8.2	8.0	6.5
142082	8.4	8.2	5.3
142083	8.5	7.0	5.0
142084	8.8	7.7	6.4
142085	8.9	9.3	5.1
142086	9.0	8.0	5.6

potential in the stock, and probably indicates descent of *Stenosisma* from a species of *Coledium*. Possibly the slight protrusion of the valve edges functioned in directing the flow of currents in and out of the shell in these species of *Coledium*, realizing its great development as a stolidium only later, in the Permian, when adult individuals of *Stenosisma* adopted the habit of living free on the sea floor. The long beak and relatively large pedicle foramen of *C. angarium* probably mean that the species lived attached throughout its life, the rudimentary stolidium having no role in adaptation to a free-living habit at this early stage in the history of the family.

Occurrence and abundance.—Barnett Formation, calcarenite 107 feet above base, at Barton Ranch, hill south of Bee Branch, 3,200 feet S. 14° W. of Whites Crossing, 10 miles southwest of Mason, Tex. (6 specimens USNM 142089); Barnett Formation, calcarenite, at Barton Ranch 1,600 feet N. 88° W. of Whites Crossing, 10 miles southwest of Mason, Tex. (9 specimens USNM 142088).

Age.—Late Mississippian (upper Meramec or lower Chester).

COLEDIUM BOWSHERI (Cooper)

Plate 9, figs. 2-2c

Stenosisma bowsheri COOPER, G. A., 1956a, Journ. Paleont., vol. 30, No. 3, p. 525, pl. 61D, figs. 42-55.

Original description (Cooper, 1956a).—Small, wider than long, subpentagonal in outline; greatest width at the middle; sides narrowly rounded; anterior margin nearly straight. Anterior commissure strongly uniplicate. Surface smooth except for the fold and sulcus which are occupied by three and two costae respectively.

Pedicle valve gently convex in lateral profile and with the maximum convexity just posterior to the middle; anterior profile broadly and gently convex. Beak small, incurved. Umbo narrowly rounded, and median region gently inflated, flanks moderately steep. Sulcus originating just anterior to the middle, shallow and bounded on each side by a short oblique and angular fold. Tongue long and truncated anteriorly.

Foramen triangular, open, no deltidial plates having been seen in any of the specimens studied.

Brachial valve deeper than the pedicle valve but with a gently convex lateral profile; anterior profile strongly arched. Fold low, originating at about the middle; flanks gently swollen and precipitous.

Pedicle valve interior with a shallow and short spondylium; interior of brachial valve having a strongly elevated but shallow torynidium (camarophorium) anteriorly trilobed, the median lobe projecting noticeably beyond the lateral ones.

Holotype.—USNM 124408a, Cooper, 1956a, pl. 61D, figs. 42–47; this paper, pl. 9, fig. 2a.

Occurrence.—Magdalena Group, Grapevine Canyon, Sacramento Mountains, N. Mex. (details in Cooper, 1956a, p. 525).

Age.—Pennsylvanian.

Measurements.—Dimensions of the holotype and four paratypes are given by Cooper (1956a, p. 525). The average length is about 8 mm., width about 9 mm., and thickness about 5 mm.

Comparisons.—*Coledium bowsheri* is characterized by its small size, transverse subpentagonal outline, moderate convexity, weak but distinct costae on the anterior of the fold, smooth flanks, short spondylium and short, strongly curved camarophorium. It most nearly resembles *C. obesum* (Clark) from the Mississippian of Montana, differing in its wider outline, more numerous costae on the fold, and smooth flanks. It is similar in size to *C. explanatum* (McChesney), but differs in its proportionately wider outline and lower convexity, and especially in its more numerous and weaker costae on the fold, and absent costae on the flanks. It is much smaller than *C. erugatum* n. sp. which lacks costae, and smaller than *C. torvum* n. sp. whose costae are very weak and located far anterior. It is not likely to be confused with the greatly different species *C. therum* (Walcott) and *C. crassum* (Hamlet) (pl. 18, fig. 6). Both *C. undulatum* n. sp. and *C. evexum* n. sp. have costae on the flanks, which differentiate them from *C. bowsheri*.

COLEDIUM CESTRIENSIS (Snider)

Plate 12, figs. 1–1d; figures 23, 24

Camarophoria cestriensis SNIDER, L. C., 1915, Okla. Geol. Survey Bull. 24, pt. 2, p. 85, pl. 4, figs. 15–16; EASTON, W. H., 1943, Journ. Paleontology, vol. 17, No. 2, p. 131.

Original description (Snider, 1915).—Shell small, subovate to subpentagonal, length and width nearly equal, the greatest width anterior to the middle of the shell. The dimensions of the largest shell and one of average size are as follows: length of pedicle valve, 13 mm. and 10.5 mm.; length of brachial valve, 11 mm. and 9 mm.; greatest width, 12.5 mm. and 9.5 mm.; thickness, 9 mm. and 6.5 mm.

Pedicle valve arched from beak to front, greatest convexity in the umbonal region, slope steep toward the cardinal margin, and very gentle to the anterolateral margin. The mesial sinus begins posterior to the middle of the valve, and deepens rapidly anteriorly being produced into a lingual extension deeply inflecting the margin of the brachial valve, with a single, ill-defined, rounded plication in the anterior portion. Beak small and incurved. The median septum usually

shows as a dark line on the surface and the spondylium is often exposed by the breaking away of the beak.

Brachial valve more convex than the pedicle, the greatest depth anterior to the middle. Slope from the middle to the beak and margins about equal except on the mesial fold; the mesial fold begins about the middle of the valve and has a single ill-defined furrow. Beak pointed and incurved beneath that of the pedicle valve.

Ordinarily the lateral slopes are without plications, but in a few of the largest specimens a very faint plication is developed at the an-



FIG. 23.—*Coledium cestriensis* (Snider), Pitkin Limestone, Okla. (Waller loc. 169-H, unit 34), USNM 142105. Longitudinal section through midline, $\times 5$, showing profiles of camarophorium, intercamarophorial plate (lined), hinge plate, and septum of spondylium.

terior margin near the mesial fold on the brachial valve and a corresponding furrow is shown on the ventral valve.

Surface markings consist of faint concentric lines of growth.

Supplementary descriptive remarks.—Spondylium in pedicle valve sessile at extreme apex, then elevated on low median septum; trough of spondylium extending anteriorly about one-third length of valve, septum continuing nearly to midlength. Camarophorium in brachial valve extending to midlength of shell, about one-third length of valve, septum supporting camarophorium slightly shorter; trough strongly curved ventrally (longitudinally), producing very high septum between it and strongly curved valve floor; hinge plate short, connected to posterior part of camarophorium by thin intercamarophorial plate.

Lectotype (here designated).—Snider, 1915, pl. 4, figs. 15–18 (Univ. Chicago coll.).

Growth.—The patterns of growth in this species are typical for the genus, with increase in width varying narrowly along a straight line relative to increase in length, and increase in thickness slightly accelerated (fig. 24). The slope of the length-width line shows that short

FIG. 24.—Scatter diagrams of dimensions of *Coledium cestriensis* from all listed localities in the Pitkin Formation, Okla.

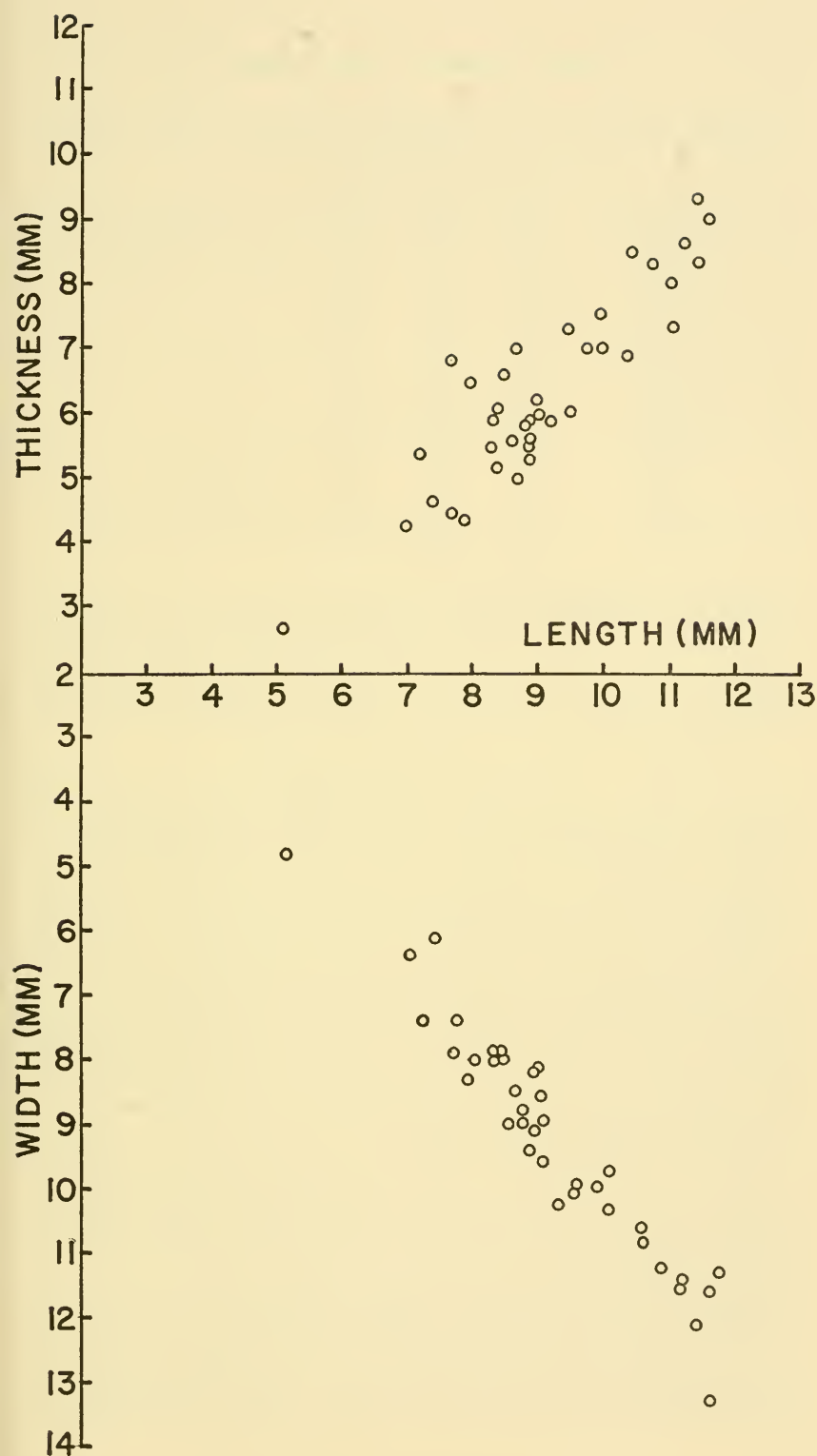


FIG. 24.—(See opposite page for legend.)

TABLE 19. *Measurements of Coledium cestriensis from the Pitkin Limestone in Oklahoma*

USNM No.	<i>Measurements, in millimeters</i>			Locality
	Length	Width	Thickness	
142091	5.1	4.8	2.7	Waller loc. 69M
142092	7.0	6.4	4.3	"
142093	7.7	7.9	4.5	"
142094	7.9	8.3	4.4	"
142095	8.4	8.0	5.2	"
142096	8.9	8.2	5.3	"
142097	9.0	8.6	6.0	"
142098	9.2	10.3	5.9	"
142099	10.0	9.8	7.0	"
142100	10.5	10.9	6.9	Mather loc. 301
142101	11.1	11.6	8.0	"
142102	11.1	11.5	7.3	Waller loc. 69M
142103	11.7	11.4	9.0	"

specimens are slightly elongate, and large specimens slightly transverse. Projection of the lower ends of both curves toward zero continues the same trends, indicating that proportional growth in early shell stages probably was similar to that in the larger shells available for measurement.

Comparisons.—*Coledium cestriensis* is characterized by its large size, two rather weak costae on the fold, and weak or absent lateral costae. It is larger than *C. explanatum* (McChesney), and has weaker costae on fold and flanks. It is about the same maximum size as *C. torvum* n. sp., but has weaker and normally fewer costae on the fold and flanks. It also attains about the same maximum size as *C. erugatum* n. sp., but that species entirely lacks costae. It is smaller, less elongate and more strongly convex than *C. therum* (Walcott), has fewer costae, and lacks the incipient stolidium that is present sporadically on that species. It differs from *C. obesum* (Clark) from the Mississippian Heath and Brazer Formations (Easton, 1962, p. 42) in its larger size, fewer and weaker costae on fold and flanks, and somewhat narrower, less pronouncedly pentagonal outline.

This species differs from *C. bowsheri* (Cooper) from the Magdalena Group of the Sacramento Mountains, N.Mex., in its larger size, proportionately narrower outline, much weaker and more variable number of costae that begin farther anterior, and its strong convexity, especially the longitudinal convexity of the brachial valve.

Occurrence and abundance.—Pitkin Limestone, sec. 35, T-16-N, R-20-E, Muskogee Quadrangle, Okla., Mather's locality 301 (3 specimens USNM 92564); Fayetteville Shale, on Oklahoma Highway 10, SE.¼ NW.¼ sec. 21, T-15-N, R-20-E, 4 miles southeast of Fort

Gibson, Okla. (1 specimen USNM 142106); Pitkin-Fayetteville boundary, on Oklahoma Highway 10, in secs. 21 and 29, T-15-N, R-20-E, 4 miles southeast of Fort Gibson, Okla. (5 specimens: Waller loc. 169-H); Pitkin Limestone, 12-20 feet below top, in abandoned Keough Quarry, along Highway 80, 1.5 miles north of Fort Gibson, in SW.¼ sec. 25, T-16-N, R-19-E, Cherokee County, Okla. (41 specimens: Waller loc. 69-M); Pitkin Limestone, in bluff at Boy Scout camp, north central sec. 19, T-16-N, R-23-E, Cherokee County, Okla. (8 specimens: Waller loc. 201-H); Pitkin (displaced blocks) at Elk Creek, secs. 5 & 8, T-14-N, R-23-E, Okla. (1 specimen: Waller loc. 159-H); top of Pitkin, along road on east side of Fort Gibson Dam, secs. 7 and 18, T-16-N, R-20-E, Cherokee County, Okla. (1 specimen: Waller loc. 191-H).

Specimens from the Pitkin Limestone collected by T. R. Waller are deposited in the U.S. National Museum. His localities containing the letter "H" refer to measured sections in Huffman (1958); those followed by "M" refer to sections by Moore (1947). Details are contained in Waller (1962) p. 40, 129-133.

Age.—Late Mississippian (Chester).

COLEDIUM DUTROI Grant n. sp.

Plate 17, figs. 1-5b; figure 25

Shell very large for genus, flatly to strongly biconvex; outline transversely subpentagonal, widest slightly anterior to midlength; commissure uniplicate at anterior; fold low to moderately high, height increasing with size of shell, crest broadly arcuate; sulcus shallow, trough of some specimens slightly convex transversely; crest of fold and midline of sulcus indented on several specimens by narrow shallow groove, producing small notch where meeting at anterior margin; costae normally absent, very weak in sulcus of few specimens; posterolateral edges of pedicle valve broadly flanged, covered by overlapping edges of brachial valve; valve margins protruding slightly around flanks and anterior, not producing distinct stolidium; growth lines weak, fine, closely and evenly spaced; growth laminae stronger, especially at anterior, widely and irregularly spaced.

Pedicle valve evenly and moderately strongly convex longitudinally, flatly convex transversely, thickest in umbonal region; beak thick, only slightly attenuate, erect to slightly incurved, not pressed tightly against brachial umbo, leaving room for small foramen; shape of foramen and possibility of modification by deltidial plates not observed.

Brachial valve strongly convex transversely, less strongly convex

longitudinally along fold, greatest swelling in umbonal region; beak bluntly pointed, apex normally hidden beneath pedicle beak.

Pedicle valve interior with dental plates joining above floor to form rather shallow spondylium, supported for entire length by median septum (spondylium not sessile in apex of valve), height of septum increasing anteriorly, becoming very high for genus, continuing anteriorly about one-third length of valve.

Brachial valve interior with short undivided hinge plate; cardinal process formed by slight swelling of apex of plate, weakly scored longitudinally for attachment of diductor muscles; camarophorium elevated on low median septum duplex in apex, height of septum increasing greatly toward anterior; sides of camarophorium reaching nearly to underside of hinge plate, midline connected to plate by intercamarophorial plate extending anteriorly slightly beyond hinge plate; septum of camarophorium extending anteriorly about one-fourth length of valve, crest of camarophorium somewhat longer; crura extending forward from anterior edge of hinge plate, curved ventrally to follow contour of crest of camarophorium; muscles and pallial marks not observed.

Holotype.—USNM 142109, pl. 17, fig. 2.

Comparisons.—*Coledium dutroi* is the largest known species of the genus, comparable in size to many species of the normally larger *Stenosisma*. In addition to its size, it is characterized by its high convexity (in large adults) broad fold that becomes high in adults and has a median groove in about half the known specimens, its broad

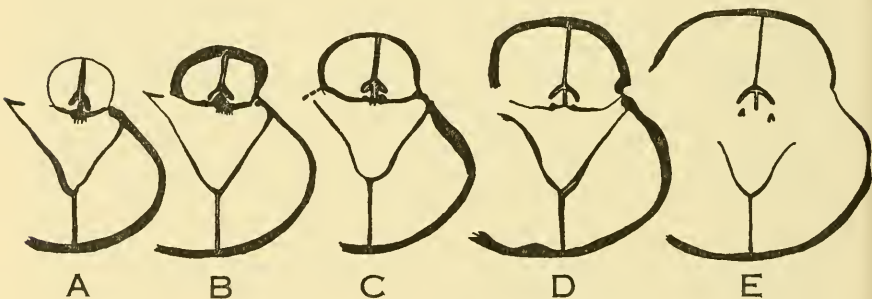


FIG. 25.—*Coledium dutroi* n. sp., Mississippian Ladronez Ids., Alaska, transverse sections $\times 4$, original length 20.0 mm. USNM 142110, distances given from pedicle valve beak.

A. 2.5 mm.: cardinal process distinct, septum of spondylium high. B. 2.8 mm.: spoon of camarophorium separate from hinge plate, septum duplex with wedged insertion into valve floor. C. 3.0 mm.: intercamarophorial plate duplex. D. 3.4 mm. E. 4.0 mm.: crura and intercamarophorial plate anterior to hinge plate; spondylium high.

TABLE 20.—Measurements of *Coledium dutroi*, from the Mississippian of Alaska

USNM No.	Measurements, in millimeters			USGS loc.
	Length	Width	Thickness	
142107	18.0	20.6	11.5	3767
142108	19.0	24.6	18.5	3767
142109	19.6	22.4	14.3	3703
142110	20.0	26.0	13.0	3747
142111	c.23.5	25.7	19.0	3703
142112	c.24.0	28.9	17.0	3703
142113	25.0	30.2	c.20	3767

sulcus also with median groove in many, and by its nearly complete lack of costation. Internally, the septum of the spondylium is usually high, elevating the spondylium nearly to the middle of the height of the valve, and consequently the spondylium is not as deep as normal for most stenoscismatids. It is named for J. T. Dutro, Jr., U.S. Geological Survey, who provided the Alaskan specimens of this species, and of species of *Camerisma*.

Only three other species resemble *C. dutroi*. One that approaches it in size is *C. therum* (Walcott) from the Mississippian of Nevada. Despite its large size for the genus, *C. therum* attains a maximum size only about half that of *C. dutroi*. In addition, *C. dutroi* differs in its broader fold, absent or nearly absent costae, and only slightly protruding valve edges. *C. erugatum* n. sp., also Mississippian, is entirely smooth, but *C. dutroi* attains a much greater maximum size, its fold is broader and, in all but large adults, is lower; furthermore, many specimens of *C. dutroi* have a median groove along the midline of the fold and sulcus.

C. crassum (Hamlet) from the Permian of Timor attains a size similar to that of *C. dutroi*, but differs in its more equilaterally pentagonal outline, proportionately broader, flatter crested fold, occasional weak costae near the anterior of the fold, more swollen brachial umbo, much shorter pedicle beak, and its nonprotruding anterior and anterolateral valve edges (see pl. 18, fig. 6).

Occurrence and abundance.—Unnamed Upper Mississippian limestone of Condon (1961), Craig Quadrangle, Southeastern Alaska, all specimens collected by G. H. Girty in 1918: U.S.G.S. loc. 3747, dark brittle limestone on south shore of Shelikof Island, one specimen (USNM 142110); U.S.G.S. loc. 3703, near middle of white limestone on east shore of island No. 250 in Ladrone Islands, three specimens (USNM 142109, 142111, 142112); U.S.G.S. loc. 3767, on east shore of island No. 250 in Ladrone Islands, three specimens (USNM 142107, 142108, 142113).

COLEDIUM EVEXUM Grant n. sp.

Plate 15, figs. 1-10; figure 26

Shell slightly below median size for genus, moderately to strongly biconvex; outline transversely subpentagonal, greatest width near midlength; commissure strongly uniplicate; fold high at anterior, rounded or somewhat flattened, beginning about 4 mm. anterior to brachial beak, not standing high above flanks posterior to margin; sulcus shallow, normally slightly raised along midline, reducing amount of depression below flanks, extending anteriorly as broad tongue into fold, beginning about 7 mm. anterior to pedicle beak; costae low, rounded, beginning far forward, absent from some specimens, numbering two or three on fold, one fewer in sulcus, normally absent from flanks but some specimens with one or two on each flank; valve edges slightly overlapping along narrow flanges on posterolateral slopes, butting elsewhere, slightly protruding around anterior margins of some specimens; growth lines fine, distinct, closely spaced; growth laminae stronger, widely and irregularly spaced.

Pedicle valve rather strongly convex for genus, greatest swelling anterior to umbonal region; beak long for genus, weakly attenuate, erect to slightly incurved, apex sharp, not pressed against brachial umbo; delthyrium small, triangular; deltidial plates not observed, probably absent; foramen coincident with delthyrium, not penetrating apex of beak.

Brachial valve similarly convex but with greatest swelling farther anterior; beak obtusely pointed, apex within pedicle valve.

Pedicle valve interior with dental plates forming boat-shaped spondylium, sessile only for about 0.5 mm. in apex, from there elevated on low median septum duplex, extending anteriorly about one-fourth length of valve.

Brachial valve interior with thin flat hinge plate in apex; camarophorium elevated on high median septum duplex, longitudinal curvature moderate, extending anteriorly about one-fourth total length of shell, trough of camarophorium relatively narrow throughout length; intercamarophorial plate connecting trough of camarophorium to underside of hinge plate, extending abnormally far forward, nearly entire length of camarophorium; crura not observed.

Holotype.—USNM 142147, plate 15, fig. 9.

Comparisons.—*Coledium evexum* is characterized by its somewhat more than normally swollen pedicle valve, transversely subpentagonal outline, very weak costae that commonly are absent from the flanks and are entirely absent from some specimens, slightly protruding anterior valve edges that presage an incipient stolidium, and its short

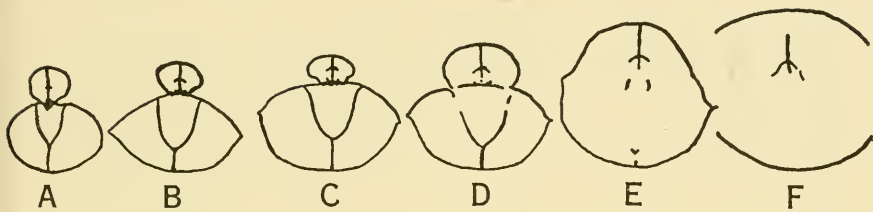


FIG. 26.—*Coledium evexum* n. sp., Chappel Limestone, McCulloch County, Tex.; transverse sections $\times 6$, USNM 142149, original length 9.4 mm., distances given from pedicle valve beak.

A. 0.1 mm.: camarophorium begins as swelling on septum; cardinal process apparent. B. 0.3 mm.: cardinal process gone. C. 0.5 mm. D. 0.7 mm.: intercamarophorial plate, hinge plate, and dental plates all detached. E. 1.1 mm.: spondylium and hinge plate gone, crura visible. F. 1.6 mm.: septum of camarophorium detached from valve floor, intercamarophorial plate still present. Camarophorium ends at 1.8 mm.

spondylium and relatively long intercamarophorial plate. Some specimens have two low and broad costae on the fold, resembling slightly those of *C. obesum* (Clark) and *C. explanatum* (McChesney). However, on *C. evexum* these costae are much lower and broader, less distinct, and begin farther anterior; the brachial valve is much less strongly convex, especially less sloping at the anterior, than in either of these two other species, and the shell outline is wider and more distinctly pentagonal. This species occurs with *C. undulatum* n. sp. but differs in its smaller size, less transverse outline, less convex brachial

TABLE 21.—Measurements of *Coledium evexum* from the Chappel Limestone of Central Texas

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
142133	c.4	3.9	2.0
142134	4.7	4.3	2.8
142135	c.5.2	5.2	2.7
142136	5.7	5.4	3.1
142137	6.3	6.3	4.0
142138	6.5	6.0	3.4
142139	6.6	7.2	4.0
142140	6.7	6.7	4.7
142141	6.9	6.6	4.9
142142	7.8	8.6	4.3
142143	8.0	8.9	6.3
142144	8.5	8.9	5.9
142145	8.9	8.8	5.9
142146	9.0	9.3	7.0
142147	9.8	11.2	7.7
142148	10.0	11.4	7.2

valve, and especially in its weaker and fewer (or absent) costae. *C. erugatum* n. sp. lacks costae, and *C. torvum* n. sp. has weak costae, but both of these species are larger and have more strongly convex brachial valves than *C. evexum*, and are proportionately not as wide. *C. bowsheri* (Cooper) is similar in outline and in the longitudinal convexity of the brachial valve, but its costae are much stronger on the fold than those of *C. evexum*, and entirely absent from the flanks. *C. evexum* attains a larger maximum size.

Occurrence and abundance.—Chappel Limestone (P. E. Cloud loc. TF-406), 0.55 mile N. 39° W. of High Lonesome Windmill, 8 miles southeast of Brady, Bald Ridge area, McCulloch County, Tex. (50 specimens USNM 142150); Chappel Limestone (Cloud loc. TF-385), east side of U.S. Highway 87, 6.7 miles south-southeast of Brady, Bald Ridge area, Tex. (2 specimens USNM 142151).

Age.—Early Mississippian (Kinderhook).

COLEDIUM EXPLANATUM (McChesney)

Plate 11, figs. 1-1c; figures 27, 28

Rhynchonella explanata McCHESNEY, J. H., 1860 (1859), Desc. new species of fossils, p. 50; McCHESNEY, 1865, Plates for new species, pl. 6, fig. 7; McCHESNEY, 1868 (1867), Trans. Chicago Acad. Sci., vol. 1, pt. 1, p. 30, pl. 6, fig. 7.

Pugnax explanatus (McChesney) HALL, J. and CLARKE, J. M., 1894, Intro. Study of Brach. pt. 2, pl. 44, figs. 14-16; HALL and CLARKE, 1894, Pal. New York, vol. 8, pt. 2, pl. 60, figs. 43-45.

Camarophoria explanata (McChesney) SCHUCHERT, C., 1897, U.S. Geol. Survey Bull. No. 87, p. 162; WELLER, S., 1910, Geol. Soc. America, Bull., vol. 21, p. 501, fig. 3; WELLER, S., 1914, Ill. Geol. Survey Monogr. 1, p. 173, pl. 23, figs. 46-51; EASTON, W. H., 1943, Journ. Paleontology, vol. 17, No. 2, p. 131.

Stenosisma explanata (McChesney) COOPER, G.A., 1944, Index Foss. No. America, p. 315, pl. 120, figs. 41-45.

Shell about average size for genus, moderately to strongly biconvex; outline subtrigonal to subpentagonal, small specimens somewhat elongate, larger specimens slightly transverse; commissure moderately to strongly uniplicate; fold high at anterior, also standing fairly prominently above flanks, beginning about 5 mm. anterior to brachial beak; sulcus shallow, broad, beginning about 5 mm. anterior to pedicle beak; costae strong, rounded to bluntly pointed, beginning about 5 mm. anterior to beaks, numbering two on fold, one in sulcus two to four on each flank; valves meeting nearly perpendicularly at anterior, without protrusion or trace of stolidium; growth lines fine, closely spaced; growth laminae slightly coarser, widely and irregularly spaced.

Pedicle valve moderately convex transversely, strongly convex longitudinally through sulcus, greatest swelling in umbonal region;

beak moderately long for genus, somewhat attenuate on some specimens, suberect to slightly incurved, apex sharply pointed; beak ridges rounded, indistinct; delthyrium open, without deltidial plates; foramen not penetrating apex of beak.

Brachial valve more strongly convex, greatest convexity near mid-length; beak obtusely pointed, apex within pedicle valve.

