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Charles D. and Mary Vaux Walcott
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(WITH EIGHT PLATES)

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U. S. National Museum
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(PUBLICATION 4602)

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INTRODUCTION

Fossil oysters are among the most common and well preserved faunal elements in Cretaceous sediments. With few exceptions, however, they have been ignored in evolutionary studies and biostratigraphy. Although countless species have been described, the taxonomy of the group is confusing and inconsistent. It seems ironic, therefore, that they are one of the groups most suited to modern population systematics. The present investigation attempts to demonstrate the feasibility of detailed systematic and evolutionary study, faunal zonation, and regional correlation based on oysters. It employs simple biometric analysis of large collections, from numerous localities, distinct stratigraphic levels, and diverse sediment types. I have chosen for this purpose a typical lophid species group centered around *Lopha lugubris* (Conrad), and including *L. bellaplicata bellaplicata* (Shumard), *L. bellaplicata novamexicana* n. subsp., and varieties of these forms.

The *Lopha lugubris* lineage is the predominant ostreid species group in Middle and Upper Turonian (Upper Cretaceous) sediments of the Western Interior and western Gulf Coast. These plicate oysters are abundant and well preserved at various stratigraphic levels in the upper Eagle Ford Shale of Texas, the Mancos Shale of New Mexico, and the Carlile Shale of Colorado, New Mexico, and, rarely, Kansas. They are ideally suited for a modern systematic study because the structural complexity of lophid oysters is greater than in many other ostreid types. Detailed analysis of this group provides a good test for the systematic, taxonomic, and evolutionary utility of morphologic features not previously considered by many ostreid workers.

Oysters of the *Lopha lugubris* group characteristically have a rounded, subovate, or subquadrate outline, asymmetrical prosocline shells with curved, opisthogyrate beaks and umbones (exogyroid in some forms), and coarse, bifurcating, radial plicae originating at the umbone on left valves, but variably developed on right valves. The shell is lamellate and moderately inequivalve, with the right (upper) valve flatter and slightly smaller than the left (lower, attached) valve. The valves are denticulate, with small cardinal areas, and a subcentral, comma-shaped muscle impression.

The lineage first appears in Western Interior and Gulf Coast sediments during the late Middle Turonian (zone of *Collignoniceras hyatti* Stanton). The youngest known representatives occur in middle Upper Turonian sediments (zone of *Prionocyclus wyomingensis elegans* Haas). It may range into even younger Carlile strata in the Western Interior, as indicated by scattered reports of small plicate oysters (indeterminate) in uppermost Turonian beds.

The *Lopha lugubris* lineage appears to have had a Gulf Coast origin, or center of dispersal, in the United States, and reached its maximum development in abundance and size in these southern waters. Its immediate ancestor is unknown. Possibly, the lineage arose from the European group of *L. syphax* (Coquand) (Early Cenomanian) or from some Early Cretaceous lophid stock, such as *Lopha marcoui* (Böse). There is a distinct gap, however, in our knowledge of the evolution of *Lopha* in sediments of Cenomanian age where representatives of this genus are not common.

ACKNOWLEDGMENTS

I am greatly indebted to Drs. Norman F. Sohl and William A. Cobban of the United States Geological Survey, and to Dr. Richard S. Boardman of the United States National Museum, for their excellent criticism of the manuscript and many suggestions during the course of the study. Conversations with Dr. H. B. Stenzel of the Shell Development Company were very helpful. Collections were kindly donated to the National Museum by Dr. Bob F. Perkins of the Shell Development Company and loaned by Dr. Donald E. Hattin of the University of Indiana. Specimens that I collected during the period 1958 to 1960 are on loan through the courtesy of the University of Michigan Museum of Paleontology. The drawings

were made by Larry Isham, the photographs by Jack Scott, both of the United States National Museum.

BIOSTRATIGRAPHY

Members of the *Lopha lugubris* group have equivalent stratigraphic distribution in Turonian sediments of Colorado, New Mexico, and Texas (fig. 1). The restricted ranges, broad geographic distribution, and abundance of individual species and subspecies render them useful as stratigraphic tools in regional correlation. In some areas they are the best available indices.

Stratigraphic distribution in Texas.—Lopha bellaplicata novamexicana n. subsp. has not yet been found in Texas. *Lopha bellaplicata bellaplicata* (Shumard) is the oldest known representative of the group on the Gulf Coast, marking a discontinuous faunal zone (zone 9 of Adkins and Lozo, 1951, p. 155) at the top of the Eagle Ford Shale (late Middle and early Late Turonian; Cobban and Reeside, 1952, chart 10b). It has been reported from the upper Arcadia Park Limestone and Shale Member, the upper South Bosque Marl Member (questionably), and the upper few feet of the "Condensed Zone" of Adkins and Lozo (1951, p. 155). Generally the species occurs only in the upper 25 feet of the Eagle Ford, but locally it has been reported ranging through as much as 70 feet of section. It apparently does not range into the Austin Chalk, although reworked fragments of shells have been found in a thin conglomeratic calcarenite bed ("reworked Eagle Ford" zone) which locally lies between the Austin and Eagle Ford, and which has been assigned by many workers to the former.

Lopha bellaplicata bellaplicata is known to occur only in upper Middle Turonian sediments in Texas, above the zone of *Collignoniceras woollgari* (Mantell) (early Middle Turonian) and locally below a widespread disconformity which, in the Western Interior, forms the Middle–Upper Turonian boundary. Faunal associates in the U. S. National Museum and U. S. Geological Survey collections from Texas include an undescribed species of *Inoceramus* closely related to *I. dimidius* White (and ancestral to it), *Cardium pauperculum* Meek, and *Cyprimeria*? sp. or *Tapes* sp. cf. *T. cyprimeriformis* Stanton, all characteristic of the middle Carlile Shale (Blue Hill and Codell Members) in the southern Western Interior. *Lopha blacki* (White) morphologically intergrades with *L. bellaplicata bellaplicata* and comes from approximately equivalent upper Eagle Ford strata. It is here considered a synonym of *L. bellaplicata bellaplicata.*

The zone of *Lopha lugubris* lies predominantly above that of *L. bellaplicata bellaplicata,* but their ranges overlap slightly (fig. 1). At two known localities in Texas, the species are found together in