Pedicle valve interior with dental plates converging on floor near apex to form sessile spondylium, becoming elevated about 1–2 mm. anterior, supported by low median septum duplex, extending anteriorly about one-fourth length of valve, septum extending slightly farther.

Brachial valve interior with short hinge plate in apex; crura extending anteriorly from forward edge of hinge plate, curving ventrally; camarophorium beginning against floor of valve immediately anterior to apex, beginning as small swelling at top of median septum, connected to base of hinge plate by low, short intercamarophorial plate, continuing anteriorly about one-third length of valve, concave transversely, strongly curved longitudinally toward end of spondylium of opposite valve.

Holotype.—McChesney (1860, 1868) plate 6, fig. 7 (Plastoholotype in Walker Museum, Univ. Chicago, No. 12424, illust. by Weller, 1914, plate 23, figs. 46–47; duplicate in U.S. National Museum, No. 62495).

Growth.—In this species both the width and the thickness are slightly accelerated with respect to increase in length, in contrast to the more common pattern where increase in width is isometric

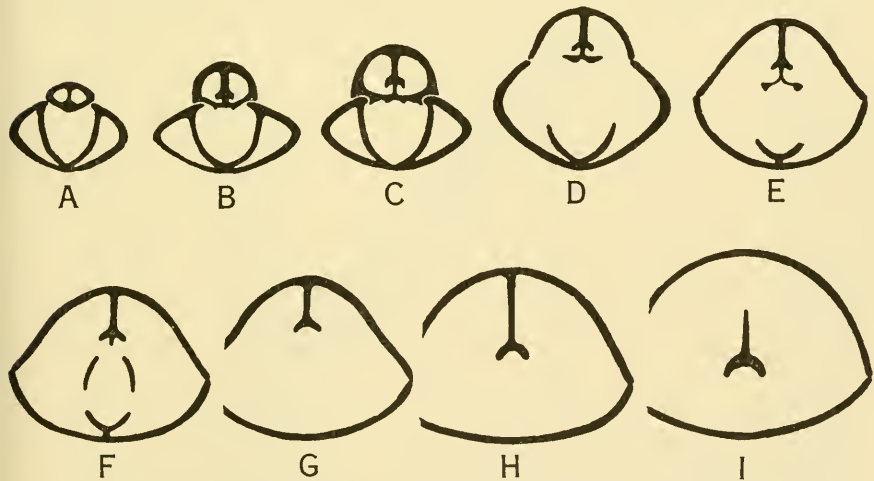


FIG. 27.—*Coledium explanatum* (McChesney), Chester Series, Chester, Ill.; sections by Weller (1914, p. 174, fig. 4, B–H, J–K), $\times 3\frac{3}{4}$.

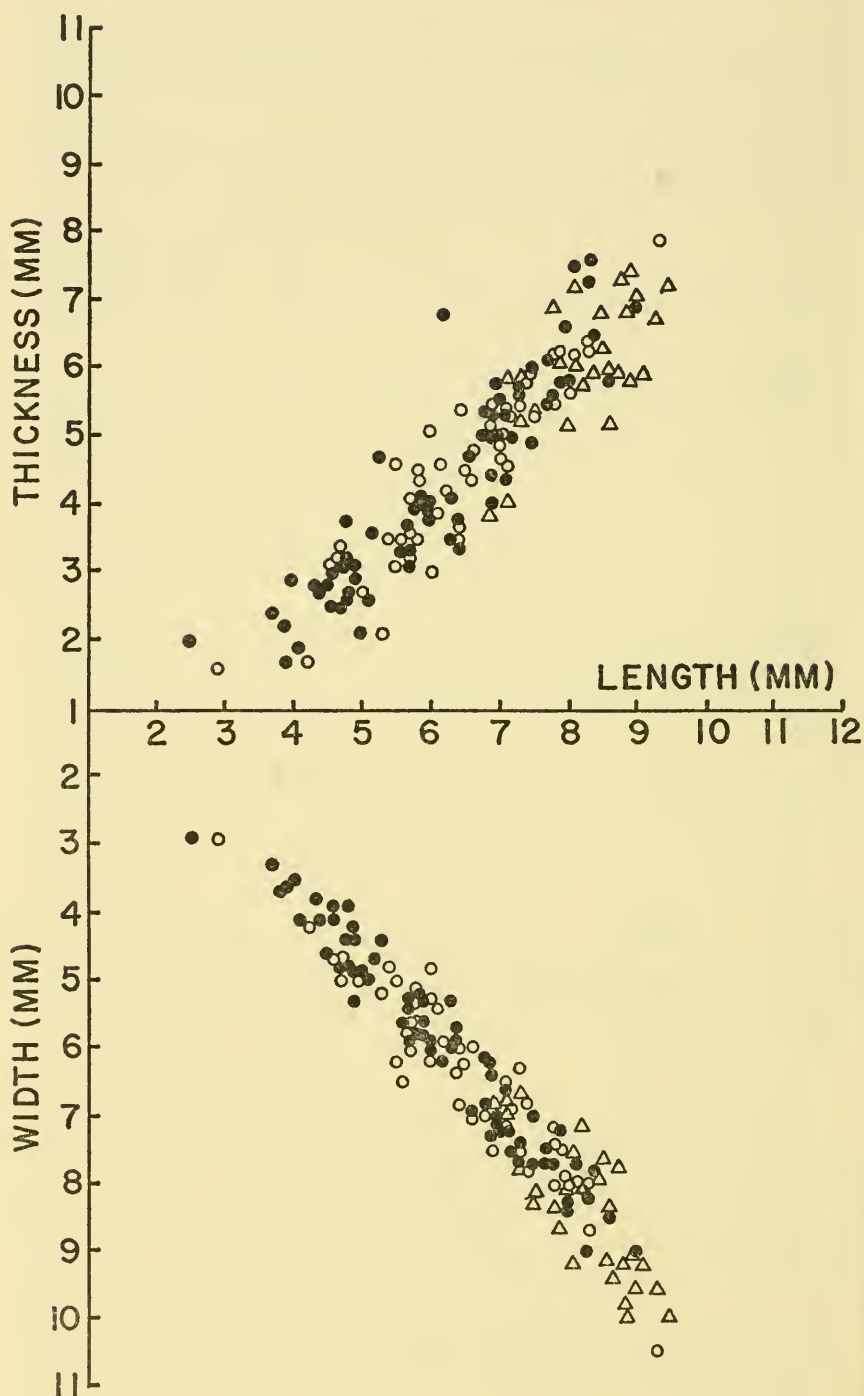


FIG. 28.—(See opposite page for legend.)

(fig. 28). If each of the two curves were projected toward a point on the length-axis somewhere less than 0.5 mm., each must necessarily bend somewhat more strongly than shown by the points on the diagrams, indicating more pronounced allometry at the earlier stages in shell growth. However, the stronger curvature of the hypothetically projected trend in thickness indicates that the length and width of early postlarval shells increased nearly commensurately, while the shells remained very flat and thin until reaching a length of about 3–4 mm.

Comparisons.—*Coledium explanatum* is characterized by its globose shape, transverse adult outline, sharp pedicle beak without apical per-

TABLE 22.—Measurements of *Coledium explanatum* from the lower part of Fayetteville Shale, 2 miles north of Habberton, Ark.

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
142153	6.9	6.9	3.9
142154	7.1	7.0	4.0
142155	7.2	7.4	5.8
142156	7.8	8.4	6.9
142157	8.5	7.7	6.3
142158	8.7	9.4	5.9
142159	8.7	8.8	5.9
142160	8.9	9.1	6.8
142161	8.9	10.0	7.4
142162	9.0	9.6	7.0
62495	8.1	9.2	7.2

TABLE 23.—Measurements of *Coledium explanatum* from the upper part of Chester Series, 2 miles south of Marion, Ky.

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
142165	2.9	2.9	1.6
142166	4.7	4.7	3.4
142167	4.9	4.9	2.9
142168	5.7	5.6	3.6
142169	5.8	5.1	3.9
142170	6.1	5.4	4.6
142171	6.6	7.0	4.8
142172	7.0	7.0	4.9
142173	7.3	6.3	5.5
142174	7.8	8.0	5.5
142175	9.3	10.5	7.9

FIG. 28.—Scatter diagrams of dimensions of *Coledium explanatum*. Circles represent specimens from 2 miles south of Marion, Ky.; solid dots represents specimens from 2 miles north of Baldwin, Ill.; triangles represent specimens from 2 miles north of Habberton, Ark.

TABLE 24.—*Measurements of Coledium explanatum from the Chester 2 miles north of Baldwin, Randolph County, Ill.*

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
142177	c.2.5	2.9	2.0
142178	3.7	3.3	2.4
142179	3.9	3.6	2.2
142180	4.1	4.1	1.9
142181	4.6	3.9	3.0
142182	4.8	4.4	2.6
142183	5.1	5.0	2.6
142184	5.7	5.4	3.7
142185	6.0	5.9	4.0
142186	6.4	5.9	3.4
142187	7.0	7.1	5.5
142188	7.8	7.7	5.6
142189	8.4	7.8	6.5
142190	8.6	8.5	5.8

foration, and especially by its strong costae that number nearly invariably two on the fold. It is about the same size as *C. obesum* (Clark) and *C. bowsheri* (Cooper), but is more strongly costate than either. It is much smaller than *C. erugatum* n. sp. and *C. torvum* n. sp., and also more strongly costate than either. McChesney (1860) compared it to *Rhynchonella wortheni* Hall, which, according to Weller (1914), lacks the internal structures of a stenoscismatacean. Its two costae on the fold recall *C. rhomboideum* (Phillips) but that species is more pentagonal, less convex, and lacks costae on the flanks (see pl. 18, fig. 1). The rather strong anterior costae of *C. explanatum* resemble those of *C. pleurodon* (Phillips) (pl. 18, fig. 3) and *C. nuculum* (Schellwien) (pl. 18, fig. 4), but the number of costae in *C. explanatum* typically is fewer than in either of those species, and the convexity of the shell much lower than in *C. nuculum*.

Discussion.—According to Weller (1914), and judging from the USNM collection, this species is the most abundant and widespread species of *Coledium*. The form of the holotype is known from casts, one of which formed the basis for Hall and Clarke's illustrations (see synonymy). This specimen is somewhat more strongly costate than most specimens in the USNM collections, and more so than specimens illustrated by Weller (1914, pl. 23) from the Chester of Illinois, the topotype area. However, agreement of the holotype with abundant specimens from the same region is close in all other features, and Weller's use of the name "*explanatum*" is here followed.

Occurrence and abundance.—Upper part of Chester Series, just east of Marion-Fredonia road, 2 miles south of Marion, Ky. (71 specimens

USNM 142176, 36539) ; Chester, at M. & O. Railroad bridge, 2 miles north of Baldwin, Randolph County, Ill. (76 specimens USNM 142191) ; lower part of Fayetteville Shale, 2 miles north of Habberton, Ark. (35 specimens USNM 142164) ; lower part of Glen Dean Formation, on road between Cloverport and Mattingly, Breckinridge County, Ky. (52 specimens USNM 142192, 93) ; Chester, near bridge over Prairie du Long Creek 3.3 miles north of Red Bud, Ill. (13 specimens USNM 142194, 95) ; upper part of Fayetteville, about 3 miles east of Elkins, Ark. (1 specimen USNM 142196) ; Chester, at Tar Park Post Office, Ky. (3 specimens USNM 142197) ; Chester, Buffalo Wallow section, Cloverport, Ky. (2 specimens USNM 142198) ; Chester, at Rileys, Randolph County, Ill. (9 specimens USNM 142199, 48892) ; Glen Dean, center of NW.¼, sec. 13, T-35-N, R-12-E, in railroad cut 1 mile southeast of Red Rock, Derry County, Mo. (2 specimens USNM 142200) ; St. Louis Limestone, Pope County, Ill. (2 specimens USNM 142201) ; Chester, Evansville, Ill. (5 specimens USNM 142202) ; Chester, on Hardinsburg Road to Stephensport, Ky. (30 specimens USNM 142203-5, 37867) ; Chester, Chester, Ill. (7 specimens USNM 142206) ; lower part of St. Genevieve Limestone, Cardens Crossroads, 6 miles south of Marion, Ky. (2 specimens USNM 48888) ; Chester near base of section at Smithland, Ky. (8 specimens USNM 48891) ; Chester, middle of section at Smithland, Ky. (3 specimens USNM 48890) ; Chester, upper part of section at Smithland, Ky. (37 specimens USNM 48898) ; upper part of Chester, north of Caneyville Quarry, Grason County, Leitchfield, Ky. (5 specimens USNM 142207) ; middle part of Chester, 4.5 miles east of Princeton, Ky. (7 specimens USNM 48887) ; middle part of Chester, 4 miles east of Scottsburg, Ky. (9 specimens USNM 48894) ; top of Chester, King's Station, Crittendon County, Ky. (1 specimen USNM 48889) ; top of Chester, Montgomery Switch, Caldwell County, Ky. (10 specimens USNM 48895) ; upper part of Chester, 1 mile west of Montgomery Switch, Caldwell County, Ky. (20 specimens USNM 48893).

Age.—Late Mississippian (Meramec to Chester).

COLEDIUM GLOBULINUM (Phillips)

Plate 18, fig. 2

Terebratula globulina PHILLIPS, J., 1834, *Encyclopedia Metropolitana*; Geol., vol. 4, pl. 3, fig. 3, (*vide* Davidson, 1858).

Terebratula seminula PHILLIPS, J., *ibid.*, p. 222, pl. 12, figs. 21-23.

Camarophoria globulina (Phillips) DAVIDSON, T., 1858, *Monogr. Brit. Perm. Brach.* (pt. 4), p. 27, pl. 2, figs. 28-31; DAVIDSON, T., 1863, *Monogr. Brit. Carb. Brach.*, (pt. 5), p. 115, pl. 24, figs. 9-22; DAVIDSON, T., 1863, *Appendix to Carb. & Perm. Monogr.*, p. 268, pl. 54, figs. 20-25.

Stenosisma globulina (Phillips) BRANSON, C. C., 1948, Geol. Soc. America Mem. 26, p. 524 (synonymy only).

Shell small for genus, moderately biconvex to subglobose; outline subelliptical to subpentagonal, length and width nearly equal; commissure uniplicate; fold moderately high at anterior but not standing much above flanks, beginning about 4 mm. anterior to brachial beak (proportionately far forward in so small a shell); sulcus shallow, hardly depressed below level of flanks; costae numbering two or three on fold, one fewer in sulcus, one or (more commonly) none on flanks; growth lines not observed; growth laminae weak, widely spaced; valves meeting nearly perpendicularly at anterior, without trace of stolidium.

Pedicle valve most strongly convex just anterior to beak region; beak sharp, suberect to slightly incurved; delthyrium apparently without deltidial plates; foramen not penetrating apex of beak.

Brachial valve more strongly convex; greatest convexity near posterior, longitudinal convexity lower toward anterior along fold.

Pedicle valve interior with dental plates forming spondylium, sessile in extreme apex, then elevated on low median septum, extending anteriorly about one-third length of valve.

Brachial valve interior with small hinge plate at posterior; camarophorium beginning as slender-sided trough on top of septum in posterior, curving ventrally, extending about one-third length of valve; intercamarophorial plate not observed, probably present.

Comparisons.—*Coledium globulinum* is characterized by its small size, globose shape, few costae, and its camarophorium that begins as a trough, not a knob, in the apex of the valve. It is the smallest known species of the genus, and is much smaller than the other species that occurs in the Permian, *C. crassum* (Hamlet) from Timor. Its shape is most like that of *C. explanatum* (McChesney) and *C. obesum* (Clark), but it is smaller and less strongly costate, especially on the flanks. It also resembles *C. bowsheri* (Cooper), differing in its smaller size, narrower and less pentagonal outline, and in the presence on some specimens of costae on the flanks.

Discussion.—The U.S. National Museum has four specimens of *C. globulinum* (USNM 96284) from the Permian of Tunstall, near Sunderland, England, a locality cited for the species by Davidson (1858). These confirm the suspicion aroused by Davidson's and Phillips' (1836) descriptions and illustrations that the species belongs to *Coledium*. As such, it is one of the youngest known species of the genus: only *H. crassum* (Hamlet) from the island of Timor also is known from the Permian.

Davidson (1863, p. 116, p. 268) concluded from examination of

Phillips' specimens and from his own collections that *C. globulinum* included specimens that Phillips had called *Terebratula seminula*. I accept his opinion in this matter, and include the name in the synonymy of *C. globulinum*.

COLEDIUM OBESUM (Clark)

Plate 16, figs. 2-2c; figure 29

Camarophoria obesa CLARK, T. H., 1917, Harvard Mus. Comp. Zoology, Bull. 61, No. 9, p. 373, pl. 2, figs. 13-24, text fig. 3.

Stenoscisma obesa (Clark) EASTON, W. H., 1962, U.S. Geol. Survey Prof. Paper 348, p. 41, pl. 4, figs. 24-27.

NOT *Stenoscisma obesa* (Clark) SHAW, A. B., 1962, Journ. Paleontology, vol. 36, No. 4, p. 633, pl. 97, fig. 27-31; pl. 98, fig. 6-8, text fig. 1, (*Atrionium* aff. *A. bisinuatum* (Rowley)).

Original description (Clark, 1917).—Shell small, subglobular in form, subcircular to subpentagonal in outline, longer than wide, wider than thick. Both valves are strongly convex; the pedicle valve is the more strongly arched longitudinally, the brachial valve transversely. In the pedicle valve the beak is prominent and overhangs the brachial valve considerably. There is a distinct but not strongly marked sinus on the pedicle valve, within which is a raised median plication. On either side of the sinus are two plications, only the pair bordering the sinus achieving any prominence; occasionally the only evidence of the outer plication is a sinuosity in the lateral margin. The brachial valve is characterized by a short and not prominent fold divided by a median furrow. On each side there may be one or two short plications. The fold, sinus, and plications on both valves are short, not extending one half the length of the specimens.

Internally, the pedicle valve shows a pair of dental lamellae near the beak, supported by a median septum. The lamellae are continued anteriorly into a spondylium, well raised from the floor of the valve. The brachial valve has a slightly longer median septum supporting both hinge plate and cruralium (camarophorium). The hinge plate is short, and the cruralium extends a short distance beyond the septum.

The surface of the valve is unornamented save for lines of growth at irregular intervals.

Supplementary descriptive remarks.—The beak of the pedicle valve is short and sharp, erect to slightly incurved; the delthyrium is open, normally not completely filled by the brachial umbo, and unobstructed by deltidial plates; the foramen penetrates the apex of the beak. Despite Clark's statement to the contrary, most specimens are nearly equal in length and width, or slightly wider than long.

The camarophorium of the brachial valve interior is short for the

genus, most similar to that of *C. bowsheri* (Cooper), and is strongly curved longitudinally, in contrast to the nearly straight camarophorium of species of *Atribonium*.

There is no trace of a stolidium on any of the numerous specimens in the Easton (1962) collection, and the form of the anterior commissure is typical of that of species in which the stolidium is absent.

Comparisons.—*Coledium obesum* is characterized by its subglobular shape, sharp, suberect beak, with open delthyrium and foramen that penetrates the apex, its short but strongly curved camarophorium, and especially by its few and gentle costation of fold and flanks. It most nearly resembles *C. bowsheri* (Cooper) in general shape, differing in its less transverse outline, and fewer weaker costae. It also resembles *C. explanatum* (McChesney), but is somewhat smaller and its costae, on both fold and flanks, are much weaker. Its maximum size is only about half that of *C. erugatum* n. sp. or *C. torvum* n. sp.; its costae further distinguish it from the former, its fewer and weaker costae from the latter. It is smaller, wider, and less triangular in outline than *C. rhomboidale* (Hall and Clarke) and *C. therum* (Walcott), and its costae are weaker. It is smaller, less convex, and has weaker costae on the fold than *C. cestriensis* (Snider).

Remarks.—Shaw (1962, p. 633) described specimens from the Lodgepole Limestone of Montana under the designation of *Stenocisma* (sic) *obesa* (Clark). Study of his illustrated specimens in the U.S. National Museum collection shows that they have the flattened anterior, and the general form that typify species of *Atribonium*, and are not closely related to *Coledium obesum*. Shaw's specimens probably belong to a new species that is related to *Atribonium bisinuatatum* (Rowley). He suggested that his new species *Stenocisma uniplicatum* Shaw probably is a variant of the one that he called *S. obesa*, but that it is stratigraphically segregated. This idea is corroborated by the fact that the range of variation of the closely related *A. bisinuatatum* (Rowley) includes specimens that resemble Shaw's two categories (see Weller, 1914, pl. 23). However, variants of the Mississippi Valley population may have become established as separate species in Montana, and as long as the two forms are stratigraphically segregated, I agree with Shaw that they should be recognized as distinct.

Growth.—Trends of growth in this species are typical for the genus, with points on the width scattergram (fig. 29) clustered narrowly along a straight line, and those on the thickness scattergram more widely spread along a curve of gentle acceleration. Small shells are

FIG. 29.—Scatter diagrams of dimensions of *Coledium obesum* (Clark) from Easton's (1962) locality 13414, Golden Valley County, Mont.

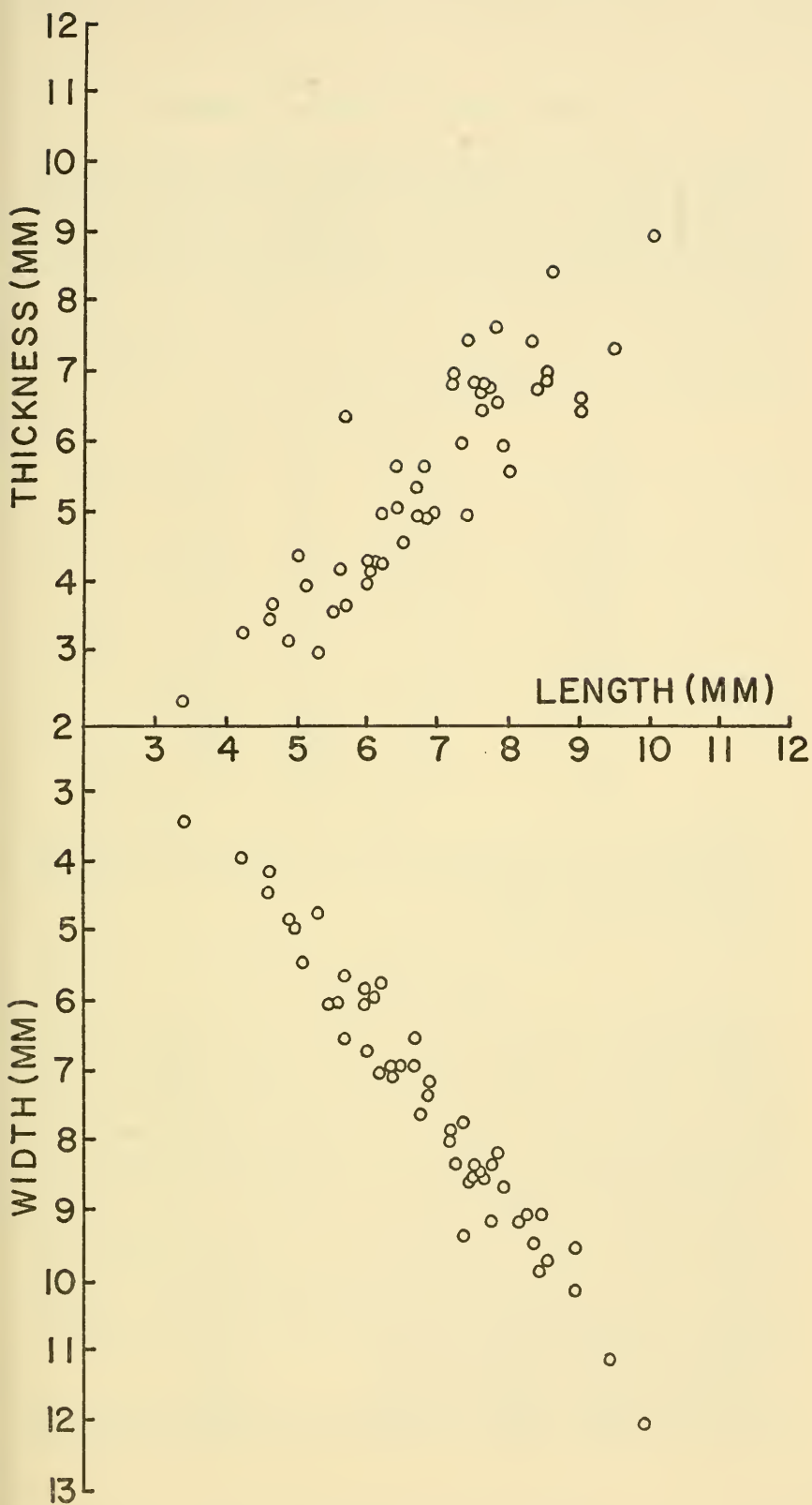


FIG. 29.— (See opposite page for legend.)

nearly as wide as they are long, but larger ones are more transverse. Only a few specimens are thicker than long, although the trend is toward increasingly equal length and thickness. Projection of the lower ends of the curves would continue the same trends, indicating little or no allometric growth in early postlarval stages.

TABLE 25.—*Measurements of Coledium obesum from the Heath Shale locality 13414 of Easton (1962), Mont.*

USNM No.	<i>Measurements, in millimeters</i>		
	Length	Width	Thickness
142208	3.4	3.4	2.3
142209	4.6	4.1	3.5
142210	5.0	4.9	4.4
142211	5.7	5.6	3.7
142212	6.2	5.7	5.0
142213	6.5	6.9	4.6
142214	6.9	7.3	5.0
142215	7.9	8.1	6.0
142442	8.3	c.9	7.5
142443	8.4	9.4	6.8
118749A	c.9.0	9.5	6.7
142444	c.9.5	11.1	7.4
142445	c.10.0	12.0	9.0

Occurrence and abundance.—Heath Shale, Montana, Easton locality No. 13414 (about 65 specimens).

Age.—Late Mississippian.

COLEDIUM OPIMUM Grant n. sp.

Plate 18, figs. 5–5a

Shell about average size for genus, juveniles flatly biconvex, adults strongly biconvex; outline rounded subpentagonal, widest near mid-length, slightly longer than wide; adults uniplicate, fold moderately high, broad at anterior margin, but standing only slightly above flanks, beginning about 5 mm. anterior to brachial beak; sulcus shallow, with flattened trough; juveniles shorter than 5 mm. with anterior margin flattened or slightly emarginate on midline, anticipating fold; costae very low, rounded, numbering two on fold, one in sulcus, none on flanks; posterolateral edges of brachial valve strongly overlapping pedicle valve; valves meeting at obtuse angle around anterior margin, slightly protruding at extreme edges, but without trace of stolidium; growth laminae weak, widely spaced.

Pedicle valve somewhat inflated, especially in umbonal region; beak thick, without beak ridges, strongly curved, pressed against brachial

umbo more or less tightly; delthyrium trigonal, entirely filled in adults by brachial beak; foramen small, slot-shaped, penetrating apex of beak.

Brachial valve more strongly convex, umbonal region greatly swollen; apex of beak curved into delthyrium of pedicle valve.

Pedicle valve interior with dental plates uniting just above floor to form large, boat-shaped spondylium, sessile or nearly so at apex, increasingly elevated anteriorly on low median septum, extending anteriorly about one-third length of valve, about one-fourth length along curvature of valve, septum extending slightly beyond anterior of spondylium.

Brachial valve interior with high cardinal process formed partly by curved apex of valve beak; hinge plate short, shallowly divided at midline; crura curving slightly ventrally from anterior edge of hinge plate; camarophorium long, shallowly spoon-shaped, widening anteriorly, curving moderately strongly toward ventral valve, supported by high but short median septum (camarophorium extending anteriorly about one-third length of valve; septum extending along floor about one-fifth length); intercamarophorial plate thick, extending from trough of camarophorium to underside of hinge plate, projecting nearly 1 mm. anterior to hinge plate.

Holotype.—USNM 142448, plate 18, fig. 5a.

Comparisons.—*Coledium opimum* is characterized by its rather large size for the genus (the large ones could not be measured accurately, so their measurements are not given below), strong convexity with swollen beak regions, strongly curved pedicle beak, foramen that penetrates the apex of the beak, and its weak or absent costae. In the last feature it resembles *C. erugatum* n. sp., differing in its larger size, more swollen pedicle beak, narrower outline, and in small juveniles, its emarginate anterior. Its weak or absent costae, more swollen beak, narrower outline and greater convexity distinguish it from *C. torvum* n. sp. which also reaches nearly the same size. *C. therum* (Walcott) attains a larger size than *C. opimum*, has stronger costae, not as thickened nor strongly curved pedicle beak, and some specimens have a short stolidium. Other species of the genus are easily distinguished from *C. opimum*, normally by their smaller size, or stronger costae.

TABLE 26.—Measurements of illustrated specimens of *Coledium opimum* from the Pennsylvanian of Chariton County, Mo.

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
142446	c.6.5	5.7	3.6
142447	c.8.4	7.0	4.4
142448	10.0	c.10	8.4

Discussion.—This species is represented in the U.S. National Museum collections by only a dozen specimens, about one-third of them well-preserved. It is described despite the small collection because all of the important features are shown, the species is distinctive, and it is one of the few stenoscismatids known from the Pennsylvanian.

Occurrence and abundance.—“Upper Carboniferous,” Chariton County, Mo. (12 specimens USNM 24405).

Age.—Pennsylvanian.

COLEDIUM RHOMBOIDALE (Hall and Clarke)

Plate 10, figs. 1-1a; plate 11, figs. 2-7; figure 30

Camarophoria rhomboidalis HALL, J., & CLARKE, J. M., 1894, Pal. New York, vol. 8, pt. 2, p. 366, pl. 62, fig. 25-29; HALL, J., 1895, 14th Ann. Rept. State Geologist, New York, p. 363, pl. 9, fig. 37-40.

NOT *Stenoscisma rhomboidalis* (Hall and Clarke) FAGERSTROM, J. A., 1961, Journ. Paleontology, vol. 35, No. 1, p. 29, pl. 9, fig. 45-47.

Shell somewhat small for genus, moderately to strongly biconvex; outline subtrigonal, normally slightly elongate, less commonly equidimensional, rarely transverse, normally widest anterior to midlength; commissure uniplicate; fold moderately high, projecting above flanks only near anterior, not prominently, beginning about 5 mm. anterior to brachial beak; sulcus shallow except at anterior, there depressed below flanks, projecting as broad tongue into fold; beginning about 6 mm. anterior to pedicle beak; costae moderately strong, crests rounded, beginning about 4 mm. anterior to beaks, numbering two or three on fold, one fewer in sulcus, from one to three on each flank; valves meeting nearly perpendicularly at anterior, some specimens with slightly larger angle, but not enough to produce flattened anterior; growth lines fine, closely spaced; growth laminae slightly stronger, irregularly spaced.

Pedicle valve moderately convex, greatest swelling anterior to beak in posterior part of valve; beak short, sharp, somewhat attenuate, suberect to slightly incurved; beak ridges rounded, distinct on some specimens, obscure on others; delthyrium triangular, nearly filled by brachial beak; deltidial plates not observed, very small if present; foramen small, not penetrating apex of beak.

Brachial valve much more strongly convex transversely, moderately convex longitudinally along fold, greatest convexity posterior to midlength, anterior to beak; apex of beak within pedicle valve.

Pedicle valve interior with dental plates forming boat-shaped spondylium, sessile on floor of valve for at least 1 mm. in apex, as much as 2.5 mm. in some specimens, then elevated on low median

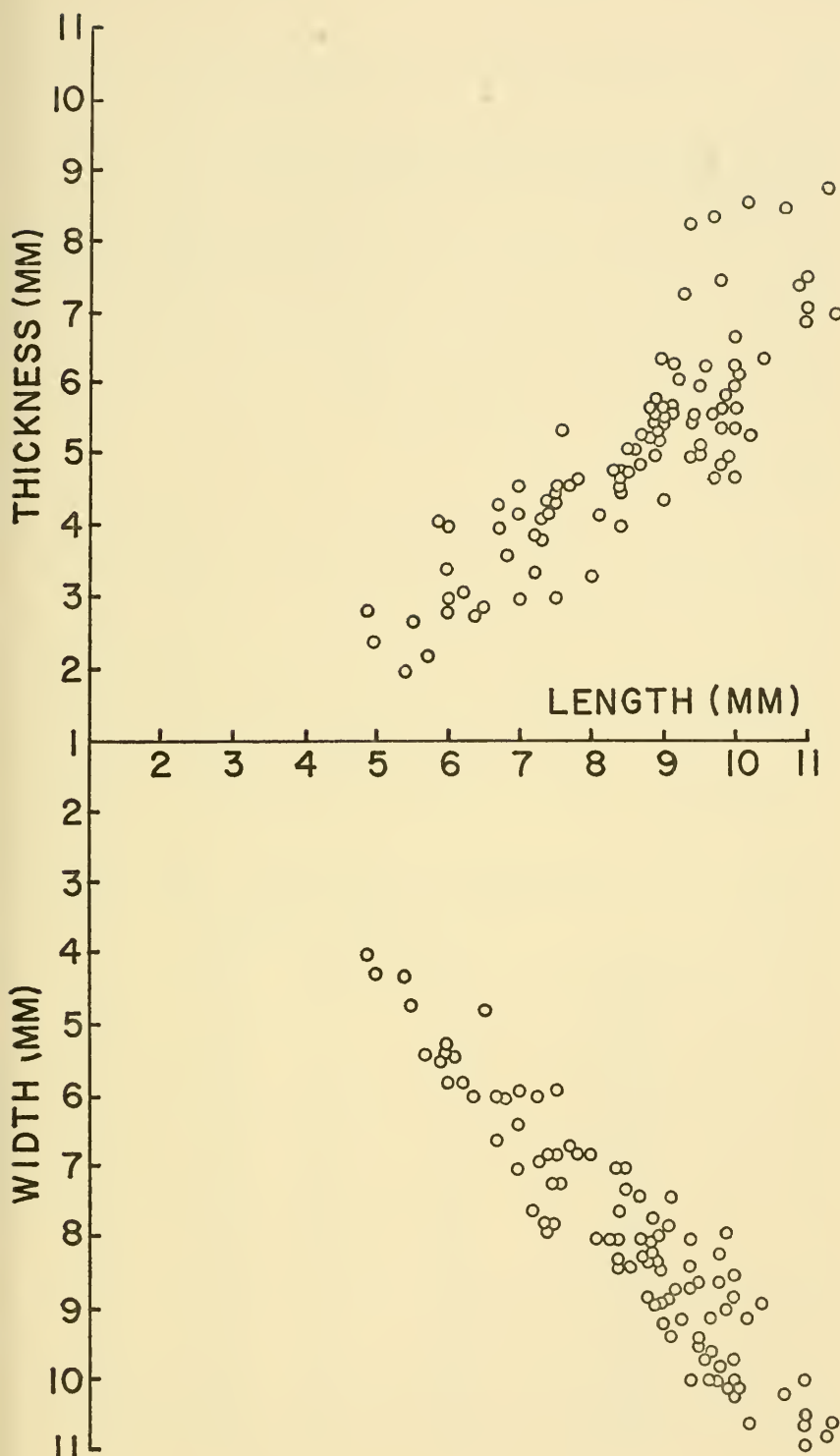


FIG. 30.—(See opposite page for legend.)

septum duplex, extending anteriorly nearly half true length of valve, about one-third length measured along floor of valve.

Brachial valve interior with camarophorium beginning as swelling of median septum in apex, widening anteriorly to form shallow trough, connected to base of hinge plate by short intercamarophorial plate; median septum extending anteriorly along floor slightly less than half length of valve, slightly beyond midlength of shell; longitudinal curvature of camarophorium not great, keeping well away from pedicle valve spondylium; hinge plate short, slightly curved ventrally away from camarophorium; crura not observed.

Holotype.—N.Y. State Museum No. 1172 (designated by Fagerstrom, 1961, p. 29).

Growth.—The width of shells of this species increases proportionately with increase in length, although nearly all measured shells are narrower than they are long (fig. 30). Increase in thickness, on the other hand, is somewhat accelerated relative to increase in length, with points on the diagram falling along a rather well-defined curve. Projection of either of the two trends toward a low number on the length-axis indicates probable allometric growth in growth stages earlier than those of specimens available for study. Very small shells probably are subequal in length and width, but very flat.

Comparisons.—*Coledium rhomboidale* is characterized by its elon-

TABLE 27.—Measurements of *Coledium rhomboidale* from the Logansport Limestone near Pipe Creek Falls, Ind.

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
142449	c.4.9	4.0	2.8
142450	5.0	4.3	2.4
142451	5.4	4.3	2.0
142452	5.5	4.7	2.7
142453	6.0	5.4	4.0
142454	6.4	6.0	2.8
142455	6.5	4.8	2.9
142456	7.0	5.9	4.2
142457	7.2	6.0	3.4
142458	7.5	7.2	4.6
142459	8.6	8.4	5.1
142460	9.0	8.9	5.7
142461	c.9.4	8.4	5.6
142462	9.4	8.0	5.5
142463	9.6	9.7	6.3
142464	9.8	8.2	5.4
142465	9.8	8.6	4.9
142466	9.8	10.0	7.5
142467	11.0	10.9	7.1

gate subtrigonal outline, by its fold that is relatively high at the anterior but does not stand high above flanks (that is, the fold slants anteriorly), its two or three low rounded costae on the fold, weakly costate flanks, and long, relatively flat camarophorium. It is nearly the same size as *C. explanatum* (McChesney), but more elongate, less strongly convex, and less strongly costate. It is smaller and more strongly costate than the smooth *C. erugatum* n. sp. or weakly costate *C. torvum* n. sp. Its outline is similar to that of *C. therum* (Walcott), but it attains a much smaller maximum size and there is no trace of a stolidium around the anterior commissure. It is not as wide as *C. bowsheri* (Cooper) and its flanks are costate; it is not as wide, as large, nor as convex as *C. undulatum* n. sp., and its costae are fewer, beginning much farther forward. It is proportionately narrower than *C. evexum* n. sp., and more strongly costate. It is similar to *C. cestriensis* (Snider), but its costae on the fold are lower, the flanks consistently and more strongly costate, the brachial valve less convex, and the camarophorium longitudinally much less strongly curved toward the ventral valve.

Discussion.—*Coledium rhomboidale* occupies a morphologic and probably phylogenetic position transitional from *Atribonium* to *Coledium*. The manner of meeting of the valves at the anterior, and its outline and costation are fairly characteristic for *Coledium*, so the species is placed in that genus. However, some individuals have a concentration of growth laminae near the anterior margin that produce a rounded rather than sharp anterior surface. This condition recalls *Atribonium*, but is not as strongly developed as in any species of that genus; it is only a rounding, rather than a strong geniculation of the two valves. Another link with *Atribonium* is the rather flat longitudinal curvature of the camarophorium. This structure is somewhat long for *Coledium*, but also longer than normal for *Atribonium*, apparently peculiar to the species. The form of the camarophorium is considered more important phylogenetically than the manner of meeting of the valves, because of the normal tendency in brachiopods for internal features to be more conservative. Therefore, this species probably constitutes a phylogenetic link between the two genera; it is the earliest known species of *Coledium*.

Fagerstrom (1961) identified specimens from the Formosa Limestone of Ontario with *Camarophoria rhomboidalis* Hall and Clarke, originally described from Cass County, Ind. Numerous topotype specimens in the U.S. National Museum collection from Pipe Creek Falls, Cass County, Ind., are comparable in size and form to Hall and Clarke's illustrated specimens. Their median length is about twice that of Fagerstrom's specimens (U.S. National Museum No. 549475,

549476), and their valves meet at the anterior nearly perpendicularly, rather than nearly in a plane as in the Ontario specimens. The manner of meeting of the valves is more characteristic of a species of *Coledium* than of a species of *Atribonium*, to which Fagerstrom's specimens clearly belong.

Fagerstrom included some of Hall and Clarke's (1894) and Hall's (1894) specimens of *C. rhomboidale* with his new species *Stenosisma halli* Fagerstrom. Direct comparison of the Indiana specimens with Fagerstrom's holotype reveals generic differences. Although the Indiana species is variable, and some specimens have the valves meeting at a larger angle than is typical for *Coledium*, the Ontario specimen is flattened at the anterior and belongs to the genus *Atribonium*. Hall and Clarke's species shows the same range of variation as do the National Museum's topotype collection of over 100 specimens. This probably represents a variable population, and in my opinion the species should remain as Hall and Clarke constituted it.

Occurrence and abundance.—Logansport Limestone, at Pipe Creek Falls, Cass County, Ind. (104 specimens USNM 142468–72); on Pipe Creek, $\frac{3}{4}$ mile northwest of Bunker Hill, Ind. (4 specimens; aff. *C. rhomboidale* USNM 142473, 74). The Logansport is the "Corniferous limestone, Peru, Indiana" of Hall and Clarke (1894); the 104 specimens are topotypes.

Age.—Middle Devonian.

COLEDIUM THERUM (Walcott)

Plate 16, figs. 1–1d

Rhynchonella thera WALCOTT, C. D., 1884, U.S. Geol. Survey Monogr. 8, p. 223, pl. 7, figs. 6–6c.

Shell large for genus, moderately to strongly biconvex; outline rounded subtrigonal or subpentagonal to elliptical, greatest width normally slightly anterior to midlength; commissure uniplicate; fold moderately high, but not standing prominently above flanks, crest broad, flat; sulcus shallow, extending anteriorly as tongue into fold; edges of valves slightly produced in many specimens, forming narrow ridge around anterior margins (probably incipient stolidium); costae weak, beginning far forward, about 6–10 mm. anterior to beaks, numbering two or three on fold, one fewer in sulcus, none to three on each flank, normally much weaker on flanks; growth lines fine and closely spaced; growth laminae slightly stronger.

Pedicle valve moderately strongly convex, greatest swelling anterior to beak but just posterior to midlength; beak short, sharp, suberect to slightly incurved; beak ridges blunt but distinct in juveniles, rounded and indistinct in large specimens; delthyrium small, trigonal,

mostly occupied by brachial beak; deltidial plates small, only slightly restricting pedicle opening; foramen not penetrating apex of beak.

Brachial valve more strongly convex, greatest swelling also just posterior to midlength, convexity increasing with length of specimen; beak short, rounded, apex within pedicle valve.

Pedicle valve interior with dental plates converging to form large boat-shaped spondylium, sessile in apex, then elevated on thin median septum for remainder of length; septum high for genus, attaining height slightly above 1 mm. in large specimens, extending anteriorly about one-fourth actual length of valve.

Brachial valve interior with hinge plate in apex; camarophorium beginning as small wings on sides of median septum, rather than as

TABLE 28.—*Measurements of Coledium therum from the Mississippian near Eureka, Nev.*

USNM No.	Measurements, in millimeters		
	Length	Width	Thickness
142475	6.9	6.0	2.4
142476	9.6	10.9	6.8
142477	10.0	10.9	6.4
142478	10.4	10.3	6.3
142479	10.6	9.4	6.4
14344	10.8	11.0	7.8
142480	11.0	13.6	6.9
142481	c.12.5	12.3	8.4
142482	12.6	11.3	9.0
142483	13.9	13.8	11.7
142484	15.8	15.0	10.3

small ball or pair of swellings, separated from hinge plate by strong intercamarophorial plate, camarophorium extending anteriorly about half length of valve.

Holotype.—USNM 14344 (Walcott, 1884, pl. 7, fig. 6–6c).

Comparisons.—*Coledium therum* is characterized by its large maximum size, normally elongate subtrigonal to subpentagonal adults, late-appearing costae that number two or three on fold and flanks of adults but are absent from juveniles, and especially by its camarophorium that is slender in cross-section at the extreme posterior (not a ball on the top of the septum), and its incipient stolidium around the anterior margins of a few specimens. It is larger than any other known species of the genus except *C. crassum* (Hamlet) and *C. dutroi* n. sp., but its median size is near that of the more bulbous and wider *C. erugatum* n. sp. and *C. torvum* n. sp. It differs further from *C. erugatum* in its costate fold and flanks; differs further from *C. torvum* in its fewer

costae that are somewhat stronger on adults. Other species are not sufficiently similar to warrant detailed comparison.

Discussion.—The specimen illustrated by Walcott (1884) is smaller than the largest specimens of the species, and therefore its costae are poorly developed. Larger specimens in the U.S. National Museum collections from the same locality have somewhat stronger and longer costae, and some have three instead of two on the fold. Smaller specimens in the collection, on the other hand, have weaker costae; some lack costae because these do not form until the shell has attained a length near 6 mm.

Convexity increases with length, as in other species of the genus. Therefore, along with the late-forming costae, this feature combines to produce what appears to be a rather variable species. The variation is not great, however, when growth factors are considered. Small and medium size specimens are rather flat and may be smooth; larger specimens are convex and may have as many as three costae on the fold and on each flank.

This species is important as the earliest known species in which the stolidium appeared, although in very rudimentary form. This species may be related to *Stenosisma*, with its strongly trigonal outline, relatively well-developed stolidium, and camarophorium that began as a trough in the extreme apex rather than as a knoblike swelling at the top of the septum as in early genera.

Occurrence and abundance.—Mississippian limestone in canyon directly south of Conical Hill, on east side of Secret-Canyon-Road Canyon, Eureka District, Nev. (Walcott Loc. 651) (18 specimens USNM 14344); Diamond Peak Formation, at Conical Hill, Windfall Canyon, SW. $\frac{1}{4}$ sec. 36, T-19-N, R-53-E, 3 miles south of Eureka, Nev. (10 specimens USNM 142485); Diamond Peak Formation, top of Conical Hill, east side of Windfall Canyon road, 3 miles east-south-east of Eureka, Nev. (4 specimens USNM 142486). All of these are from essentially the same locality; one in the lot from loc. 651 is the holotype, the rest are paratypes; those listed separately are topotypes.

Age.—Late Mississippian (probably Chester).

COLEDIUM TORVUM Grant n. sp.

Plate 13, figs. 1-2; figure 31

Shell medium to large for genus, strongly biconvex; outline ovate, slightly elongate in youth, slightly transverse as adult; commissure uniplicate; fold moderately high at anterior commissure, broad, with gently rounded or slightly flattened crest, but standing only slightly above flanks of valve anterior to about 5 mm. from brachial beak; sulcus shallow, beginning about 7 mm. anterior to pedicle beak, de-

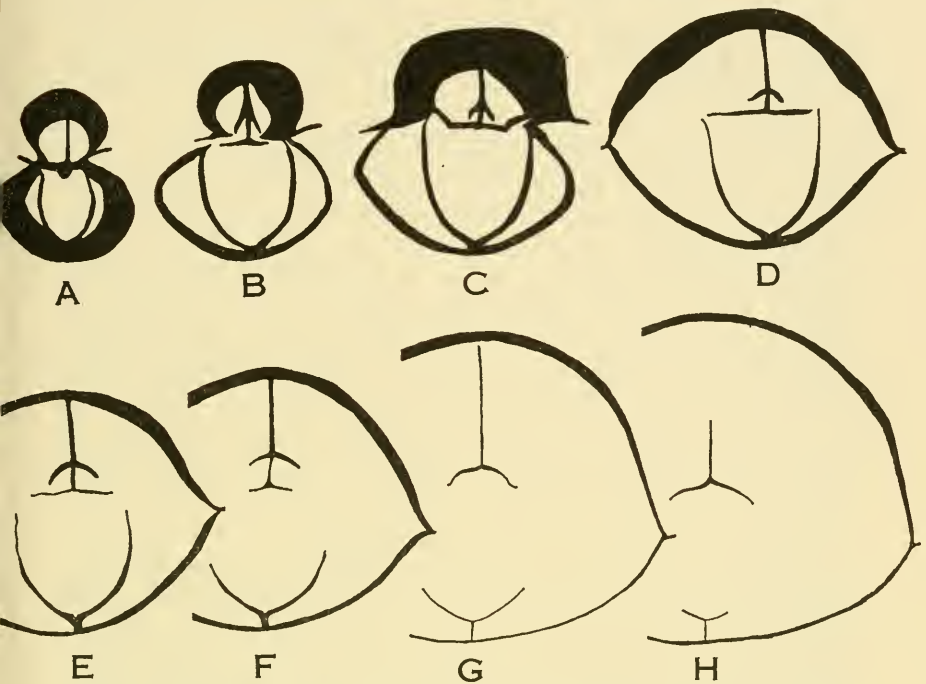


FIG. 31.—*Coledium torvum* n. sp., Morrow Series, Okla., transverse sections $\times 6$, original length 11.1 mm. YPM 23260, distances given from pedicle valve beak.

A. 0.4 mm.: camarophorium not apparent. B. 1.6 mm.: camarophorium large, hinge plate detached from walls. C. 1.8 mm.: low edge of cardinal process visible. D. 2.0 mm. E. 2.4 mm. F. 2.7 mm.: hinge plate narrow. G. 4.1 mm.: intercamarophorial plate ended at 3.4 mm. H. 4.8 mm.: base of septum detached from floor; septa in both valves mere cracks at 5.2 mm.

pressed only slightly below flanks, but extending anteriorly as broad tongue into fold; valves meeting nearly perpendicularly around anterior, at fold and flanks, brachial valve overlapping flattened flange of pedicle valve on posterolateral slopes; costae beginning 5–8 mm. anterior to beaks, rather weak, strongest at anterior margins, numbering from three to five on fold, one fewer in sulcus, one to three, rarely four, on each flank, some bifurcated; growth lines fine, closely and rather evenly spaced; growth laminae somewhat stronger, interrupting contours of valves only slightly.

Pedicle valve somewhat swollen in umbonal region, flattening toward flanks; then curving more strongly through sulcus; beak short, bluntly pointed, with short dull beak ridges; delthyrium small, trigonal, constricted by pair of small, conjunct deltidial plates, leaving small elongate oval foramen to pierce slightly apex of beak.

Brachial valve more strongly convex, with greatest convexity about one-third distance anterior from beak; beak short, with apex hidden by deltidial plates.

Pedicle valve interior with dental plates meeting to form sessile spondylium in apex of valve, about 1 mm. anterior to apex forming low median septum duplex, elevating spondylium slightly; median septum extending anteriorly about one-third length of valve, spondylium slightly shorter.

Brachial valve interior with short camarophorium beginning as slight expansion of median septum in apex of valve, height above floor increasing rapidly toward anterior as strongly convex valve and strongly convex camarophorium curve away from one another; intercamarophorial plate short, connecting camarophorium to base of hinge plate in apex of valve; hinge plate short, with low cardinal knob at apex, crura extending anteriorly from forward edge of hinge plate, curving with nearly same contour as camarophorium.

Holotype.—Y.P.M. No. 23258, plate 13, fig. 1c.

Comparisons.—*Coledium torvum* is characterized by its moderate-to-large size for genus, strongly convex brachial valve, and especially by its rather numerous, although weak, costae on the fold and flanks. It differs from smooth *C. erugatum* n. sp. in possession of costae, and from *C. cestriensis* (Snider) in its more numerous and weaker costae. It is larger than *C. explanatum* (McChesney), and also has more and weaker costae and stronger convexity.

Occurrence and abundance.—Morrow Series at Keough Switch

TABLE 29.—*Measurements of Coledium torvum from the Morrow Series in Oklahoma*

YPM No.	<i>Measurements, in millimeters</i>		
	Length	Width	Thickness
23246	7.4	7.7	4.5
23247	8.0	7.9	5.4
23248	8.2	8.9	6.1
23249	8.7	9.9	5.4
23250	9.8	9.7	5.8
23251	9.8	10.5	6.6
23252	10.3	11.0	7.7
23253	10.9	11.2	7.6
23254	11.2	10.9	7.6
23255	11.5	11.2	7.9
23256	11.7	11.3	8.1
23257	11.9	13.1	9.4
23258	11.7	13.4	8.4
23259	c.12.0	13.0	9.0

above Fort Gibson, Okla. (15 specimens), Yale Peabody Museum collection.

Age.—Early Pennsylvanian (Morrow).

COLEDIUM UNDULATUM Grant n. sp.

Plate 14, figs. 1-2a; figure 32

Shell about average size for genus, strongly biconvex; outline transversely subpentagonal, greatest width posterior to midlength; commissure uniplicate; fold high at anterior but not standing prominently above flanks, crest broad and flat; sulcus broad, shallow, with flattened trough, depressed proportionately to elevation of fold; costae low, distinct, beginning at beaks or within 5 mm. of beaks, numbering normally three on fold, rarely as many as seven, from three to five on each flank somewhat weaker on flanks; valve edges meeting nearly perpendicularly, without protruding and without trace of stolidium; growth lines fine, closely spaced; growth laminae slightly stronger, widely and irregularly spaced.

Pedicle valve moderately strongly convex, with greatest convexity in umbonal region anterior to beak; beak short, obtusely pointed, sub-erect to erect; delthyrium small, trigonal, deltidial plates not observed, probably absent; pedicle opening through delthyrium, not penetrating apex of valve.

Brachial valve much more strongly convex, with greatest convexity posterior to midlength, just anterior to beak in umbonal region; beak curved into pedicle valve.

Pedicle valve interior with dental plates forming boat-shaped spondylium, sessile for fraction of millimeter in apex, from there forward elevated on low median septum duplex, extending anteriorly about one-fourth length of valve.

Brachial valve interior with camarophorium relatively wide and transversely concave, curving longitudinally toward pedicle valve, trough extending anteriorly about one-third length of valve, somewhat beyond anterior extent of median septum; hinge plate and crura not observed, due to coarse calcite crystallization of specimens.

Holotype.—USNM 142501, plate 14, fig. 2.

Growth.—Increase in width and thickness both are accelerated relative to increase in length, with points on both diagrams falling along well defined curved paths (fig. 32). Length and width of median size shells are nearly equal, but larger shells are strongly transverse. Only the largest shells are as thick or thicker than they are long. Projection of the trends toward very small dimensions would continue the even curvature of both curves, with only slight flattening in the length-thickness curve, indicating only minimal allometry in early stages.

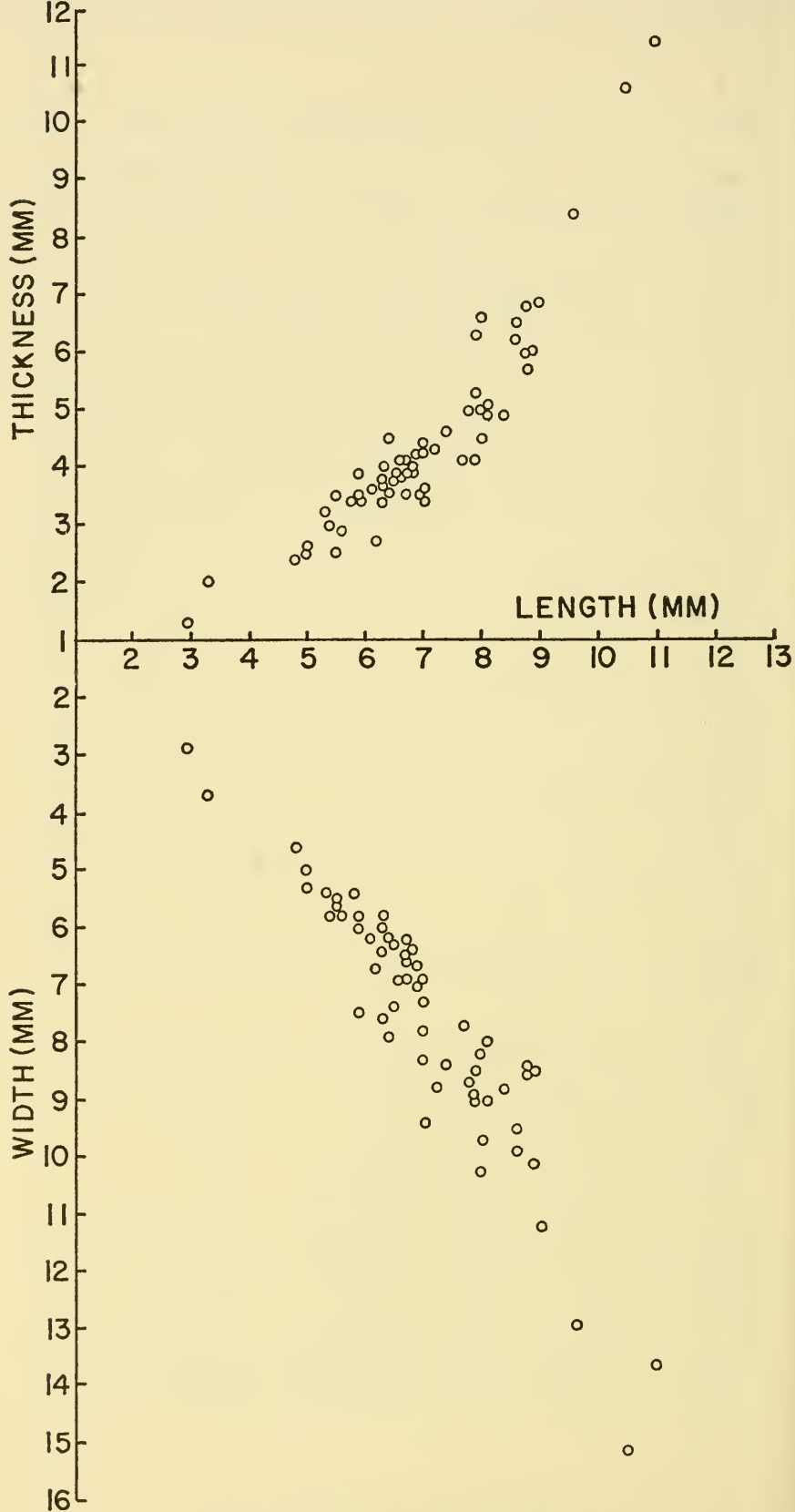


FIG. 3z.— (See opposite page for legend.)

TABLE 30.—*Measurements of Coledium undulatum from the Chappel Limestone in Texas*

USNM No.	<i>Measurements, in millimeters</i>		
	Length	Width	Thickness
142487	2.9	2.9	1.3
142488	3.3	3.7	2.0
142489	4.8	4.6	2.4
142490	5.3	5.4	3.2
142491	5.8	5.4	3.4
142492	6.3	7.6	3.8
142493	6.4	7.9	4.5
142494	7.4	8.4	4.6
142495	7.9	8.9	4.1
142496	8.0	8.2	5.0
142497	8.0	10.3	6.6
142498	8.4	8.8	4.9
142499	8.6	9.9	6.0
142500	8.9	10.1	6.0
142501	9.0	11.2	6.9
142502	10.5	15.1	10.6
142503	11.0	13.6	11.6

Comparisons.—*Coledium undulatum* is characterized by its broadly subpentagonal outline, moderately convex pedicle valve combined with very strongly convex brachial valve which becomes increasingly convex with overall size of the shell, its numerous fine costae on fold and flanks, short pedicle beak, and total lack of a stolidium or its beginnings. It occurs with *C. evexum* n. sp. in the Chappel Limestone, differing from that species in its larger size, wider outline, shorter beak, and numerous costae on fold and flanks that begin farther posterior. It is larger and has more numerous costae than *C. explanatum* (McChesney), *C. cestriensis* (Snider) or *C. obesum* (Clark), attaining a size similar to that of *C. erugatum* n. sp. which has no costae and a narrower outline, or *C. torvum* n. sp. whose costae are short and weak and outline narrower. It is larger and more convex than *C. bowsheri* (Cooper) and differs further in its costate flanks.

Occurrence and abundance.—Chappel Limestone, 0.55 mile N. 39° W. of High Lonesome Windmill, 8 miles southeast of Brady, Bald Ridge area, McCulloch County, Tex. (Cloud loc. TF-406) (200 specimens USNM 142505); Chappel, north side of draw, 0.6–0.7 mile up Honey Creek from county road crossing, 8 miles southwest of Mason, Bear Spring area, Mason County, Tex. (Cloud loc. 417c) (4 specimens USNM 142506); on San Saba River, 0.25 mile below

FIG. 32.—Scatter diagrams of dimensions of *Coledium undulatum* n. sp. from 8 miles southeast of Brady, Tex.

Joe Davis Hollow, 1.7 miles N. 60° E. of Lost Creek, McCulloch County, Tex. (Cloud loc. TF-392) (4 specimens USNM 142507); Chappel, 3,800 feet northeast of Elm Pool, Johnson City area, Blanco County, Tex. (1 specimen USNM 142503).

Age.—Early Mississippian (Kinderhook).

Genus STENOSCISMA Conrad 1839

Figures 1, 2, 33

- Stenoschisma* CONRAD, T. A., 1839, New York Geol. Survey, 3d Ann. Rept., p. 59.
- Camerophoria* KING, W., 1844, Annals and Mag. Nat. Hist., vol. 14, p. 313 (nom. nud.); KING, W., 1845, Neues Jahrb., p. 254 (nom. nud.) KING, W., 1846 (Aug.), Annals and Mag. Nat. Hist., vol. 18, p. 89.
- Camarophoria* King, HERRMANNSEN, 1846 (Dec.), Indices generum malacozoorum primordia, p. 161 (emended spelling); KING, W., 1850, Permian foss. of Eng., Paleont. Soc. Monogr., p. 113.
- Seminula* M'COY, F. (part), 1844, Carb. foss. Ireland, p. 150 (*vide* BUCKMAN, S. S., 1906, Annals and Mag. Nat. Hist., vol. 18, p. 325).
- Stenoschisma* Conrad, DALL, W. H., 1877, U.S. Nat. Mus., Bull. No. 8, p. 65 (altered spelling); COOPER, G. A., 1942, Wash. Acad. Sci. Journ., vol. 32, No. 8, p. 229; SHAW, A. B., 1962, Journ. Paleontology, vol. 36, No. 4, p. 633.
- Stenoschisma* Conrad, OEHLERT, D. P., 1887, in FISCHER, P., Manuel de Conchyliologie, p. 1309 (emended spelling).
- Stenoschisma* Conrad, COOPER, G. A., 1944, in Shimer and Shrock, Index foss. No. America, p. 315.
- Camaropholia* King, NONAKA, 1944, Jap. Journ. Geol. & Geog., vol. 19, art. 7, p. 85, (*lapsus pro Camarophoria*).
- NOT *Stenoschisma* Conrad, HALL, J., 1847, Paleont. New York, vol. 1, p. 142; (for *Atrypae* like *Producta modesta* Say).
- NOT *Stenoschisma* CONRAD-HALL, in HALL, J., 1867, Paleont., New York, vol. 4, pt. 1, p. 335 (for group containing *Rhynchonella formosa* Hall).
- NOT *Stenoschisma* Conrad, HALL, J. and CLARKE, J. M., 1894, Paleont., New York, vol. 8, Brachiopoda, pt. 2, p. 187 (*Rhynchonella formosa* Hall designated as type and only known species).
- NOT *Stenoschisma* Conrad, GRABAU, A. W. and SHIMER, H. W., 1907, p. 288 (cites *S. formosum* (Hall)); KOZLOWSKI, R., 1929, Paleont. Polonica, vol. 1, p. 146 (cites *S. formosa* (Hall) as type species).

Shell rhynchonelliform, biconvex; outline bluntly subtrigonal to rhombic, transverse or elongate; commissure strongly uniplicate, with high, gently costate fold, gently costate flanks, valves overlapping at posterior, butting along lateral and anterior margins, with edges of adults extended to form large, thin, wrinkled stolidium, bearing pallial markings on inner surfaces, normally extending from both valves at crest of fold and flanks, also on sides of fold in some species. Costae low, rounded, simple or less commonly bifurcating, beginning at or slightly posterior to midlength of shell, normally weaker on flanks

than on fold, number greatly variable. Growth lines fine, closely crowded; growth laminae slightly stronger, irregularly spaced; radial striae absent.

Pedicle valve flatly convex transversely, more strongly convex longitudinally through sulcus; beak short to slightly prominent, blunt or weakly attenuate, nearly straight or suberect to erect, with sharp apex; beak ridges distinct or absent; delthyrium small, triangular, normally constricted by small, triangular, conjunct or disjunct deltidial plates, leaving small, oval foramen; posterolateral flanges broad, elongate, normally covered by edge of brachial valve, marked by weak growth lines.

Brachial valve strongly convex transversely and longitudinally, umbonal region normally somewhat swollen; beak blunt to slightly attenuate, apex within pedicle valve, covered by pedicle beak or deltidial plates.

Pedicle valve interior with small blunt hinge teeth elongate parallel to sides of valve; dental plates nearly parallel where connected to hinge teeth, converging near floor of valve to form deep, scoop-shaped spondylium, joined along median line to form low supporting septum increasing in height slightly toward anterior, extending forward somewhat less than one-third length of valve. Muscle marks in spondylium, weak and poorly differentiated, bounded at posterior by light transverse line or ridge dividing off posterior third of spondylium; pallial trunks diverging from anterior end of median septum, each bifurcating repeatedly toward margins, producing numerous short branches at margins, extending to proximal edge of stolidium, there each splitting into several branches radiating across stolidium. Transverse gonocoel troughs originating near anterior of median septum (fig. 2).

Brachial valve interior with subtrigonal hinge plate striated or thickened at apex to form cardinal attachment for diductor muscles; hinge sockets short, narrow, finely denticulate, located at lateral extremes of hinge plate; crural bases diverging narrowly from anterior of cardinal knob, filled between and laterally to form hinge plate, becoming free anteriorly, extending forward as slender crura, outwardly bowed and ventrally curved, ends nearly touching anterior edges of ventral spondylium in closed shells. Median septum thin, high, height increasing anteriorly, anterior edge nearly perpendicular to floor of valve, upper edge capped by spoon-shaped camarophorium with slight elongation of anterior along median line; posterior part of inner surface of camarophorium braced to hinge plate by median intercamarophorial plate. Muscle marks within camarophorium, anterior adductors elongate, narrow, median, extending out onto median lobe of camarophorium; posterior adductor marks lateral, somewhat broader,

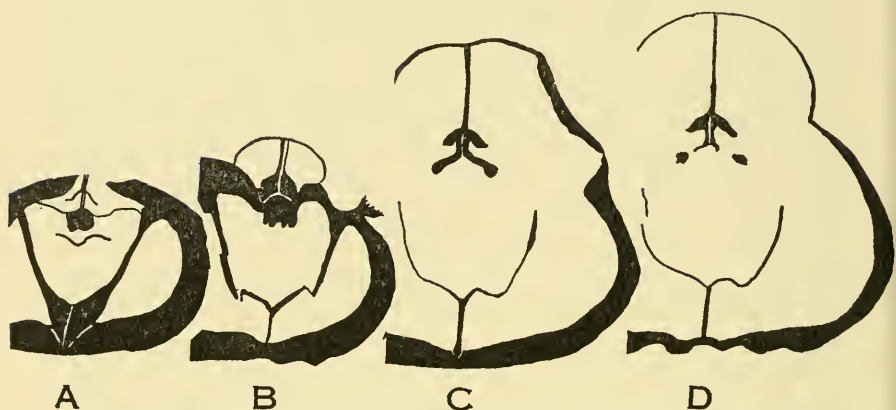


FIG. 33.—*Stenoscisma* sp., Hess Formation, Glass Mountains, Tex., transverse sections $\times 4$.

A. Spondylium nearly sessile, septum thick, with wedged insertion into floor; hinge plate and cardinal process thick, form indistinct. B. Cardinal process high, edges of spondylium broken. C. Duplex intercamarophoral plate attached to hinge plate and crural bases. D. Crura extend anterior to hinge plate.

shorter, occupying remainder of camarophorium. Pallial trunks originating in posterior of valve, diverging anteriorly, each bifurcating several times toward margins, there each branch splitting into several and radiating across stolidium.

Type species.—*Terebratula schlotheimi* von Buch, L., 1835, Akad. der Wissenschaften, Berlin, Abhand., Jahrgang 1833, p. 59–60, pl. 2, figs. 32a–c; by monotypy in Conrad, T. A., 1839, Geol. Survey New York, 2d Ann. Rept., Assembly Document 275, p. 59.

Discussion.—*Stenoscisma* is the most important and most abundantly represented genus in the Stenoscismatacea. Its greatest development occurred in the Permian; more than 60 Permian species had been described by 1948 (Branson, C. C., 1948), and fully 20 more have been discovered since then, both published and unpublished. The genus was worldwide, an important constituent of nearly all Permian brachiopod faunas.

Only a few species are described here as examples of the genus. It would be futile to try to comment meaningfully upon every species; such full treatment would add little to the understanding of this well known genus whose descriptions in the literature are numerous. Examples chosen are the type species, *S. schlotheimi* (von Buch) abundantly represented in the collections of the U.S. National Museum and Yale Peabody Museum, a few species from the Permian of West Texas, known from the work of R. E. King (1931), Girty (1909, 1929) and Stehli (1954) and represented by abundant and/or well

preserved specimens in the U.S. National Museum collections, and a species from the Permian of Timor, known through work by Broili (1916). Species of *Stenosisma* will be discussed more fully in a forthcoming paper by Cooper and Grant on Permian brachiopods of West Texas.

Stenosisma is the culmination of the development of the Stenosismatacea. Its species attain greatest development of the features that typify the superfamily, and its evolution seems to have embodied the dominant trends in the history of the superfamily. The stolidium is best developed in species of *Stenosisma*, although it is only sporadically present on some species (e.g. *S. hueconianum* (Girty)). Costation varies from fine and nearly complete (*S. multicostum* Stehli) through broad and covering only about half the shell (*S. venustum* (Girty)) to erratic, with some individuals nearly smooth (*S. schlotheimi* (von Buch)). No species of *Stenosisma* develops sharp, fine, numerous costae such as those of the uncinuliform genus *Torynechus*; such costae are atypical for the superfamily. Internally, the spondylium and camarophorium are large and well-formed in most species of *Stenosisma*, the muscle marks visible, and the pallial markings strongly inscribed.

No descendants of *Stenosisma* are known. Apparently the entire superfamily became extinct in the Late Permian after having attained its greatest morphologic development, widest distribution, and greatest number of species and of individuals in that period.

Nomenclature.—The name *Stenosisma* was proposed by Conrad (1839), who designated its type species by monotypy, *Terebratula schlotheimi* von Buch. He referred to *T. schlotheimi* as a “. . . common Silurian bivalve,” thus introducing an element of confusion that has influenced use of the name *Stenosisma* throughout its history. Conrad implied that *Stenosisma* was common in the “Silurian” of New York, and Hall (1867) concluded that the species Conrad mistook for *T. schlotheimi* was the Lower Helderberg species *Rhynchonella formosa*. Hall cited an unpublished lithographed plate by Conrad as evidence that Conrad used the name *T. schlotheimi* for that species. Hall then used *Stenocisma* (sic) for the group typified by *R. formosa*, and subsequent authors used the name in the sense that Hall emended it, with several variations in the spelling (e.g. *Stenoschisma* Hall and Clarke, 1894; *Stenochisma* Grabau and Shimer, 1907; Maynard, 1913, and Kozłowski, 1929).

King proposed the name *Camerophoria* in 1844 and 1845, but it remained a *nomen nudum* until 1846 when he designated *Terebratula schlotheimi* von Buch as the type species. Later in 1846 Herrmannsen

pointed out to King the mixture of Greek and Latin roots in his spelling of *Camerophoria*, and King (1850) accepted the corrected spelling as *Camarophoria*. From that time until 1952 the two spellings were used indiscriminately, each with about the same frequency.

Dall (1877) was first to recognize the error in Hall's procedure, and to recommend use of the name *Stenoscisma* for the group containing *S. schlotheimi*, and for consigning *Camerophoria* King to its synonymy. Oehlert (1887, p. 1309) described and illustrated *S. schlotheimi* in the Fischer Manuel de Conchyliologie, using the name in the sense recommended by Dall, but emending the spelling to *Stenoschisma*. Hall and Clarke (1894) accepted Oehlert's change in the spelling of the name, but reiterated Hall's earlier (1847, 1867) arguments that Conrad did not have *S. schlotheimi* in mind when he assigned it to his genus, but actually was thinking of *Rhynchonella formosa*. Hall and Clarke state clearly (1894, p. 188) that they consider *R. formosa* to be the typifying species of *Stenoschisma*; this did not establish a new genus with a new type species, however, because they continued to accredit the genus to Conrad, 1839, thus merely emending *Stenoscisma*.

Grabau and Shimer (1907) in their book on North American index fossils continued to use the name in the sense of Hall (1847) and Hall and Clarke (1894), but provided yet another variation in the spelling: *Stenochisma*. Subsequent authors (e.g. Maynard, 1913; Kozłowski, 1929) continued to use the name in the Hall and Clarke sense, with the Grabau and Shimer spelling.

In the meantime, the group typified by *Terebratula schlotheimi* von Buch was recognized widely and designated by the name *Camerophoria* (or *Camarophoria*) King (1844 or 1850). Davidson used it thus in 1853, 1858, 1863, and 1880; Geinitz (1861), Meek and Worthen (1866), Waagen (1883), Hall and Clarke (1894), Tschernyshev (1902, 1914), Weller (1910, 1914), Kozłowski (1914), R. E. King (1931), Licharev (1936), Reed (1944), Sarycheva and Sokolskaya (1952) and Dunbar (1955) are important references employing W. King's name for the genus.

Despite Dall's clear exposition of the case, obviously there was strong reluctance to put King's name into the synonymy of *Stenoscisma*. Hall's argument that Conrad's original intent for *Stenoscisma* included an American Devonian form rather than the Permian *S. schlotheimi* was restated as late as 1955. Cooper (1942, p. 229) recalled attention to Dall's (1877) statement, pointed out the clear designation of the type by Conrad, and revived *Stenocisma* (sic) in favor of *Camarophoria* King. In 1944 Cooper illustrated specimens related to *S. schlotheimi*, included *Camerophoria* in synonymy, and used the name

Stenosisma with Conrad's original spelling. Since then most authors have used the name in this manner for species related to *S. schlotheimi*; examples are Stehli (1954); Fagerstrom (1961); Shaw (1962); and Easton (1962).

A few authors have preferred to retain the name *Camerophoria* (or its variant spelling) for the group related to *S. schlotheimi*. Sarycheva and Sokolskaya (1952, p. 170) used *Camarophoria*, and dated it from King's *nomen nudum* of 1844 when he had spelled it *Camerophoria*. Dunbar (1955, p. 119) noted Conrad's mistaken interpretation of *S. schlotheimi*, and cited opinions of the International Commission on Zoological Nomenclature as justification for continued use of *Camerophoria*. He indicated intent to appeal for a ruling to retain the name, but no such appeal has been received by the Commission (Spillane, written communication, 1961). No further attempts to retain King's name have been made: current usage recognizes its objective synonymy with *Stenosisma*. Licharev (1960) in the Russian treatise on brachiopods, *Osnovi Paleontologii*, uses *Stenosisma* with Conrad's original spelling, and the *Treatise on Invertebrate Paleontology* (Moore, ed.) will employ *Stenosisma* similarly.

Range.—The range of *Stenosisma* begins in the Lower Carboniferous of England and the nearby Continent with *S. crumenum* (Martin) (see Davidson, 1858). It is very rare in the Pennsylvanian, (Upper Carboniferous) but is abundant throughout the Permian.

STENOSCISMA SCHLOTHEIMI (von Buch)

Plate 21, figs. 1-12; figure 34

Terebratulata schlotheimii VON BUCH, 1835, p. 59, pl. 2, figs. 32a-c.

Stenosisma schlotheimii (von Buch) CONRAD, 1839, p. 59.

Camerophoria schlotheimi (von Buch) KING, W., 1846, p. 89.

Camarophoria schlotheimi (von Buch) KING, W., 1850, p. 113, pl. 7, figs. 10-21.

Shell outline subtrigonal to subpentagonal, commonly transverse, some specimens slightly elongate, larger specimens normally proportionately wider, greatest width anterior to midlength; convexity moderate, greatest swelling in brachial valve; commissure strongly and narrowly uniplicate; fold beginning 3-6 mm. anterior to brachial beak, standing increasingly high above flanks, crest arched, less commonly flattened; sulcus strongly depressed toward anterior, extending as long tongue into arch of fold; posterolateral edges of valves strongly overlapping, edges from midlength forward butting; stolidium present on adults longer than 10 mm. extending from both valves at crest of fold and trough of sulcus, normally extending from pedicle valve at anterolateral extremities, also present there on brachial valve of many speci-

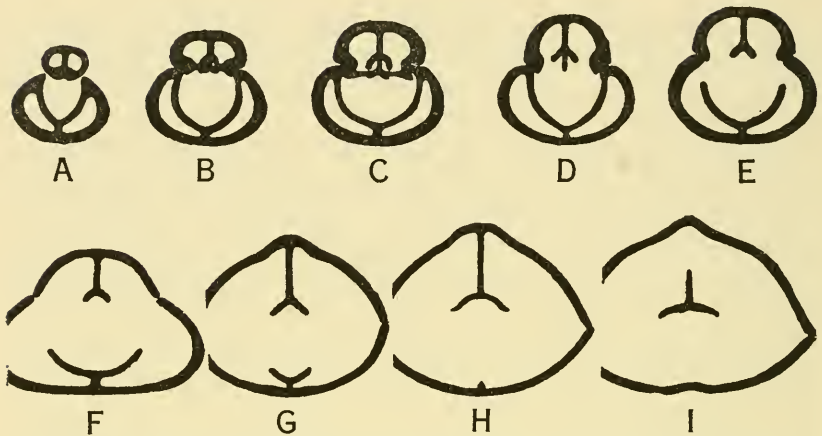


FIG. 34.—*Stenosisma schlotheimi* (von Buch), Permian, Pössneck, Germany; sections by Weller (1914, p. 109, fig. 1, C–K), $\times 3\frac{3}{4}$.

mens; costation variable, normally beginning at least 3 mm. anterior to beaks, some adults nearly smooth, with only one or two weak costae on anterior of fold, others with low rounded costae numbering up to five (normally three) on fold, one fewer in sulcus, and up to six on each flank: most specimens between these extremes, none strongly costate; growth lines weak, closely spaced; growth laminae only slightly stronger, more widely and irregularly spaced.

Pedicle valve rather flat transversely, with greatest swelling just anterior to umbo, greatest convexity longitudinally through sulcus; beak short, sharp, suberect to erect, with gently rounded beak ridges; delthyrium small, triangular, constricted by pair of small conjunct or disjunct deltidial plates; foramen open, small, subtrigonal to slitlike; posterolateral flanges long, broad, overlapped by edges of brachial valve, normally completely covered.

Brachial valve more strongly convex, greatest convexity transversely, longitudinal profile along crest of fold only gently curved; beak bluntly angular, apex within pedicle valve.

Pedicle valve interior with spondylium formed by junction of dental plates, line of junction meeting floor along midline of valve in apex, becoming elevated upon low median septum duplex somewhere beyond 1 mm. from apex; height of septum increasing anteriorly, reaching height near 1 mm., length of spondylium about one-third length of valve.

Brachial valve interior with camarophorium on short high median septum, shallowly spoon-shaped, rather broad, beginning very near

underside of hinge plate in apex; intercamarophorial plate low, increasing in height toward anterior, occupying less than one-third length of camarophorium; length of top of camarophorium slightly more than one-third length of valve, terminating somewhat farther anterior than pedicle spondylium; median septum extending 2 or 3 mm. along floor of valve, only about one-third length of camarophorium, with concave

TABLE 31.—*Measurements of Stenosisma schlotheimi from the Middle Zechstein near Pörsneck, Thuringia, (East) Germany*

YPM No.	<i>Measurements, in millimeters</i>			Costae on brachial valve
	Length	Width	Thickness	
23263	3.8	3.8	2.0	0
23264	4.0	4.0	2.4	0
23265	4.7	5.0	2.0	0
23266	4.8	4.5	2.8	0
23267	4.9	4.4	2.3	0
23268	5.1	5.3	3.0	2
23269	5.2	5.6	3.2	4
23270	5.5	5.6	3.5	5
23271	6.7	6.6	3.2	2
23272	6.9	7.4	3.5	8
23273	7.7	8.2	3.9	2
23274	8.2	8.8	4.7	10
23275	8.4	8.9	5.8	3
USNM 142525	8.7	10.3	5.7	9
23276	9.1	9.0	5.0	2
23277	9.7	11.6	5.8	8
23278	10.0	11.9	6.7	3
USNM 142526	10.1	11.3	5.6	6
23279	10.4	11.0	7.8	5
USNM 142527	11.0	12.6	8.2	5
23280	11.0	13.2	6.7	4
23281	11.5	13.0	8.0	9
23282	11.8	15.5	7.8	4
23283	12.5	17.1	10.0	4
23284	12.7	13.7	8.7	12

anterior edge, leaving greater part of length of camarophorium unsupported; crura extending anteriorly from hinge plate, slightly divergent, curving ventrally slightly more than top of camarophorium, thus diverging from camarophorium toward anterior, length about equal to length of camarophorium.

Comparisons.—*Stenosisma schlotheimi* is characterized by its small size, transverse outline, short, sharp pedicle beak, prominent fold, rounded costae greatly variable in number, and a stolidium that is directed mostly toward the anterior, from the anterolateral flanks and

the crest of the fold. It is about the same size as *S. hueconianum* (Girty) but is much less globose and with fewer, broader costae, and more consistently present stolidium. It is much smaller than *S. venustum* (Girty); its outline normally is more transverse, stolidium somewhat shorter, fold proportionately higher, and costae are much broader, fewer, and begin farther anteriorly. *S. schlotheimi* is less strongly convex and has a much smaller number of costae than *S. inequale* (Girty). It is much less convex and more transverse than *S. thevenini* (Kozłowski) from the Permian of Bolivia, and has fewer costae, especially on the fold. It is similar to the Texas Permian species that King (1931) identified as *S. thevenini*, differing primarily in its higher fold, somewhat more transverse outline, weaker costae, and shorter pedicle beak.

This species is much smaller and more weakly costate than *S. multicrostum* Stehli and, although only about half as large as typical for *S. kalum* Stehli, it has many fewer and much weaker costae. *S. schlotheimi* is much smaller than *S. purdoni* (Davidson) identified by Broili (1916) from the Permian of Timor. Furthermore, it is proportionately wider and less convex than the Indonesian species. It is much smaller, also, than *S. giganteum* (Diener) from the same island, and has fewer costae that begin farther anterior.

S. schlotheimi is smaller and has fewer and weaker costae than any of the species described by Waagen (1883) from the Permian of the Salt Range, excepting "*S.*" *superstes* (Verneuil) (now considered a species of *Cyrolexis*) and "*S. globulinum*" (Phillips); it is much wider and less globose than either of those two species. Among the species identified from the Permian of the Urals and Timan by Tschernyshev (1902), only *S. crumenum* (Martin) and some specimens of *S. mutabile* (Tschernyshev) resemble the type species. But neither of these is as wide, both are more globose, and *S. mutabile* is much more strongly costate in the adult stages.

Among British species, *S. multiplicatum* (King) is larger and more costate than *S. schlotheimi*; *Terebratula globulina* Phillips (now in *Coledium*) is smaller, rounder in outline, and has proportionately more prominent mesial costae. *S. crumenum* (Martin) is larger and its costae are more numerous and begin farther posterior, in addition, the profile is more strongly convex.

Occurrence and age.—The species is abundant in the fossiliferous part of the Zechstein near Pössneck, Germany (Late Permian according to Gignoux, 1955, p. 214). It has been identified widely throughout Europe, but these citations probably do not reflect accurately its true distribution. Until European specimens can be compared in detail, only those from the type area can be considered reliably identified.

STENOSCISMA HUECONIANUM (Girty)

Plate 19, figs. 1-1b

Camarophoria hueconiana GIRTY, G. H., 1929, Journ. Wash. Acad. Sci., vol. 19, No. 18, p. 412, 414, figs. 14-21.

Camarophoria deloi KING, R. E., 1931, Univ. Texas Bull. 3042, p. 110, pl. 34, fig. 24 (holotype); STAINBROOK, M. A. and MADERA, R. F., 1941, Journ. Paleontology, vol. 15, No. 4, p. 378, pl. 55, figs. 15-27.

Shell small for genus; outline transversely subelliptical to subpentagonal or trigonal, sides diverging between 70 and 105 degrees, maximum width located anterior to midlength of shell; profile strongly biconvex; commissure uniplicate, fold low to moderately high, broad, beginning about 5 mm. anterior to brachial beak; sulcus very shallow, beginning 5-7 mm. anterior to pedicle beak. Costae strong, sharp to blunt, commonly bifurcating on fold or sulcus, beginning 3-5 mm. anterior to beaks, numbering from three to five (normally five) on fold, one less in sulcus, three to five on each flank; stolidium rudimentary or absent; growth lines faint.

Pedicle valve moderately convex transversely, strongly convex longitudinally through sulcus; beak relatively long, moderately strongly hooked but not normally pressed against brachial umbonal region; posterolateral flanges broad, covered by edge of brachial valve; delthyrium broadly triangular, normally without deltidial plates, leaving large open foramen.

Brachial valve strongly convex transversely, less strongly convex longitudinally along crest of fold; beak bluntly pointed, apex within pedicle valve.

Pedicle valve interior with hinge teeth fused to sides of valve; dental plates converging just above floor of valve to form boat-shaped spondylium, fused together beneath spondylium forming low median septum extending slightly anterior to spondylium; apical region between spondylium and side of valve may be filled with shell material. Muscle marks in anterior two-thirds of spondylium, faint and undifferentiated, set off from posterior third by sharp line; pallial marks on floor of valve, vascula media diverging at straight angle from forward edge of median septum, crossing valve to sides; marks of gonocoels posterior to transverse vascula, on floor of valve beside spondylium.

Brachial valve interior with broadly triangular to crescentic hinge plate, thickened at apex to form cardinal process; hinge sockets short, located at lateral extremities of hinge plate; crural bases extending forward from base of cardinal process, space between them filled by crural plates, joining them to top of intercamarophorial plate; crural processes continuing free beyond crural bases, outwardly bowed and ventrally bent, conforming to shape of edge of camarophorium; median

septum high, thin, relatively short on floor but length increasing with height, capped by spoon of camarophorium with unusually broad median projection at anterior edge; intercamarophorial plate short, may be buried in callus. Muscle marks in camarophorium and pallial marks on floor of valve not observed.

TABLE 32. *Measurements of selected specimens of Stenosisma hueconianum from locality 712e*

USNM No.	Measurements, in millimeters		
	Length	Maximum width	Thickness
142508	9.2	10.5	7.4
142509	10.2	12.0	9.3
142510	10.5	13.6	9.5
142511	11.1	14.0	10.7
142512	12.0	15.8	12.0

Discussion.—*Stenosisma hueconianum* is small for a Permian species of the genus. It is larger than *S. schlotheimi* (Buch) but smaller than *S. venustum* (Girty), *S. multicostum* Stehli, and a large number of undescribed species that I have studied from the Glass Mountains, Tex. In addition, it is smaller than most of the Permian species from the Salt Range, the Urals and Timan, or Timor.

The stolidium of this species is narrow, and on many specimens it is not preserved. The manner of meeting of the valves indicates that the missing stolidium is not simply a matter of preservation, but that the stolidium never developed on many individuals.

The species is illustrated as a further example of variation within the genus *Stenosisma*.

Occurrence.—Hueco Limestone, 100 yards W. of USGS Bench Mark 5318, 1.5 miles NNE. of Hueco Inn, Hueco Mountains, Tex. (USNM loc. 712e).

Age.—Early Permian.

STENOSCISMA MULTICOSTUM Stehli

Plate 19, figs. 3-3a

Stenosisma multicosta STEHLI, F. G., 1954, Amer. Mus. Nat. Hist. Bull., vol. 105, art. 3, p. 339, pl. 25, figs. 7-9.

Discussion.—This species is illustrated as an example of a large species whose numerous costae increase in number by bifurcation. It is proportionately wider than *S. venustum* (Girty) and has more and finer costae. The full breadth of the stolidium of *S. multicostum* is unknown, but its extent along the valve edges indicates that it probably is

less well developed than the stolidium of *S. venustum*. It is present on the anterior edge of the pedicle valve of *S. multicostum*, but absent from the flanks of that valve. On the brachial valve it occurs at the edges of both flanks and the fold.

This trigonal and multicostate species is mimicked to some degree by a Cretaceous rhynchonellid, *Cyclothyris vesperilio* (Brocchi) (pl. 7, fig. 1).

TABLE 33.—*Measurements of Stenosisma multicostum*

USNM No.	<i>Measurements, in millimeters</i>	
	Length	Width
	Pedicle valve	
142515	25.0	37.5
142516	25.5	c.35
	Brachial valve	
142517	21.6	c.31
142518	23.0	34.6

Occurrence.—Permian Bone Spring Limestone, locality 629 of Stehli (1954), one-fourth mile south of Victorio Canyon on scarp of Sierra Diablo, north of Van Horn, Tex.

Age.—Early Permian.

STENOSCISMA PURDONI (Davidson)

Plate 20, figs. 1-4

Camarophoria purdoni Davidson, BROILI, F., 1916, Perm. Brach. Timor, p. 55, pl. 125 (11), figs. 7-23.

Discussion.—This large species from Timor is illustrated as an example of a Late Permian *Stenosisma* whose pedicle foramen is completely closed by tight curvature of the beak of the pedicle valve onto that of the brachial valve. The anterior margins show clearly the former presence of stolidia on adults, although the stolidia are not preserved on these calcareous specimens. This species undoubtedly lived its adult life on the sea floor, free of peduncular attachment.

These specimens correspond closely to those called *C. purdoni* by Broili (1916). However, they bear little resemblance to Davidson's (1863, pl. 2, fig. 4) Salt Range specimens of that name. Correct specific identification would require study and comparison of adequate collections from Timor and the Salt Range; therefore, Broili's name for the species is used, advisedly, without citing the comprehensive synonymy that appears in his book.

STENOSCISMA VENUSTUM (Girty)

Plate 21, fig. 13; plate 22, figs. 1-10; plate 23, figs. 1-5

Camarophoria venusta GIRTY, G. H., 1909, U.S. Geol. Survey Prof. Paper 58, p. 303, pl. 31, fig. 6-6c; KING, R. E., 1931, Univ. Texas Bull. 3042, p. 110, pl. 34, figs. 29-31, pl. 35, figs. 1-5.

Stenosclisma venusta (Girty) COOPER, G. A., 1944, in Index foss. No. Amer., p. 315, pl. 120, figs. 38-40.

Stenosclisma venustum (Girty) COOPER, G. A., 1956a, Journ. Paleontology, vol. 30, No. 3, p. 522, text fig. 1a.

Adult shell large for genus; outline broadly subtrigonal, sides diverging between 65 and 115 degrees, averaging about 90, divergence typically increasing with shell size; profile moderately biconvex; commissure uniplicate; fold high, broad and only gently arched over crest, beginning about 8-15 mm. anterior to brachial beak; sulcus rather shallow except at anterior, beginning 12-18 mm. anterior to pedicle beak. Costae moderately strong, blunt crested, beginning 1-5 mm. anterior to beaks, numbering five to eight, normally five or six on fold, one less in sulcus, four to six on flanks, becoming lower and weaker laterally, rarely one or two on fold or sulcus bifurcating anteriorly; stolidium broad, fanlike, finely concentrically ornamented, beginning just behind widest part of shell, not continuous from flanks to fold, better developed on brachial valve, may be reduced or absent; growth lines fine and closely spaced, with a few stronger laminae at irregular intervals.

Pedicle valve gently convex transversely and from beak to flanks, more strongly convex through sulcus; umbonal region relatively low, not swollen; beak about normal length for genus, suberect to erect but not strongly hooked; beak ridges short, blunt; delthyrium triangular, small, constricted along sides and at anterior by conjunct deltidial plates, leaving narrow, slitlike foramen normally opening directly dorsally; posterolateral flanges elongate, narrow, normally covered by overlapping edge of opposite valve.

Brachial valve strongly convex transversely, moderately strongly convex along crest of fold, convexity rather uniform, valve nowhere strongly swollen or flattened; beak bluntly pointed, apex within pedicle valve, hidden by deltidial plates.

Pedicle valve interior with blunt hinge teeth elongate parallel to sides of valve; dental plates continuous with hinge teeth, slightly convergent toward floor of valve, more abruptly curved immediately above floor, joining one another to form boat-shaped spondylium, supported by low median septum; space between floor of valve and outside of spondylium may be filled with callus. Relatively deep, transverse

troughs present in some individuals, crossing floor of valve just anterior to end of median septum; muscle marks in spondylium weak.

Brachial valve interior with broadly triangular hinge plate, apex thickened to form cardinal process which is a single small node in young individuals, becoming greatly thickened and binodose in adults, with surface textured for muscle attachment; hinge sockets elongate, narrow, finely denticulate, laterally bounding anterior one third of hinge plate; crural bases fused to hinge plate, extending from base of cardinal process to anterior edge of plate, there continuing free as slender crural processes, outwardly bowed and gently curved ventrally; median septum high, thin, length increasing with height; camarophorium spoon-shaped, widest just behind anterior end, slightly produced at anterior apex; intercamarophorial plate somewhat shorter than median septum, forming support between camarophorium and hinge plate, median part of hinge plate may extend forward between crural processes and dip from sides to top of intercamarophorial plate; space between hinge plate and camarophorium may be filled with callosity, burying intercamarophorial plate. Muscle marks weak, elongate, located in camarophorium (*see* fig. 1B).

Holotype.—*Camarophoria venusta* GIRTY, G. H., 1909, U.S. Geol. Survey Prof. Paper 58, p. 303, pl. 31, figs. 6–6c (USNM 118557).

Discussion.—This species illustrates great development of the stolidium and of internal features characteristic of Permian species of *Stenosisma*. The species attains a maximum size much greater than that of *S. schlotheimi* (v. Buch) and is more strongly costate. It is slightly smaller than the largest specimens of *S. multicostum* Stehli, but the costae are coarser, fewer, normally simple, and the outline is less strongly trigonal.

The stolidium of *S. venustum* is broad on both valves, and occupies the anterolateral flanks and the crest of the fold (and trough of sulcus) but is not continuous from the fold to the flanks. Pallial marks are visible on internal surfaces.

Internal features of *S. venustum* are typical of Permian species of the genus, with the spondylium deep, the camarophorium large, ventrally curved, spoon-shaped, and the gonocoels linear, troughlike, extending laterally from the median septum of the pedicle valve. Exceptionally well preserved silicified specimens from the Glass Mountains, Tex., provided material for study of the interior and for its illustration (fig. 1, 2; pl. 23). Diagrammatic drawings showing the possible courses of the muscles are based on examples of this and other well preserved species from the same area (fig. 1).

Occurrence and age.—Leonard Formation (Early Permian), Glass Mountains, Texas.

Subfamily TORYNECHINAE Grant n. subfam.

Uncinuliform Stenoscismatidae with stolidium greatly reduced (or absent) ; costae at beaks.

Genus TORYNECHUS Cooper and Grant 1962

Uncinuloides KING, R.E., 1931, Univ. Texas Bull. 3042, p. 112 (part).

Torynechus COOPER, G. A. and GRANT, R. E., 1962, Journ. Paleontology, vol. 36, No. 5, p. 1128.

Shell uncinuliform ; transversely subtrigonal to subpentagonal ; commissure uniplicate, fold and sulcus with low relief ; edges of valves slightly protruding to form rudimentary stolidium ; anterior and anterolateral surfaces flattened, with each costa there deeply grooved ; costae fine, numerous, sharp or blunt, beginning at beaks, added anteriorly by intercalation or bifurcation, producing shallow serration of commissure ; concentric ornamentation fine, closely spaced.

Pedicle valve moderately convex ; beak rather long, attenuate, slightly hooked ; beak ridges blunt, not obvious ; delthyrium triangular, constricted by small deltidial plates ; flanks may be slightly reflexed ; lateral valve edges covered by edges of brachial valve ; anterior margin abruptly bent to meet levigate surface.

Brachial valve more strongly convex except along crest of fold ; beak somewhat swollen, slightly attenuate ; anterior edge sharply bent toward commissure.

Pedicle valve interior with one small hinge tooth fused to each side ; dental plates large, converging on or just above floor of valve, forming elongate, boat-shaped spondylium and low, supporting median septum : space between floor and spondylium may be filled by callus, enveloping septum. Muscle marks in anterior two-thirds of spondylium, faint and undifferentiated ; pallial marks on floor of valve ; gonocoels forming deep straight troughs, slanting slightly backward from edge of median septum and weakly texturing posterior valve floor ; vascula media producing two slightly raised trunks, diverging forward from edge of median septum, each splitting nearby to produce lateral and anterior branches, each branch bifurcating at least once, splitting again at extremities, sending slender apophyses to edge of valve.

Brachial valve interior with large, subtrigonal to crescentic hinge plate greatly thickened at apex of valve to form large cardinal process, striate or serrate radially for attachment of diductor muscles ; hinge sockets at lateral extremities of hinge plate, wide, deep, short, coarsely denticulate ; crural bases diverging forward from near base of cardinal process, space between them filled by callus or extension of cardinal process or short crural plate, uniting with top of intercamarophorial plate ; crural processes extending free into living chamber, conforming

to shape of outline of camarophorium, outwardly and ventrally bowed; camarophorium deep, spoon-shaped, with anterior median projection; intercamarophorial plate short, low, may be buried in callus; median septum high, thin, rather short on floor of valve, length increasing with height. Muscle marks in camarophorium faint; pallial marks on floor of valve with vascula media diverging anteriorly from edge of median septum, each trunk bifurcating two or three times, finally splitting into many small apophyses near valve margins.

Type species.—*Torynechus caelatus* Cooper and Grant, 1962, p. 1129.

Comparisons.—*Torynechus* is characterized by its fine, numerous, intercalating and bifurcating costae that begin at the beaks, rather thick pedicle beak without sharp beak ridges, somewhat swollen brachial beak, fold that is high at commissure but does not stand prominently above flanks behind commissure, flattened anterior and anterolateral surfaces with each costa there deeply grooved, commissure with rudimentary stolidium, hinge plate with thick cardinal process, and a large camarophorium as in *Stenoscisma*. Internally, the genus most nearly resembles *Stenoscisma*, although the camarophorium is deeper and the intercamarophorial plate is shorter. It differs externally from *Stenoscisma* in its greater number of finer costae, flattened anterior surfaces, and rudimentary stolidium. Externally, *Torynechus* is similar to *Rhynchopora*, differing in its impunctate shell, thicker pedicle beak without prominent beak ridges, less elevated brachial valve, more swollen brachial beak, intercalate costae, and by its deeply grooved costae on the anterior levigate surfaces. Internally the two genera are entirely dissimilar.

Torynechus also resembles *Septacamera* Stepanov, and probably is fairly closely related to that genus. It differs from the Russian genus in its more nearly flat anterior surface produced by sharp corners on the shell, its much more numerous and bifurcating costae, and the slightly protruding valve edges that probably represent the remains of a relict stolidium. As far as can be determined, the two genera are nearly alike internally, although if in fact *Septacamera* has lateral buttress plates to the spondylium, they constitute a further generic difference.

Discussion.—Robert E. King (1931) established the genus *Uncinuloides* for *Rhynchonella guadalupae* Shumard (1859) and for the specimens from the Glass Mountains which he (King, 1931) and Girty (1909) assigned to that species. Shumard's holotype was lost, apparently even at the time of Girty's writing, and Girty also lost his specimen from the Glass Mountains, composing its description from memory. King's specimens from the Glass Mountains are from a much

lower level in the Permian, and it is doubtful that they are conspecific or congeneric with *R. guadalupae*.

Judging from the only extant illustrations of *R. guadalupae* Shumard (1859, pl. 11, figs. 6a-c) reproduced by Girty (1909, pl. 16, figs. 10-10b), it differs from the Glass Mountains specimens in its less attenuate pedicle and brachial beaks, less inflated brachial beak, less distinct fold, sulcus that begins farther posterior, more distinct beak ridges and finer, more crowded costae. These are specific characters; to determine the genus of specimens in this group it is necessary to study internal structures, shape of the anterior external surfaces, and the nature of the anterior commissure. None of these features is present on Shumard's illustrations or described in his account of the species.

Girty's (1909) description of his lost specimen from the Glass Mountains mentions flat costae, a small cruralium, and a small, horizontal hinge plate with an apical perforation. These are features entirely unrelated and dissimilar to King's specimens or his description of *Uncinuloides*. Aside from the fact that the specimens are missing, difficulty arises from the general similarity of the shape of species belonging to several genera. Cooper and Grant (1962) argued that Shumard's species is unidentifiable, but certainly not conspecific with King's specimens; the generic position of Girty's specimen is unknown. Unfortunately, King's generic name is tied to Shumard's indeterminate species, so they introduced *Torynechus* as a new genus, citing King's (1931, p. 112, pl. 35, fig. 6-7) specimen as holotype for the type species *T. caelatus* Cooper and Grant (1962).

Range.—Known species of *Torynechus* are confined to the Leonard Series of the West Texas Permian.

TORYNECHUS CAELATUS Cooper and Grant

Plate 24, figs. 1-10

Uncinuloides guadalupensis (Shumard) KING, R. E., 1931, Univ. Texas Bull. 3042, p. 112, pl. 35, figs. 6-7; COOPER, G. A., 1944, in Shimer and Shrock, Index foss. No. America, p. 315, pl. 120, fig. 49-51.

Torynechus caelatus COOPER, G. A., and GRANT, R. E., 1962, Journ. Paleontology, vol. 36, No. 5, p. 1129.

Shell about average size for genus; outline moderately to broadly subtrigonal or subpentagonal, sides diverging between 65 and 115 degrees, averaging about 90; profile narrowly subtrigonal; commissure uniplicate, fold behind commissure low, standing above flanks only at anterior extreme, point of beginning not ascertainable; sulcus shallow, beginning 8-12 mm. anterior to pedicle beak. Costae fine, blunt crested, beginning at beaks, adding anteriorly by intercalation or more rarely by bifurcation, numbering 9 to 14 on fold, one less in sulcus, 10 to 22 on each flank; anterior margins of shell abruptly bent to form flattened,

levigate anterior and anterolateral surfaces, each costa there deeply grooved along crest, slightly extended at commissure to produce serrated margin interlocking with serrations of opposite valve; edges of valves protruding to form rudimentary stolidium. Concentric ornamentation fine, normally showing best in troughs between costae; growth laminae faintly visible.

Pedicle valve flatly convex transversely, moderately convex longitudinally through sulcus, abruptly flexed at anterior margin to form levigate surfaces; beak long, somewhat attenuate, thickened, slightly hooked, with obscure beak ridges; posterolateral valve edges elongate, narrow, covered by edges of brachial valve; delthyrium triangular, constricted by pair of small, disjunct deltidial plates, leaving elongate foramen opening directly ventrally.

Brachial valve moderately convex transversely flatly convex along crest of fold, except for stronger convexity at somewhat swollen, attenuate beak.

Pedicle valve interior with small, denticulate hinge teeth, one fused to each side; dental plates strong, converging just above floor to form elongate, boatlike spondylium, continuing to floor as low median septum; floor may be thickened, hiding septum. Muscle marks in spondylium and pallial troughs and trunks as described for genus.

Brachial valve interior with triangular to crescentic hinge plate, greatly thickened at apex to form large, knoblike cardinal process, serrated for muscle insertion; hinge sockets at lateral extremes of plate, wide, deep, short, coarsely denticulate; crural bases extending forward from near base of cardinal process, space between filled by callous or plate attaching to top of intercamarophorial plate; crural processes extending free, outwardly and ventrally bent to conform to outline of top of camarophorium; median septum high, thin, rather short on floor, length increasing slightly with height; camarophorium large, spoon-shaped, deep, with short intercamarophorial plate. Muscle marks in camarophorium and pallial marks on floor as described for genus.

Holotype.—King, 1931, plate 35, fig. 6 (Tex. Bur. Econ. Geol. No. 10167).

Comparisons.—*Torynechus caelatus* is characterized by its fine, blunt costae that normally add anteriorly by intercalation, attenuate beaks, somewhat swollen brachial beak, and levigate anterior that does not extend far along the sides toward the posterior. The blunt, normally intercalating costae, more swollen brachial beak, and less extensive levigate region distinguish it from another less abundant species that also occurs in the Leonard of the Glass Mountains, Tex.

Occurrence and abundance.—*Torynechus caelatus* has been found in the Leonard Formation in the Glass Mountains, Tex. Nearly 50 speci-

TABLE 34.—*Measurements of selected specimens of Torynechus caelatus from the Leonard Formation in the Glass Mountains, Tex.*

USNM No.	<i>Measurements, in millimeters</i>			Divergence of sides (degrees)
	Length	Maximum width	Thickness	
142548	14.2	13.8	8.9	74
142549	14.8	13.9	9.0	74
142550	15.1	17.7	11.4	88
142551	15.9	17.8	14.6	95
142552	17.3	20.9	14.7	95
142553	19.0	22.2	13.0	92
142554	18.2	23.6	13.8	101
142555	20.4	23.8	18.4	98

mens were collected at U.S. National Museum locality 702, about the same number at 702un, and about 30 at other localities in the formation. These are in the vicinity of Split-tank on the old Word Ranch, Hess Canyon Quadrangle, Tex., near R. E. King's (1931) locality No. 128.

Genus SEPTACAMERA Stepanov 1937

Septacamera STEPANOV, D. L., 1937, *Uchenie Zapiski, Leningrad*, No. 16, p. 146, 149.

Septacamera Stepanov, LICHAREV, B., 1960, *Osnovi Paleont.*, p. 249 (altered spelling).

Shell large, uncinuliform strongly biconvex; outline transversely subtrigonal to subelliptical or subpentagonal, widest near midlength; profile subtrigonal, with anterior surface gently arcuate, valves meeting at high angle, butting at anterior, apparently with little or no overlap of edges on posterolateral slopes; commissure strongly uniplicate, but fold not standing high above flanks; sulcus shallow, tongue extending into fold strongly bent to form flattened anterior surface; costae strong, sharp or sharply curved in cross-section, beginning at beaks or only slightly anterior, somewhat broadened and lowered on anterior surface, normally simple, without bifurcation or intercalation; stolidium entirely absent; growth lines fine, closely spaced; growth laminae slightly stronger.

Pedicle valve flatly to moderately convex for most of length, strongly convex near anterior, bending toward commissure; beak short, blunt, suberect to erect; delthyrium small, triangular, largely occupied by brachial beak; deltidial plates small, leaving oval foramen open.

Brachial valve more strongly convex, especially laterally toward flanks, strongly bent near anterior of fold, meeting pedicle valve at

nearly straight angle; beak slightly swollen, apex within pedicle valve.

Pedicle valve interior with dental plates forming large, boat-shaped spondylium, lying nearly on valve floor in posterior, elevated farther anteriorly on rather high median septum; lateral buttress plates from spondylium to valve walls doubtfully present (see discussion, below).

Brachial valve interior with large spoon-shaped camarophorium elevated on high septum; other internal details unknown.

Type species.—*Camarophoria kutorgae* Tschernyshev, T., 1902, Mem. Com. Geol. vol. 16, No. 2, p. 90 and 500, pl. 22, figs. 16–17, fig. 28, by original designation of Stepanov, 1937.

Comparisons.—*Septacamera* is characterized by its large size, strong costae that begin at the beaks, flattened or gently arcuate anterior surface, and complete lack of stolidium. It resembles some large species of *Stenosisma* Conrad, differing in its greater thickness, wedge-shaped profile, flattened rather than acute angle of meeting of the valves at the anterior, and by lack of a stolidium. It is most similar to *Torynechus* Cooper and Grant, differing in its broader and stronger costae that neither bifurcate nor intercalate, its less flattened anterior surface, entire lack of a stolidium, and possibly by the lateral buttress plates on the spondylium of some species.

Discussion.—The morphology and taxonomic position of *Septacamera* are uncertain at present. New evidence bearing on these questions is unavailable because specimens from Russia could not be obtained for study. Analysis of the literature seems to point to the conclusions that (1) *Septacamera* is a valid genus; and (2) it belongs to the Stenoscismatacea.

Stepanov (1937, p. 149) stated that the major difference between *Septacamera* and *Camarophoria* (i.e. *Stenosisma*) is in transverse buttress plates that extend from the distal sides of the dental plates, bracing the spondylium to the valve walls. Other workers have not observed these buttress plates. Tschernyshev (1902, text-fig. 28) presented a clear illustration of a specimen of the type species, *Camarophoria kutorgae* Tschernyshev, broken longitudinally along the midline to show the spondylium and camarophorium. No transverse buttress plates are apparent.

Licharev (1960, text-fig. 290) illustrated a cross-section through the beak area of a specimen identified as *Septocamera kutorgae* (Tschernyshev) in which little other than a median septum duplex in the brachial valve is apparent. The walls and internal structures of the specimen seem to have been thickened, obscuring all details of the spondylium, or perhaps the section was cut in the thick posterior part of the shell. In either case, evidence for the buttress plates is inconclusive. However, Licharev classified *Septacamera* with *Rotaia* Rzhon-

snitskaya and *Tetracamera* Weller, the former with high and the latter with low lateral buttress plates. Apparently Licharev agreed with Stepanov that lateral buttress plates are present.

Transverse buttress plates could have been destroyed in Tschernyshev's specimens when he broke them along the midline. Therefore, I incline to accept tentatively the opinion of Stepanov and, inferentially, of Licharev that they are present in the genus. Presence of such buttress plates certainly would make the genus separate from *Stenoscisma* and *Torynechus* which lack them.

Concerning the presence of a camarophorium in *Septacamera*, authorities again are divided, although majority opinion favors it. Tschernyshev's illustration, which may be considered authoritative, shows clearly the presence of a normal camarophorium, although the anterior part is missing. Stepanov states unequivocally, "There is a camarophorium in the dorsal valve" (p. 149). Licharev (1960) by classifying the genus with the Tetracameridae, seems to argue that no camarophorium is present. However, possibly he considered presence of lateral buttress plates taxonomically more important than a camarophorium, and placed *Septacamera* in that family despite a camarophorium. Only examination of topotype specimens can settle this question. Inasmuch as Tschernyshev and Stepanov indicate clearly the presence of a camarophorium, and Licharev is ambiguous on the subject, it seems reasonable to believe that one is present.

If *Septacamera* has a camarophorium it belongs with the *Stenoscismataceae*, rather than with any other group. Dental plates that unite to form a spondylium definitely are present in the genus; only the presence of lateral buttress plates is in doubt, and their presence is not sufficiently important to remove the genus from the *Stenoscismataceae*.

Stepanov cited the lateral buttress plates as sufficient to separate *Septacamera* from *Stenoscisma*. Despite doubt that such plates are present, other valid distinctions from *Stenoscisma* are notable. Most obvious is lack of a stolidium in *Septacamera*. The genus occurs in the Permian where nearly all species of *Stenoscisma* have the stolidium present in full-grown adults. It is absent from large specimens of *Septacamera*. In addition, the valves of *Septacamera* meet at the anterior in a very gentle (nearly straight) angle, or in a broad arc. Furthermore, they tend to become flattened in some species that mimic the uncinuliform anterior of *Torynechus* (e.g., *S. plicata* (Kutorga)), although not to the same degree.

Until it is possible to examine specimens from the Urals, available evidence indicates that *Septacamera* is a stenoscismatacean genus related to *Torynechus*.

The only species of *Septacamera* examined at first hand is *S. cf. S.*

plicata (Kutorga) from the Permian of Oregon (Cooper, 1957). Specimens in the U.S. National Museum collections have the external generic features of the genus, but lack the lateral buttress plates of the spondylium. This constitutes the only evidence from specimens that such plates may be lacking in the genus; it does not preclude their presence in other species of *Septacamera*.

Range.—Species of *Septacamera* have been found in the Lower Permian (Sakmarian) in the Ural foothills, and in the Lower Permian of Oregon (Word equivalent). According to Licharev (1960, p. 249), its range extends doubtfully into the Upper Carboniferous in the Ural area and Timan.

SEPTACAMERA KUTORGAE (Tschernyshev)

Plate 4, fig. 4

Camerophoria kutorgae TSCHERNYSHEV, T., 1902 Mem. Com. Geol. (Russ.), vol. 16, No. 2, p. 90, 500, pl. 22, figs. 16–17, text fig. 28; TSCHERNYSHEV, T., and STEPANOV, P., 1916, Rept. 2d. Exped. in "Fram," p. 56.

Septacamera kutorgi (Tschernyshev) STEPANOV, D. L., 1937, Uchenie Zapiski, Leningrad, No. 16, p. 146, 149.

Septacamera kutorgae (Tschernyshev) LICHAREV, B., 1960, Osnovi Paleont., p. 249, 250, text fig. 290, pl. 48, fig. 6.

Remarks.—*S. kutorgae* is about average size for the genus, as well as can be determined from the literature. It is strongly plicate and has a high fold at the anterior, but the fold is not prominent above the flanks, and the sulcus is not deeply depressed. The anterior is uncinuliform, with valves meeting in a broad arc, not acutely and not in a plane. *S. kutorgae* differs from *S. cf. S. plicata* (Kutorga) in its sharper costae, fewer costae on the fold, and less strongly geniculate anterior surface (although the last feature may have been exaggerated by crushing of the anterior of the Oregon specimens). No evidence in Tschernyshev's (1902) work indicates that lateral buttress plates are present in the pedicle valve as Stepanov (1937) contended (see discussion of genus, above).

SEPTACAMERA cf. *S. PLICATA* (Kutorga)

Plate 4, figs. 3–3a

Stenosisma cf. *S. plicatum* (Kutorga) COOPER, G.A., 1957, Smith. Misc. Coll., vol. 134, No. 12, p. 54, pl. 10E, figs. 32–35.

Stenosisma plicatum (Kutorga) HARKER, P. and THORSTEINSSON, R., 1960, Geol. Surv. Canada, Mem. No. 309, p. 62, pl. 18, figs. 1–4.

Shell about average size for genus; profile somewhat wedge-shaped; outline subtrigonal to subpentagonal; commissure uniplicate, with high fold at anterior; fold not prominent above flanks; sulcus only moderately depressed, broad and flat, beginning about 15 mm. anterior to

beak; costae strong, simple, crests obtusely pointed, beginning at beaks, numbering about 6 on fold, one fewer in sulcus, 10–12 on each flank; valves geniculate at anterior to form flattened or gently arcuate anterior surface: bent sharply on crest of fold and lateral flanks of pedicle valve, more gently through sulcus and on lateral flanks of brachial valve.

Pedicle valve flatly convex transversely and laterally toward flanks; more strongly convex through sulcus; beak short, thick, sides nearly perpendicular, coming to right-angle point, apex curved slightly: full extent not observed, probably suberect; delthyrium broadly triangular, nearly filled by brachial beak, sides constricted slightly by small deltidial plates; foramen not observed, probably small but open.

Brachial valve more strongly convex, beak blunt, apex within pedicle valve.

Pedicle valve interior with large boat-shaped spondylium formed by convergence of dental plates, supported by low median septum; no lateral buttress plates observed.

Brachial valve interior with camarophorium; other internal features not observed.

Comparisons.—*S. cf. S. plicata* is characterized by its strong, obtuse-crested, numerous costae, high fold at the anterior, and its outline with the greatest width anterior to the midlength. It differs from *S. kutorgae* (Tschernyshev) in its somewhat larger size, more trigonal rather than elliptical outline with the greatest width farther anterior, higher fold, and more numerous costae on fold and flanks. The Oregon specimens resemble Tschernyshev's (1902) specimen illustrated on plate 50 more than the two on his plate 22. However, the only complete Oregon specimen is slightly crushed at the anterior, so detailed comparison is impossible. I agree with Cooper (1957) that this species most nearly resembles *S. plicata*, but may not be conspecific.

Discussion.—These specimens are described and illustrated as examples of the genus *Septacamera*. They appear to retain all characters of the genus except for the controversial lateral buttress plates of the pedicle valve.

SPECIES DOUBTFULLY STENOSCISMATACEAN

CAMAROPHORIA SUTSCHUANENSIS Loczy (fide Grabau, 1931b)

Camarophoria sutschuanensis Loczy GRABAU, A. W., 1931b, Pal. Sinica, vol. 3, fasc. 3, p. 83, text figs. 6, 7, pl. 9; figs. 1–3.

Discussion.—Grabau (1931b) cited this species in his collection from the Devonian of China, quoting Loczy's (1899) description in

translation. The following excerpt is relevant here: "About the inner structure of the shell, I can say nothing. With a strong lens two diverging dark lines can be seen on the shell surface near the beak of the ventral valve. These correspond to the characteristic septa [of this genus]" (insert by Grabau). The genus meant is *Camarophoria*. Obviously, if there are two diverging septa (dental plates) along the floor of the ventral valve, no spondylium is present, and the species does not belong to "*Camarophoria*."

Text-figure 7 of Grabau (1931b, p. 86) shows sketches of apical cross-sections of two specimens that he identified with Loczy's species. If they are accurate (and there is no reason to doubt that they are) a spondylium clearly is present in the pedicle valve, elevated on a median septum, and no diverging septa could appear along the valve floor. Two explanations are plausible, one that Loczy saw the septa near the apex, where the spondylium is sessile, the other that Grabau's and Loczy's specimens are not conspecific (nor congeneric).

Grabau's sketches (1931b, text-fig. 7) show a spondylium in the pedicle valve, the shape of which is normal for stenoscismataceans in fig. a, slightly different in fig. b. Either would be considered well within the limits for the superfamily if accompanied by a camarophorium in the brachial valve. However, neither sketch shows a camarophorium, only an unmodified short median septum. If these specimens were stenoscismatacean, the septum would not extend anteriorly farther than the camarophorium, so the sketches cannot be explained simply as sections anterior to the camarophorium; furthermore, they purport to show sections fairly near the beaks, and are labeled by Grabau as "apical sections."

The internal structure of Grabau's *Camarophoria sutschuanensis* Loczy is not that of a stenoscismatacean genus; probably the species belongs to an undescribed genus. Possibly it is an off-shoot from the stenoscismatacean line, in which the camarophorium has degenerated. It may represent a more normal rhynchonelloid genus in which no camarophorium ever existed, but the dental plates united to form a spondylium. The usual trend in brachiopods is for the structures of the brachial valve to be more conservative than those of the pedicle valve (Ulrich and Cooper, 1936). Study of brachiopods shows that the spondylium is a structure that recurs in many groups. These considerations favor the alternative that *C. sutschuanensis* is unrelated to the Stenoscismatacea, but externally Grabau's specimens closely resemble other stenoscismatacean species from the Chinese Devonian. This equivocal evidence leaves the position of *C. sutschuanensis* indeterminate, until the type specimens can be studied directly in relation to other species from the Chinese Devonian as well as to species of other genera in the superfamily.

Internal structures of Chinese Devonian species that Grabau assigned to *Camarophoria* (other than *C. sutschuanensis* and *C. bitingi*) are neither described nor illustrated. Externally they resemble species of *Coledium* n. gen. but, in absence of knowledge of internal structures, their relationships cannot be determined.

GENERA NO LONGER INCLUDED IN STENOSCISMATACEA

Genus **LIOCOELIA** Schuchert and Cooper 1931

Genus **NANTANELLA** Grabau 1936

Discussion.—Grabau (1936, p. 70) described the genus *Nantanella*, with type species *N. mapingensis* Grabau from the Early Permian of China, assigning it to the superfamily Camerophoriacea Grabau, family Camerophoridae Waagen. Externally it resembles stenoscismatids as well as many other general rhynchonelloid forms. Grabau's sketch of the internal structures (1936, text-fig. 1) is ambiguous; the cut was made so far posterior that the hinge plate is visible; it is impossible to tell whether the branches of the brachial median septum are parts of the hinge plate, or of a camarophorium. In most stenoscismataceans, however, the edges of the camarophorium are visible dorsal to the hinge plate, where none show in Grabau's sketch. In his discussion of the interior of *Nantanella*, Grabau mentioned only the spondylium, median septum, and hinge plate, comparing them to internal structures of *Liocoelia* Schuchert and Cooper (1932, p. 189, text-fig. 36).

Schuchert and Cooper (1932) compared *Liocoelia* with *Camarophoria*: "It would thus appear that *Liocoelia* is essentially a smooth *Camarophoria* having an external form like that of *Clorinda*, *Merista* or *Meristella*." Cooper (1956, p. 523) in his discussion of the genus *Psilocamara*, said that "This genus differs from *Stenoscisma* and *Nantanella* in having a smooth, non-plicated exterior; otherwise it is similar to other members of the Stenoscismatidae." Thus he implied that *Nantanella* and, by inference, *Liocoelia* belong to the Stenoscismatacea. Cooper now (oral communication, 1962) agrees that these two genera are not Stenoscismatacea, inasmuch as the diagnostic camarophorium is absent. Only the spondylium provides internal similarity to the Stenoscismatacea; that structure occurs widely throughout the Brachiopoda and is not, in itself, a reliable criterion of relationship.

Genus **CAMAROPHORELLA** Hall and Clarke 1894

Camarophoria (*Camarophorella*) HALL, J., and CLARKE, J. M., 1894, New York, 13th Ann. Rept. State Geologist, p. 838; 1894, Paleont. New York, vol. 8, pt. 2, p. 215.

Camarophorella Hall and Clarke, HYDE, J. W., 1908, Boston Nat. Hist. Soc. Proc., vol. 34, No. 3, p. 35–65, pl. 6–10.

Discussion.—Hall and Clarke based this genus on *Pentamerus lenticularis* White and Whitfield (1862) from the “yellow sandstones beneath the Burlington Limestone at Burlington, Iowa.” They remarked its external differences from species of *Camarophoria*, but treated it as a subgenus in the belief that its internal structures were essentially similar. Hyde (1908) made an exhaustive study of *C. lenticularis* and similar Mississippian *C. mutabilis* Hyde, concluding that *Camarophorella* is a distinct genus of the spire-bearing meristelloid group.

Weller (1914) in his comprehensive study of the Mississippian brachiopods of the Mississippi Valley, investigated *C. lenticularis* from the yellow sandstones of the upper Kinderhook at Burlington, Iowa. He failed to find spiralia in his specimens, but accepted Hyde’s analysis and assigned *Camarophorella* to the Meristellidae. These conclusions appear to be sound; the genus is not considered a member of the Stenoscismatacea.

Genus PSEUDOCAMAROPHORIA Wedekind, 1926

Pseudocamarophoria WEDEKIND, R., 1926, in Salomon, et al., Grundz der Geol., bd. 2, p. 197.

Septalaria LEIDHOLD, C., 1928, Abh. Preuss. Geol. Lands., p. 35; SCHMIDT, H., 1941, Abh. Senck. Nat. Gesell., 459, p. 35; HAVLICEK, V., 1961, Roz. Ustr. Usta. Geol., No. 27, p. 180.

Diagnosis.—Rhynchonelliform, fold and sulcus strong, costae normally present, strong near anterior; high median septum in brachial valve (wing-shaped in longitudinal profile), hinge plate undivided; neither dental plates nor spondylium in pedicle valve.

Discussion.—This Middle Devonian genus from the German Eifelian has been compared closely with *Stenoscisma* (then *Camarophoria*) although not formally classified with the Stenoscismatacea (Leidhold, 1928; Schmidt, 1941). The profile of the median septum of the brachial valve is closely similar to that of the camarophorium (and its septum) of the Stenoscismatacea (Leidhold, 1928, pl. 3, fig. 3). However, the septum of *Pseudocamarophoria* is unmodified, without the troughlike ventral edge that forms the camarophorium. The pedicle valve of *Pseudocamarophoria* has no dental plates, and no spondylium. Therefore, the genus is merely a rhynchonelloid with a high median septum, whose external shape is similar to that of some later genera of Stenoscismatacea.

Pseudocamarophoria may be related to the Stenoscismatacea. The probable ancestor of that superfamily might have had a high septum in

the brachial valve that subsequently modified to form the camarophorium. Available evidence argues against this relationship, however. Serial sections of the type species of *Pseudocamarophoria* by Schmidt (1941, pl. 7, fig. 25), *P. microrhyncha* (Roemer), show the median septum extending to the hinge plate in the posterior of the valve. The septum of the camarophorium in the Stenoscismatacea is entirely separate from the hinge plate and an accessory low septum, the intercamarophorial plate, joins the hinge plate to the camarophorium. The intercamarophorial plate, therefore, is the analogue of the septum of *Pseudocamarophoria*, not the camarophorium whose profile happens to be similar.

Unfortunately, Schmidt's (1941) sections do not indicate the manner of insertion of the septum in species of *Pseudocamarophoria*. If the fibers of the septum are continuous with those of the valve floor, indicating derivation of the septum from the floor, they postulate remote relationship to the Stenoscismatacea whose brachial septum inserts wedgelike with obvious discontinuity into the valve floor.

Nomenclature.—Wedekind (1926, p. 197) established the name *Pseudocamarophoria* casually in a general discussion of Devonian faunas, citing the genotype *Terebratula microrhyncha* Roemer in a footnote. Leidhold (1928, p. 35) apparently missed this obscure designation, and included *T. microrhyncha* in his genus *Septalaria*; no reference to Wedekind appears in his (or Schmidt's, 1941) synonymy of that species. *T. microrhyncha* is not the type species of *Septalaria* (the type is *Terebratula subtetragona* Schnur), but to judge from discussion and illustrations by Leidhold (1928) and Schmidt (1941), both of whom assigned *T. microrhyncha* to *Septalaria*, the species certainly is congeneric with *T. subtetragona*. Therefore, *Septalaria* should be considered a junior subjective synonym of *Pseudocamarophoria*.

Neave (1940, vol. 3, p. 973) cited *Pseudocamarophoria* as a *nomen nudum*. However, under the Code of Zoological Nomenclature (Stoll, et al., 1961) the indication by Wedekind (1926) is sufficient to establish the name validly. It predates *Septalaria*.

Genus CAMEROPHORINA Schmidt 1941

Camerophorina SCHMIDT, H., 1941, Senckenbergischen Nat. Gesell., Abh. 459, p. 43.

NOT *Camarophorina* LICHAREV, B., 1934, Doklady Akad. Nauk, Leningrad, vol. 1, No. 4, p. 211, 213.

Discussion.—Schmidt named this genus for its superficial resemblance to *Camerophoria*, but did not classify it with that genus. She characterized the genus by its spondylium in the pedicle valve, but

stated clearly that no septum or "septalium" is present in the brachial valve.

Rzhonsnitskaya (1956) established the family Camerophorinidae for the genus *Camerophorina* including it with others in the superfamily Stenoscismatacea. Havlicek (1961) removed the Camerophorinidae to the Rhynchonellacea, where it properly belongs on the basis of its internal structures.

The genus *Camarophorina* Licharev is entirely distinct from *Camerophorina*, and belongs with the Stenoscismatacea. Despite similarity of the two names, they have been spelled differently from the time the later one was proposed; both are valid names, not homonyms.

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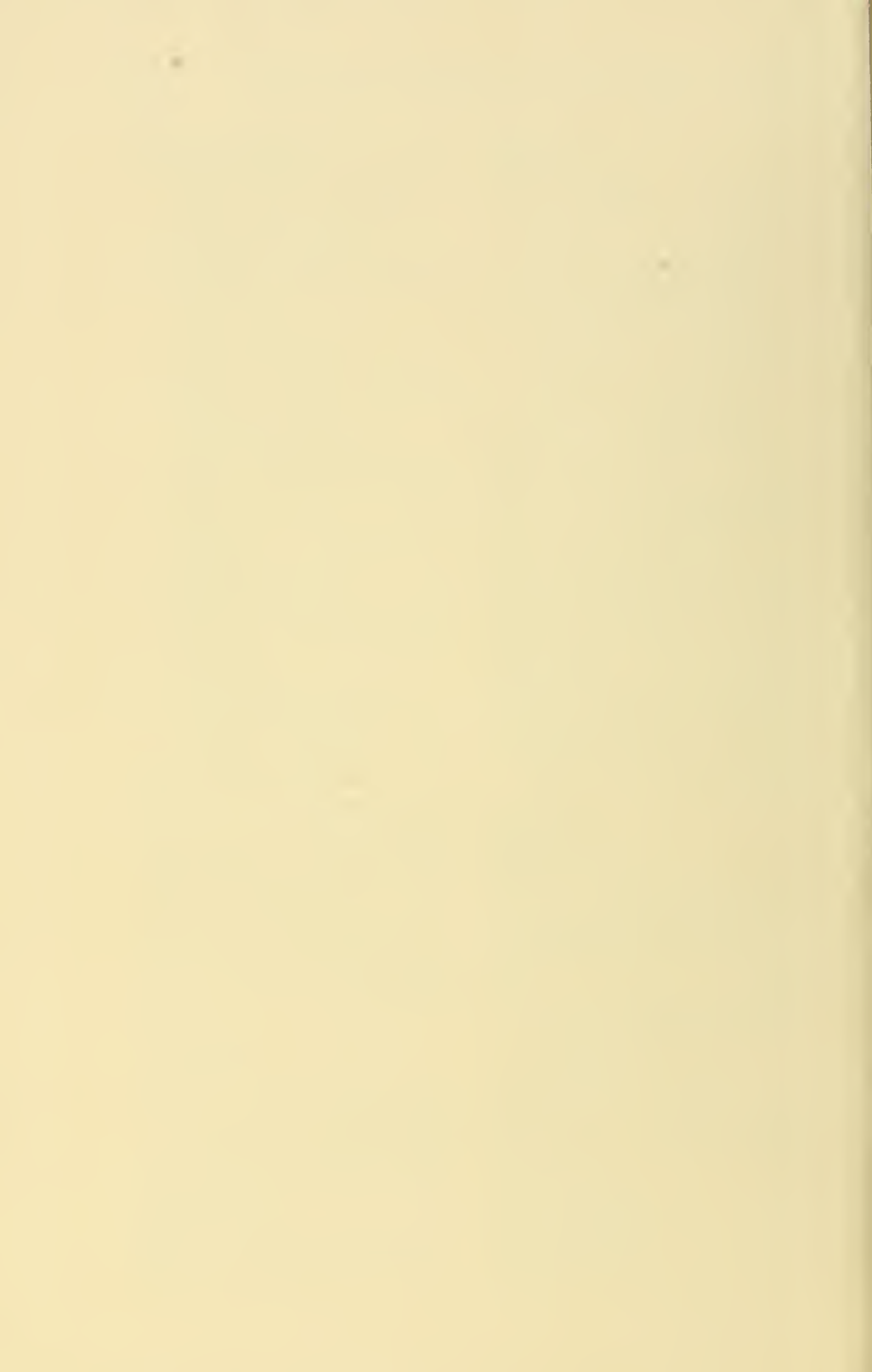
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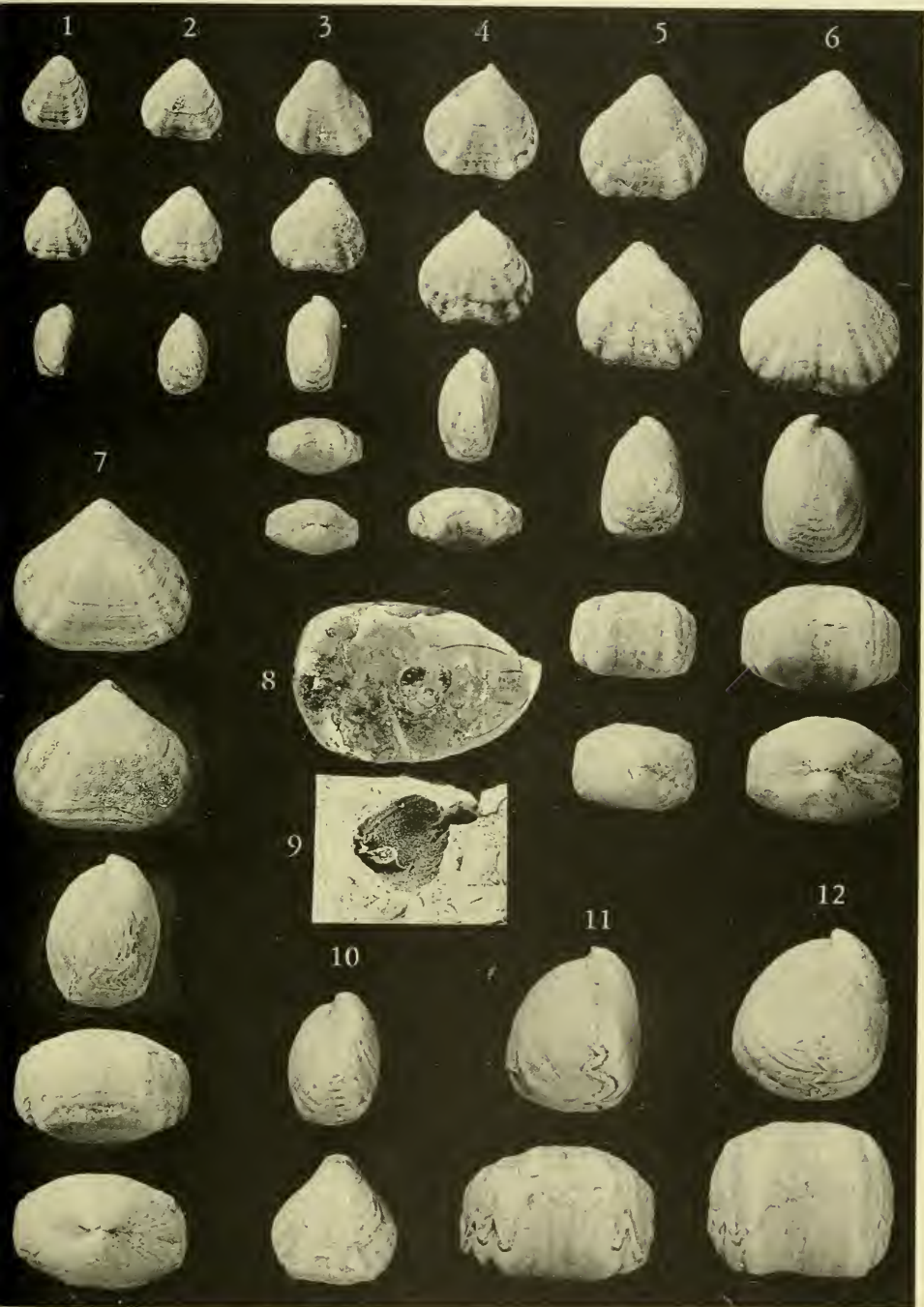
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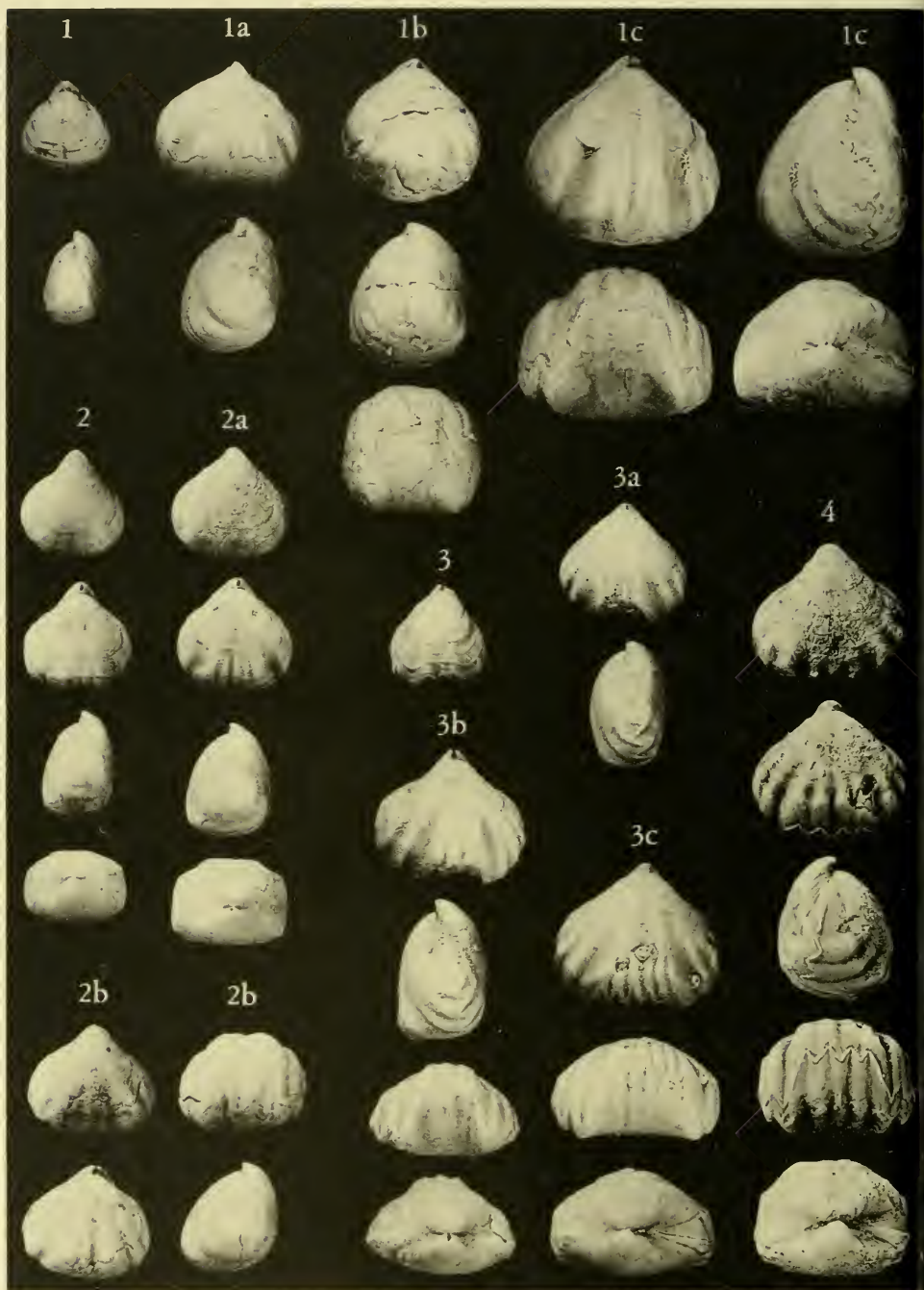
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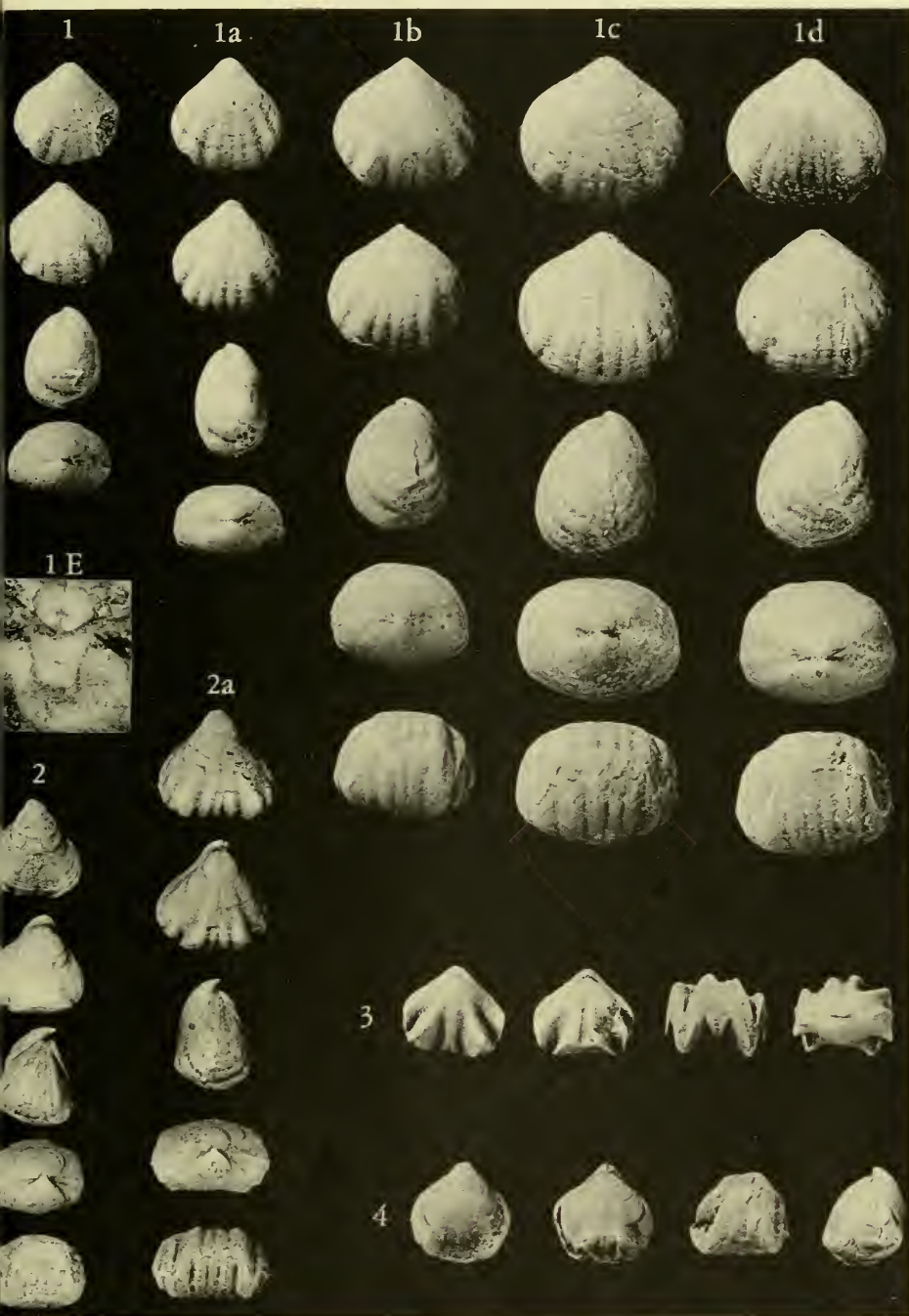




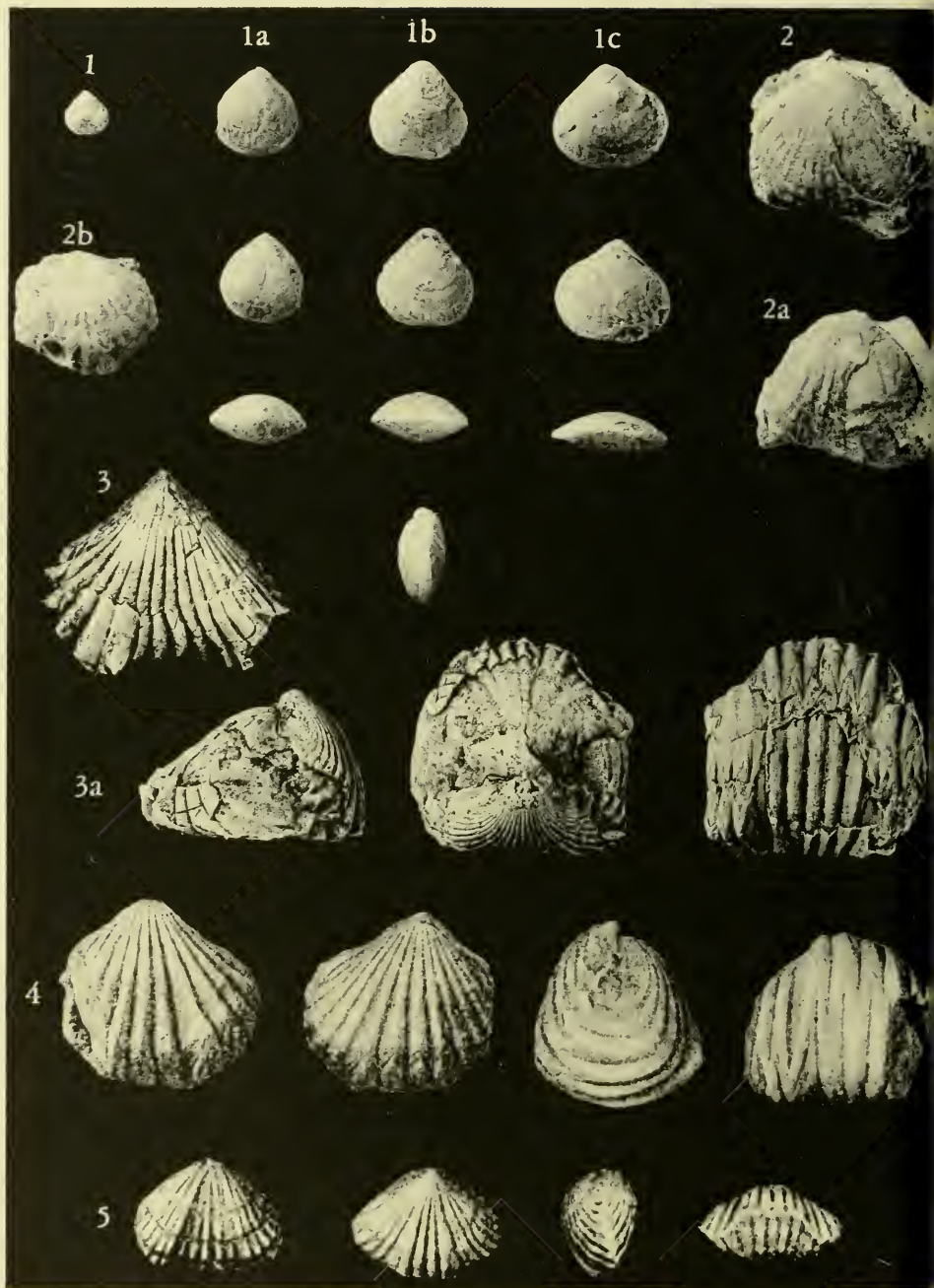
1-12, *ATRIONIUM SIMATUM*.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



1-1C. ATRIBONIUM PINGUE; 2-2B, ATRIBONIUM SUCCIDIUM;
 3-3C, ATRIBONIUM COOPERORUM; 4, ATRIBONIUM SP.
 (SEE EXPLANATION OF PLATE AT END OF TEXT.)



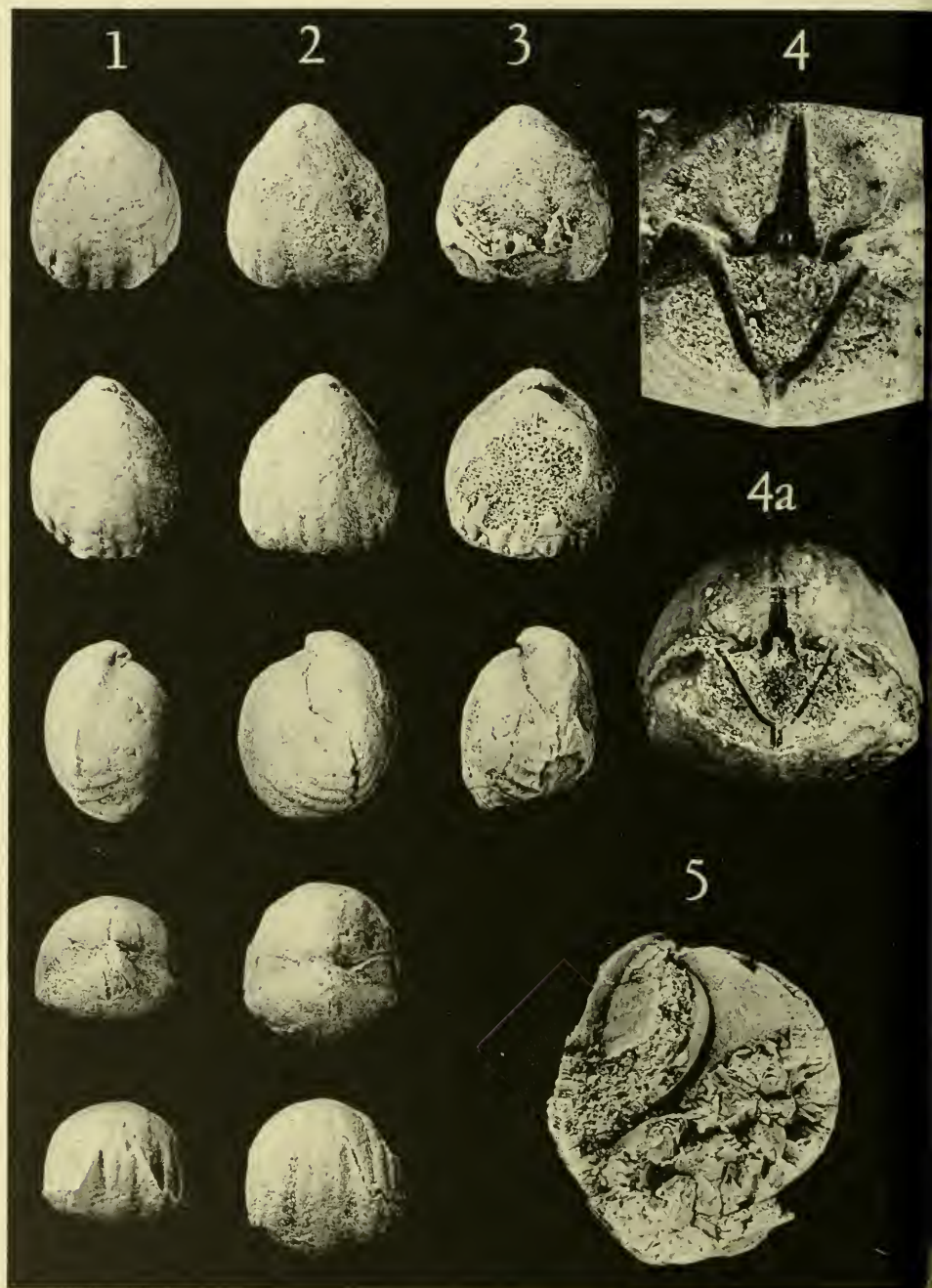
1-1E, *ATRIBONIUM GREGERI*; 2-2A, *ATRIBONIUM ROSTRATUM*;
 3, *ATRIBONIUM PAUPERUM*; 4, *ATRIBONIUM KERNAHANI*.
 (SEE EXPLANATION OF PLATE AT END OF TEXT.)



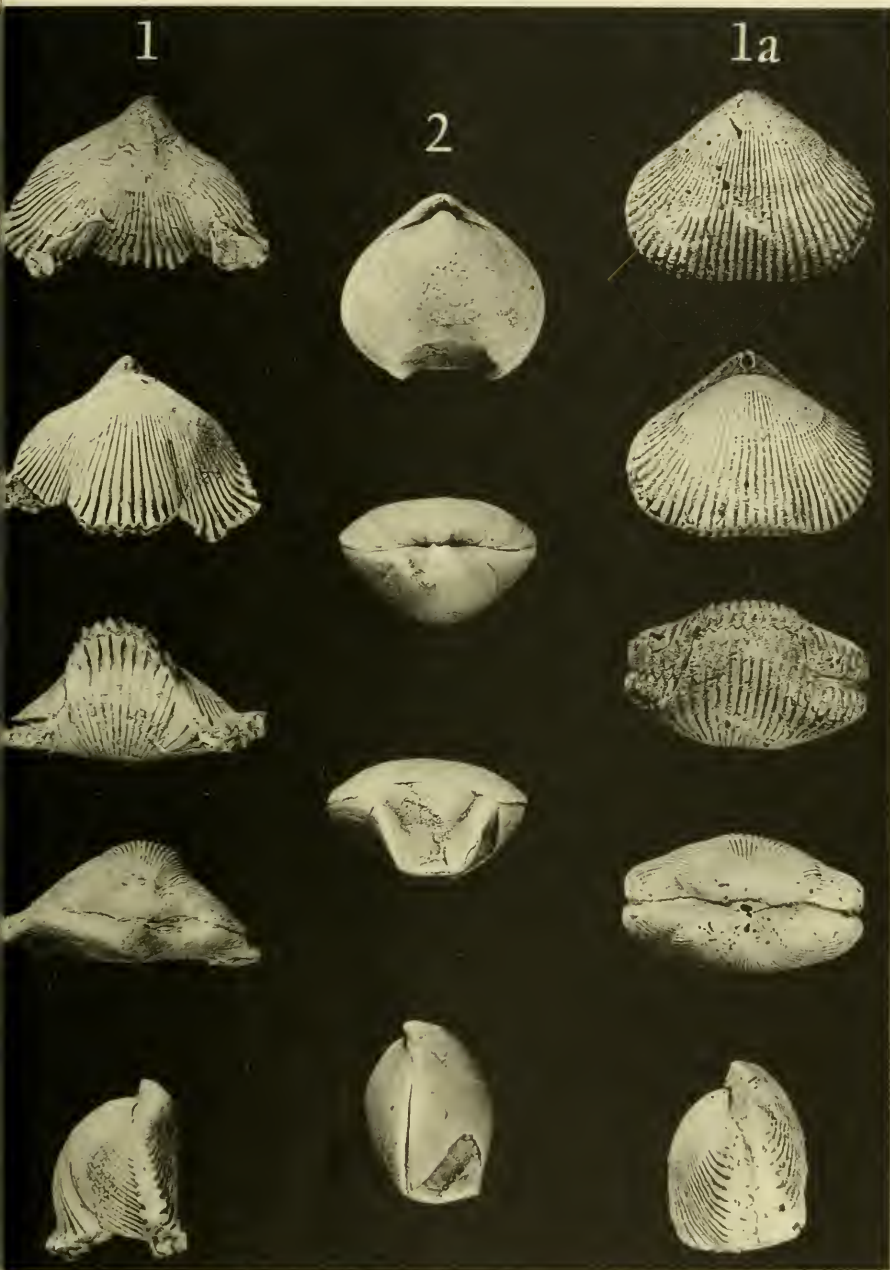
1-2B. *SEDENTICELLULA HAMBURGENSIS*; 3-3A, *SEPTACAMERA* CF. *S. PLICATA*;
 4, *SEPTACAMERA KUTORGAE*; 5, *CAMAROPHORINELLA CAUCASICA*.
 (SEE EXPLANATION OF PLATE AT END OF TEXT.)



1-9. SEDENTICELLULA SACRA
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



1-5, *CYROLEXIS HAQUEI*.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



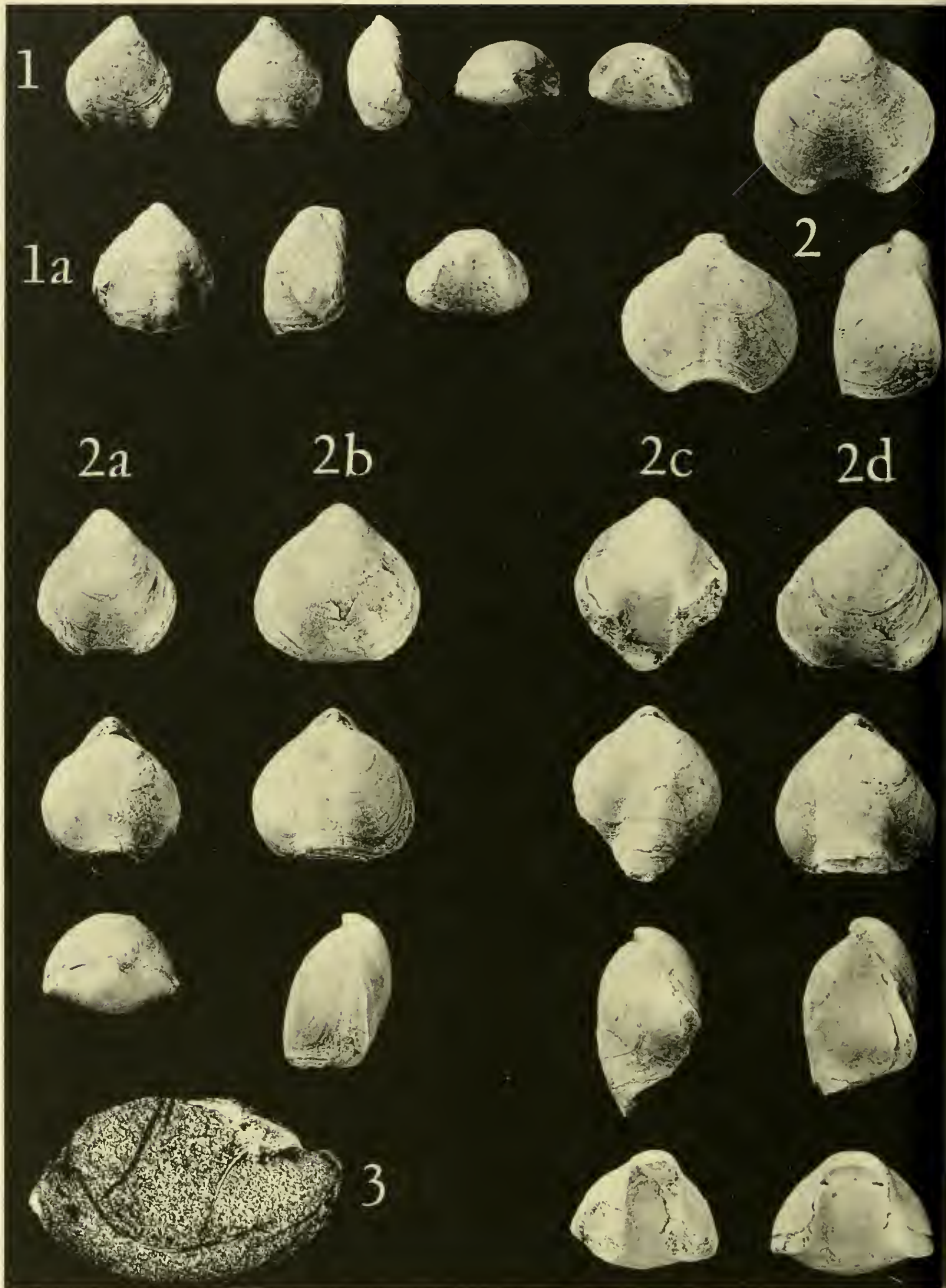
CYCLOTHYRIS VESPERTILIO; 1A, CYCLOTHYRIS COMPRESSA; 2, CAMAROPHORINA ANTISELLA.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



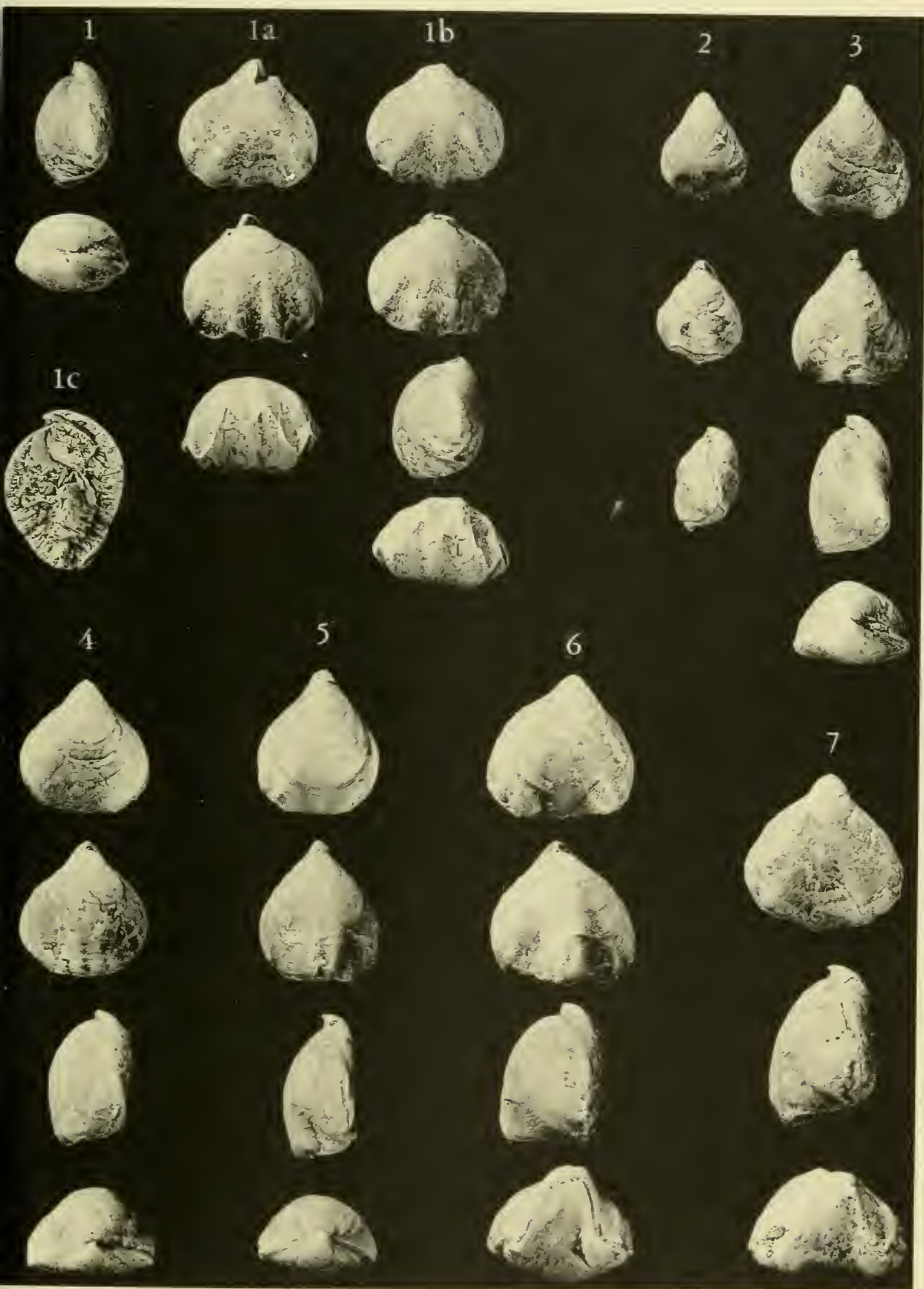
1-1B, CAMERISMA PRAVA; 2-2A, CAMERISMA SAGMARIA; 3-3A, CAMERISMA GIRTYI.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



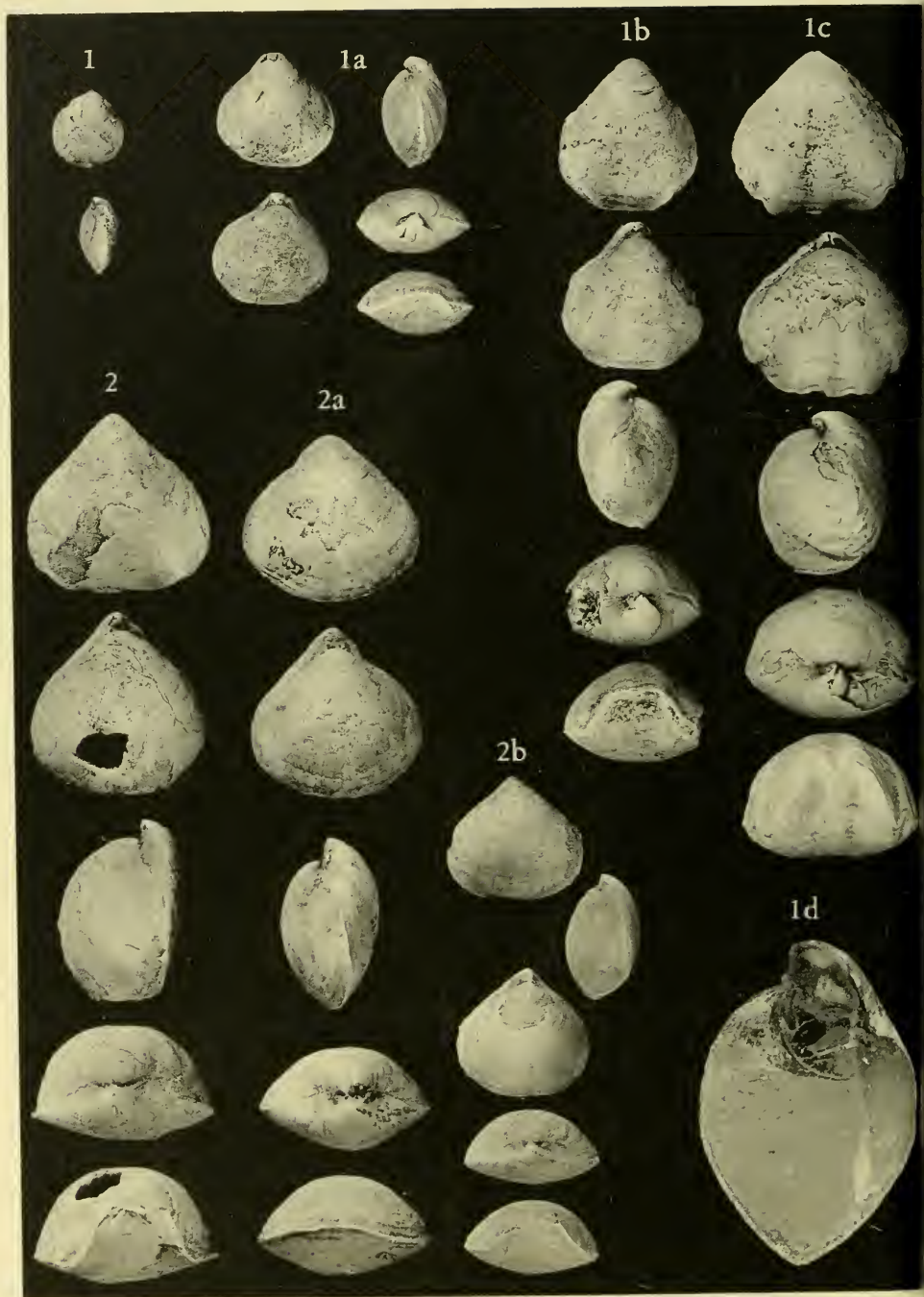
1-1D, PSILOCAMARA RENFROARUM; 2-2C, COLEDIUM BOWSHERI.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



1-1A, COLEDIUM RHOMBOIDALE; 2-3, COLEDIUM ERUGATUM.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



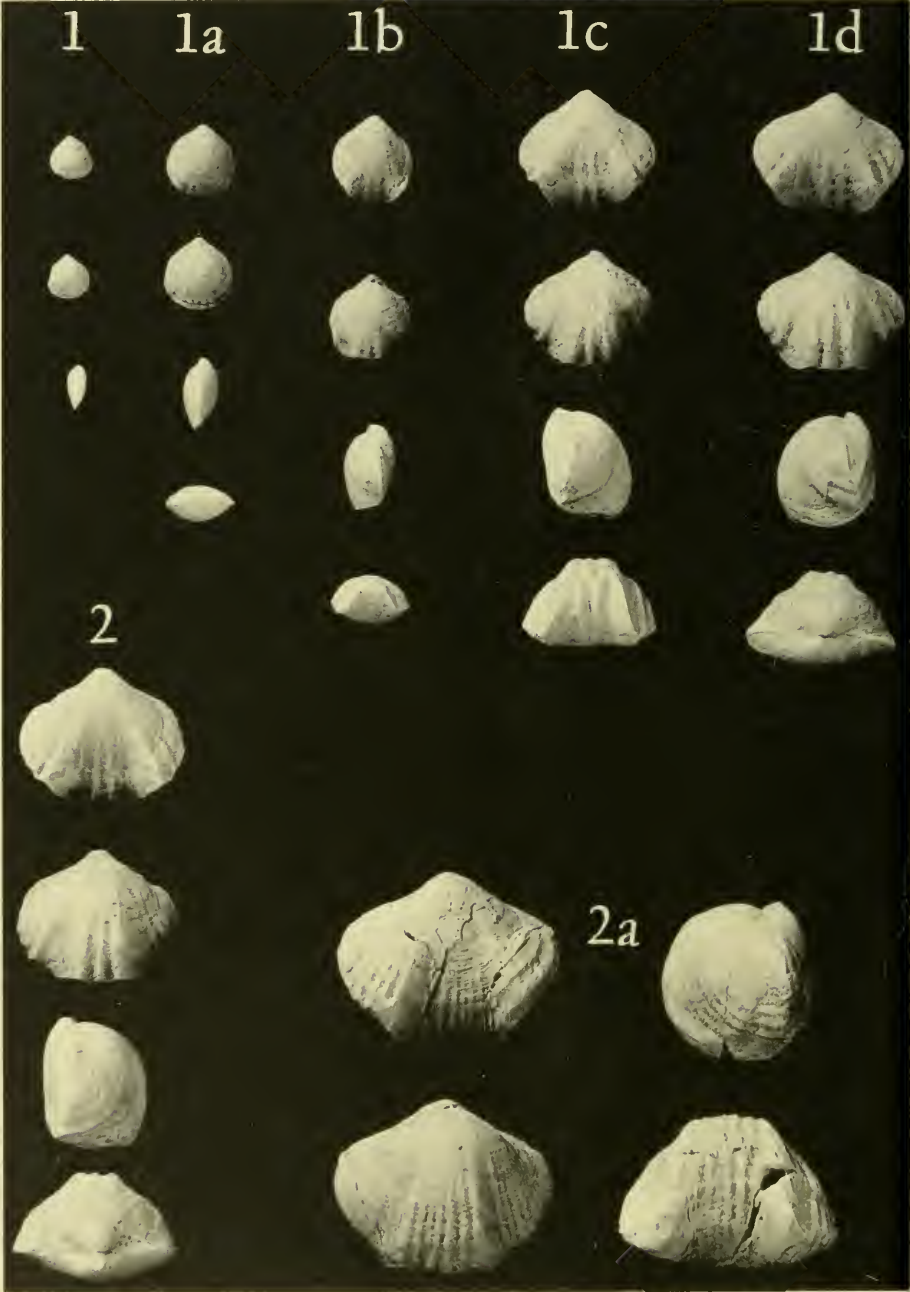
1-1c, COLEDIUM EXPLANATUM; 2-7, COLEDIUM RHOMBOIDALE.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



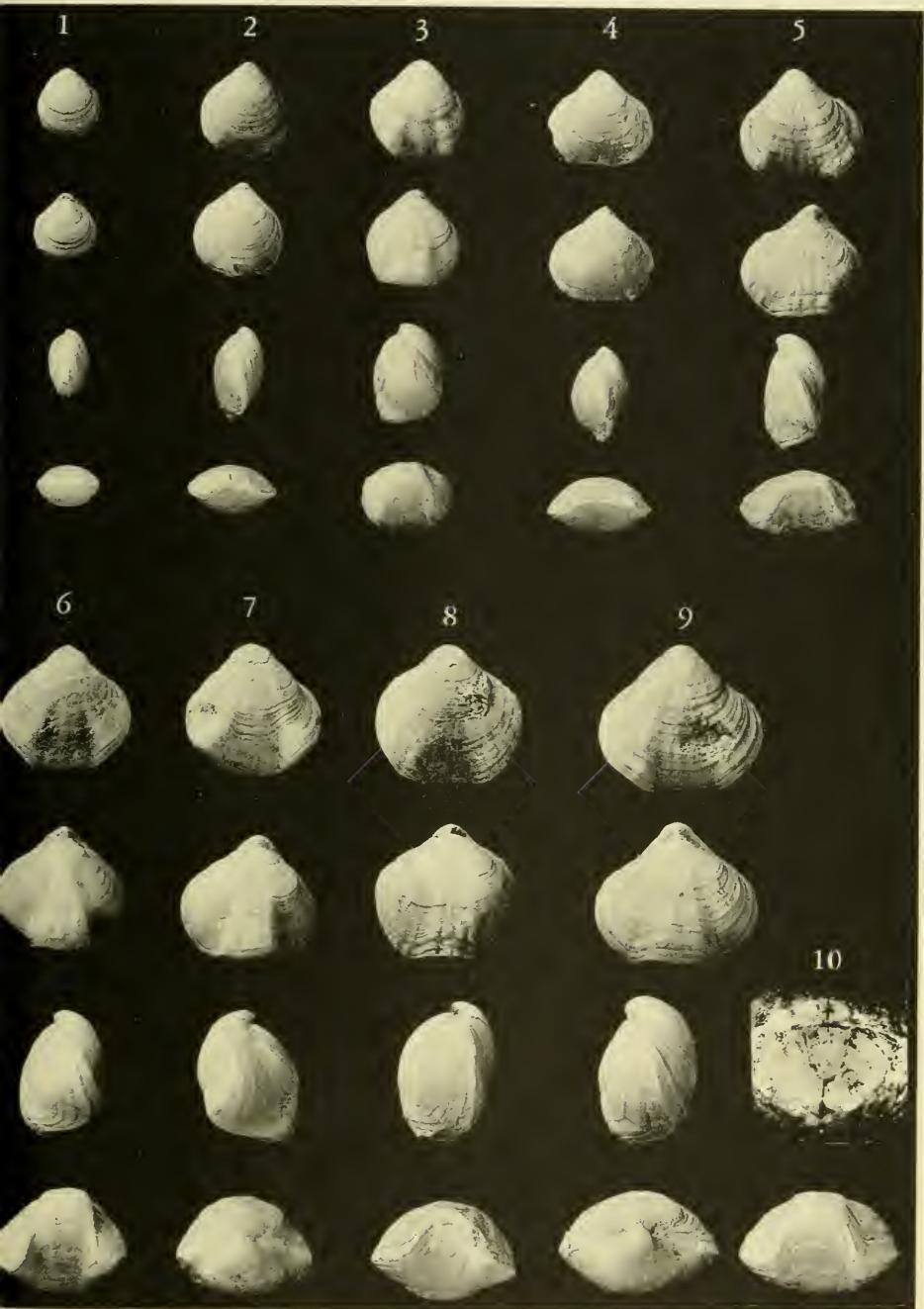
1-1D, COLEDIUM CESTRIENSIS; 2-2B, COLEDIUM ANGARIUM.
 (SEE EXPLANATION OF PLATE AT END OF TEXT.)



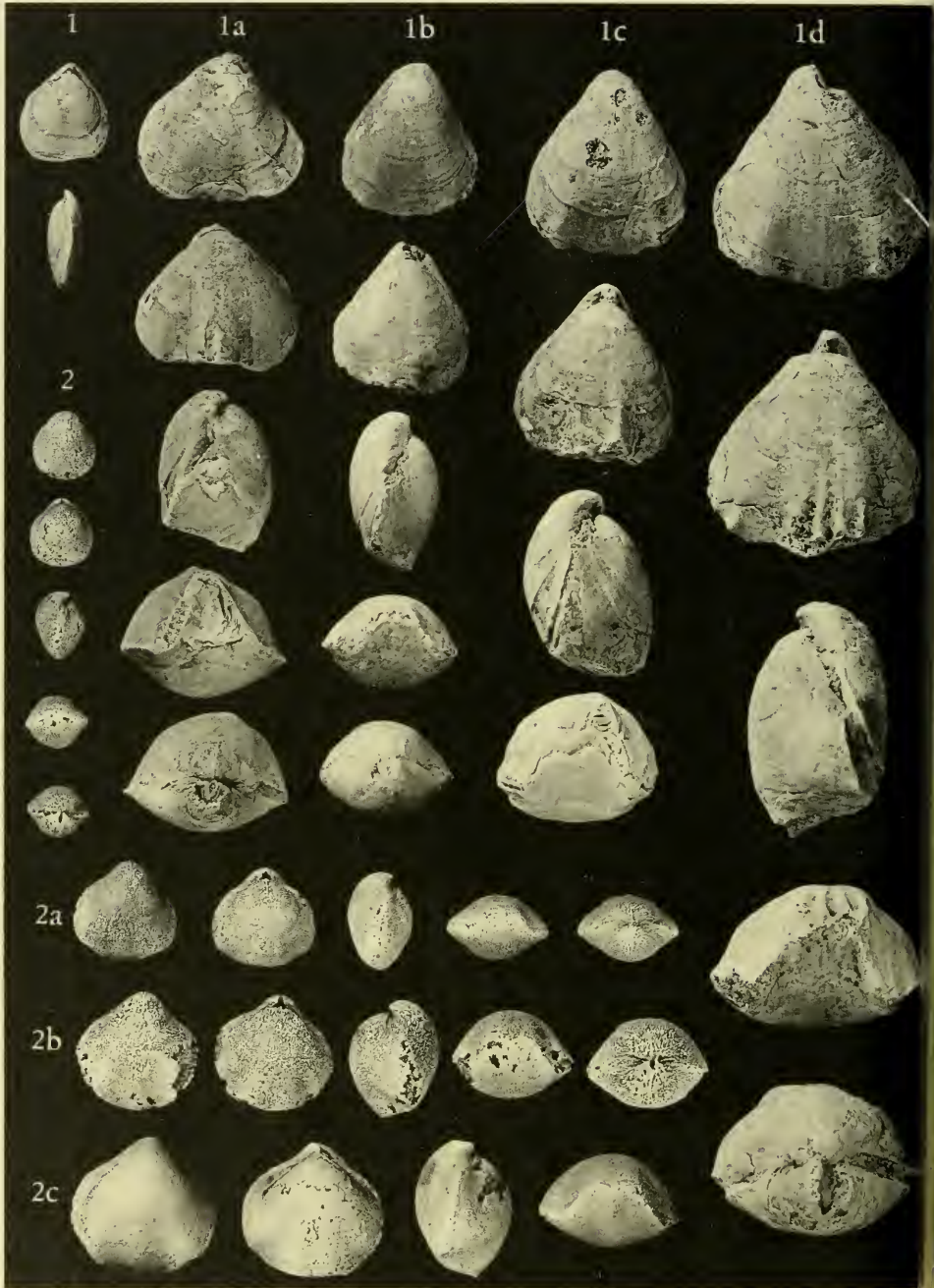
1-2, COLEDIUM TORVUM.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



1-2A, COLEDIUM UNDULATUM.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



1-10, COLEDIUM EVEXUM.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



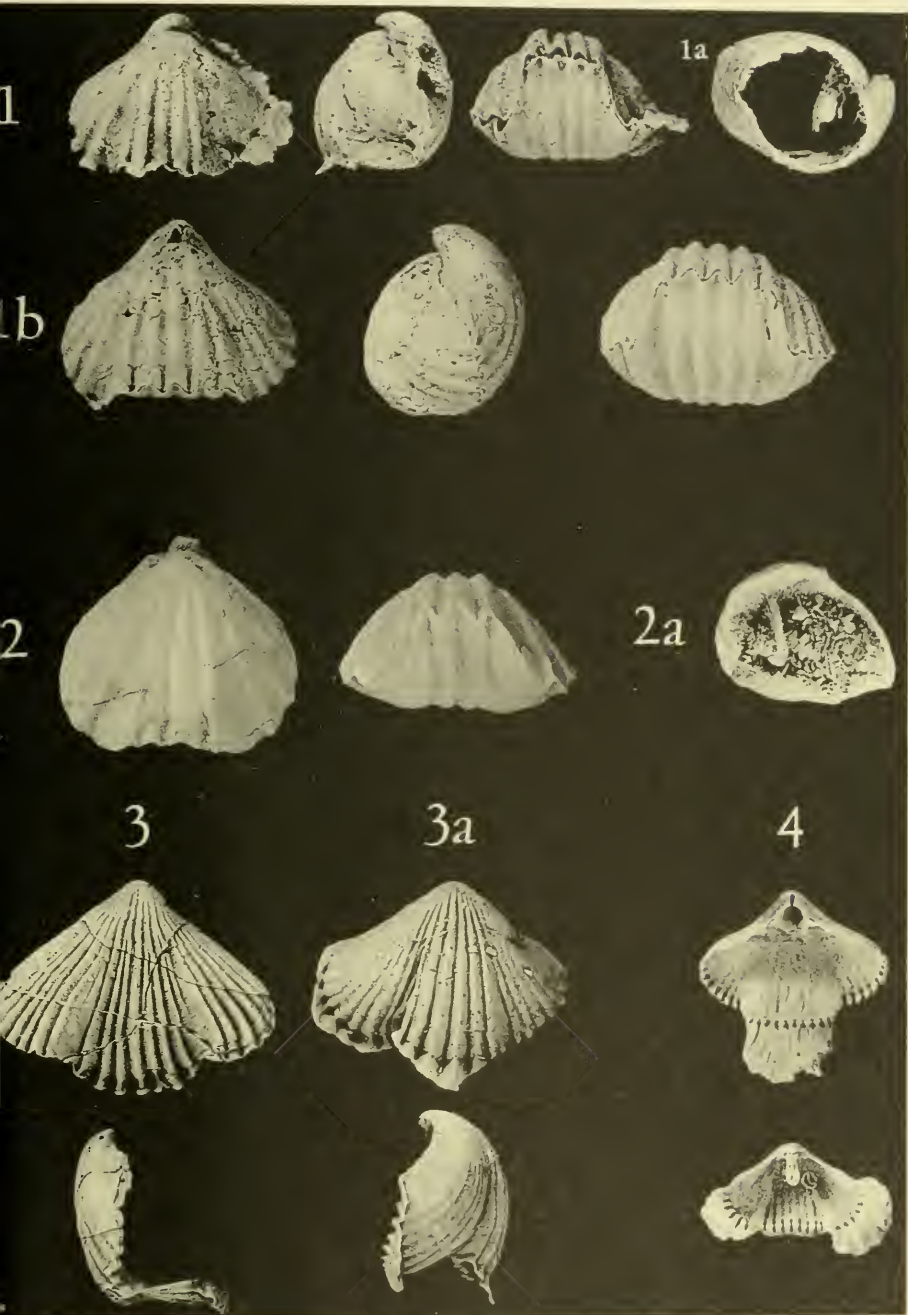
1-1D, COLEDIUM THERUM; 2-2C, COLEDIUM OBESUM.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



1-5B, COLEDIUM DUTROI.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)

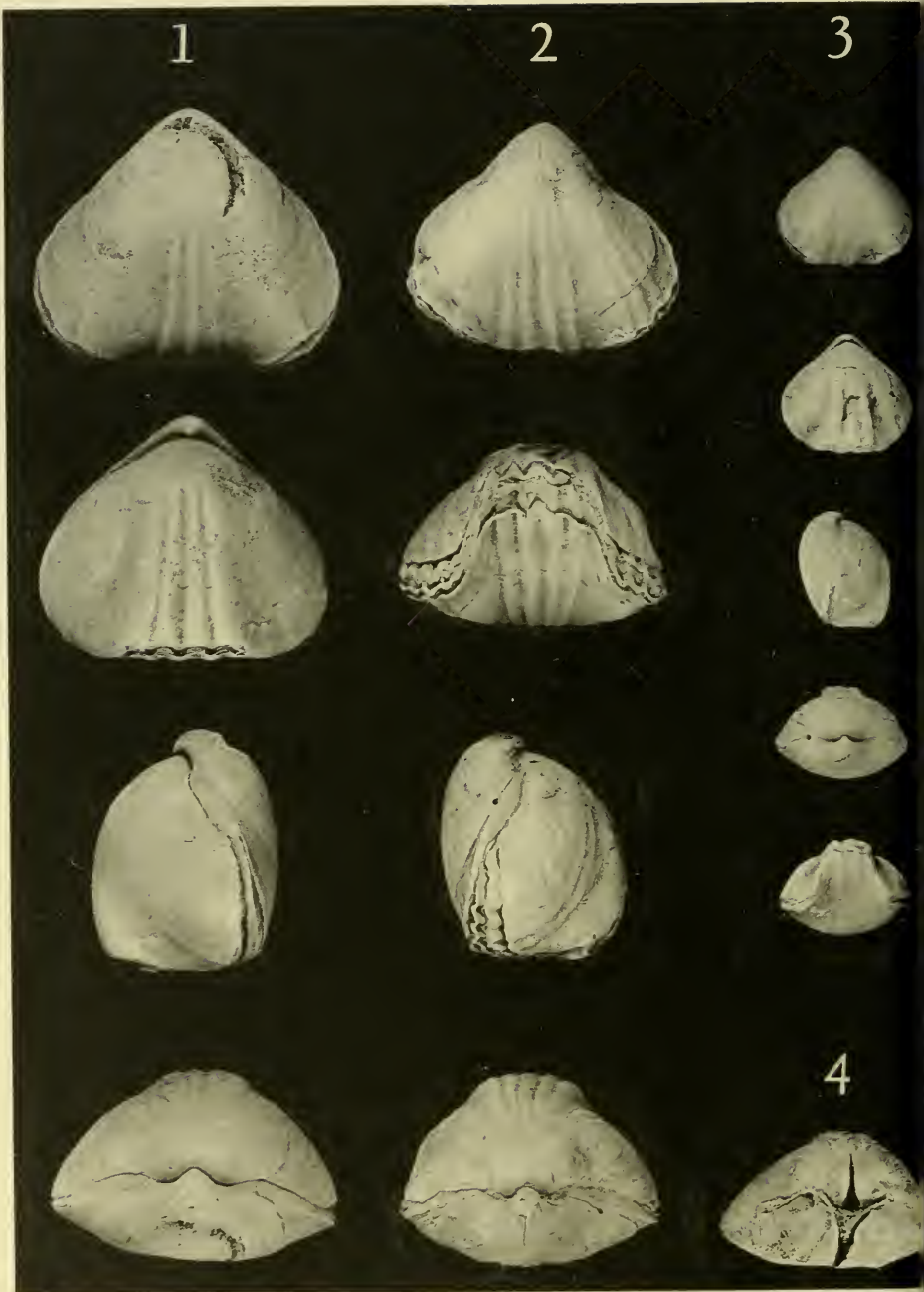


1-1c, COLEDIUM RHOMBOIDEUM; 2, COLEDIUM GLOBULINUM; 3, COLEDIUM PLEURODON;
 4, COLEDIUM NUCULUM; 5-5a, COLEDIUM OPIMUM; 6, COLEDIUM CRASSUM.
 (SEE EXPLANATION OF PLATE AT END OF TEXT.)

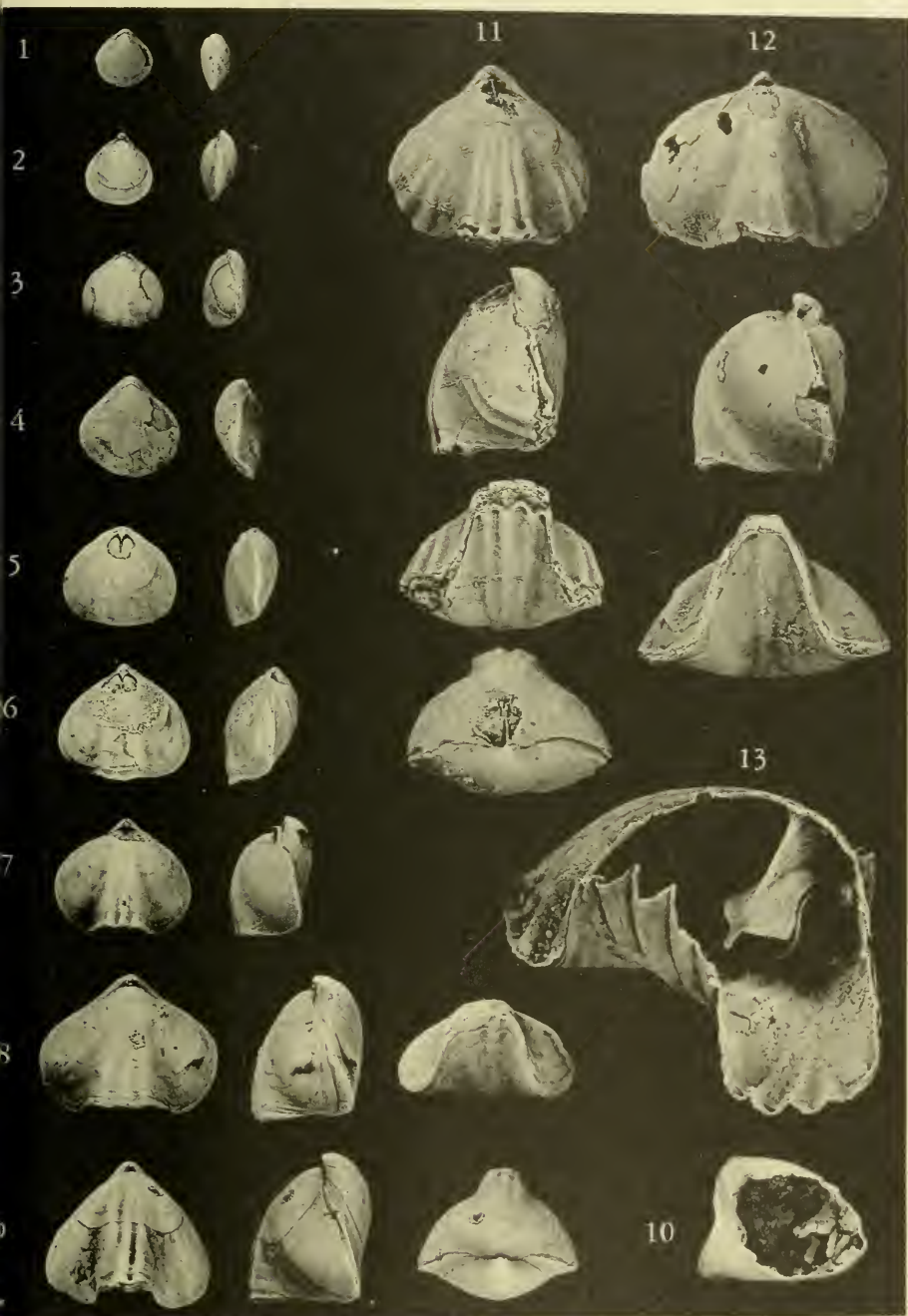


1-1B, *STENOSCISMA HUECONIANUM*; 2-2A, *STENOSCISMA BIPPLICATUM*;
 3-3A, *STENOSCISMA MULTICOSTUM*; 4, *STENOSCISMA KALUM*.

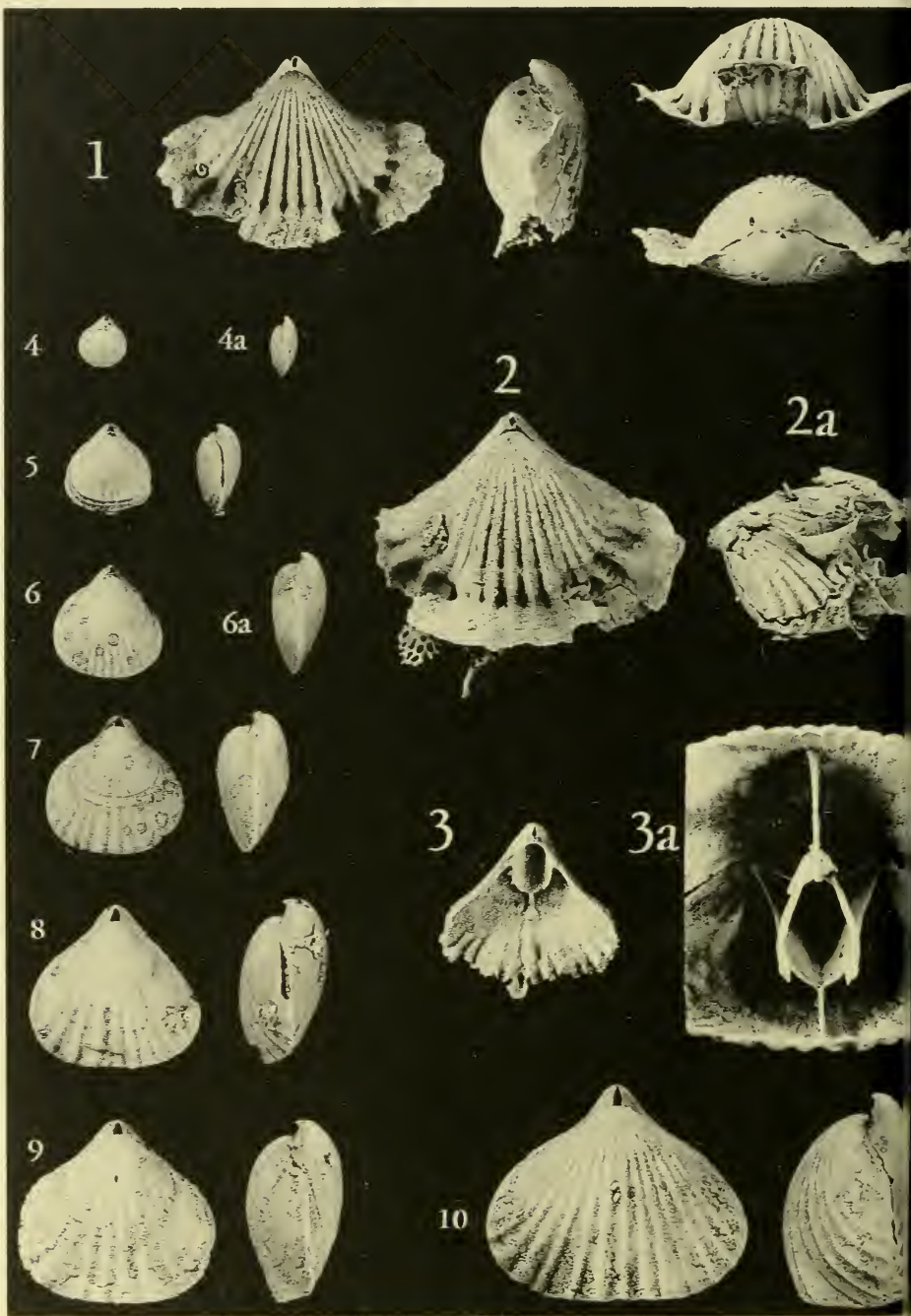
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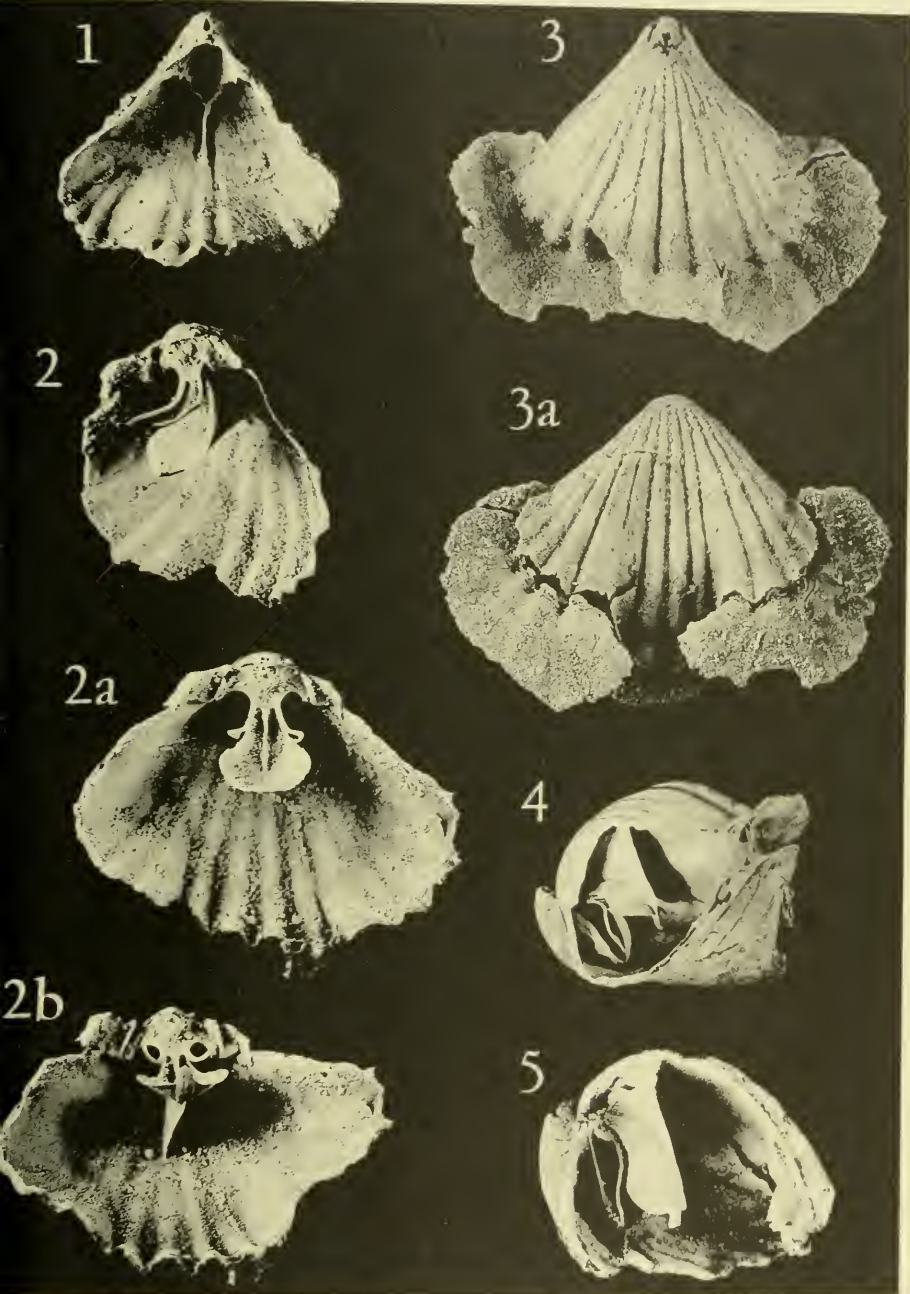
1-4, *STENOSCISMA PURDONI*.
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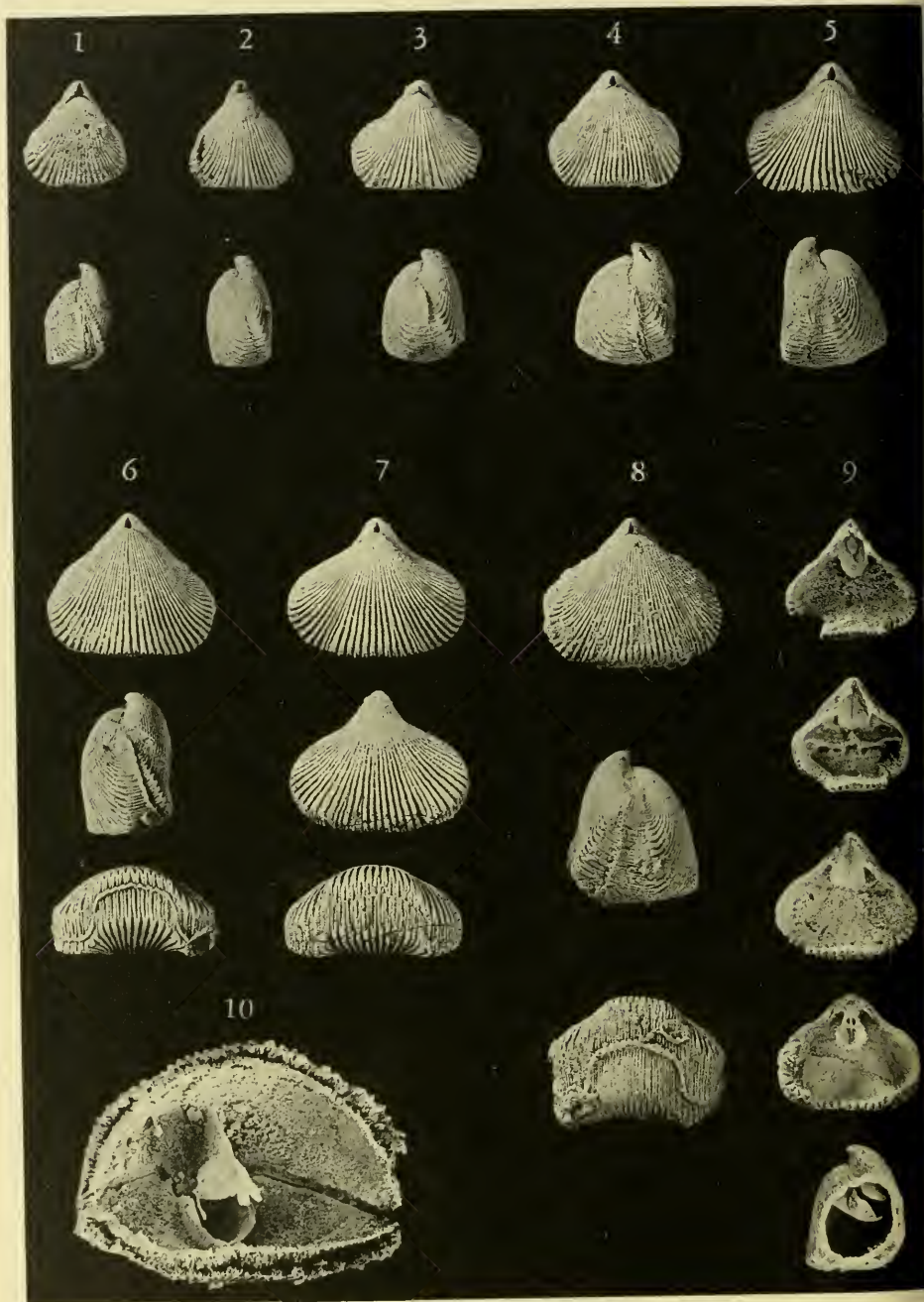
1-12, *STENOSCISMA SCHLOTHEIMI*; 13, *STENOSCISMA VENUSTUM*.
(SEE EXPLANATION OF PLATE AT END OF TEXT)



1-10, *STENOSCISMA VENUSTUM*.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



1-5, *STENOSCISMA VENUSTUM*.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)



1-10, *TORYNECHUS CAELATUS*.
(SEE EXPLANATION OF PLATE AT END OF TEXT.)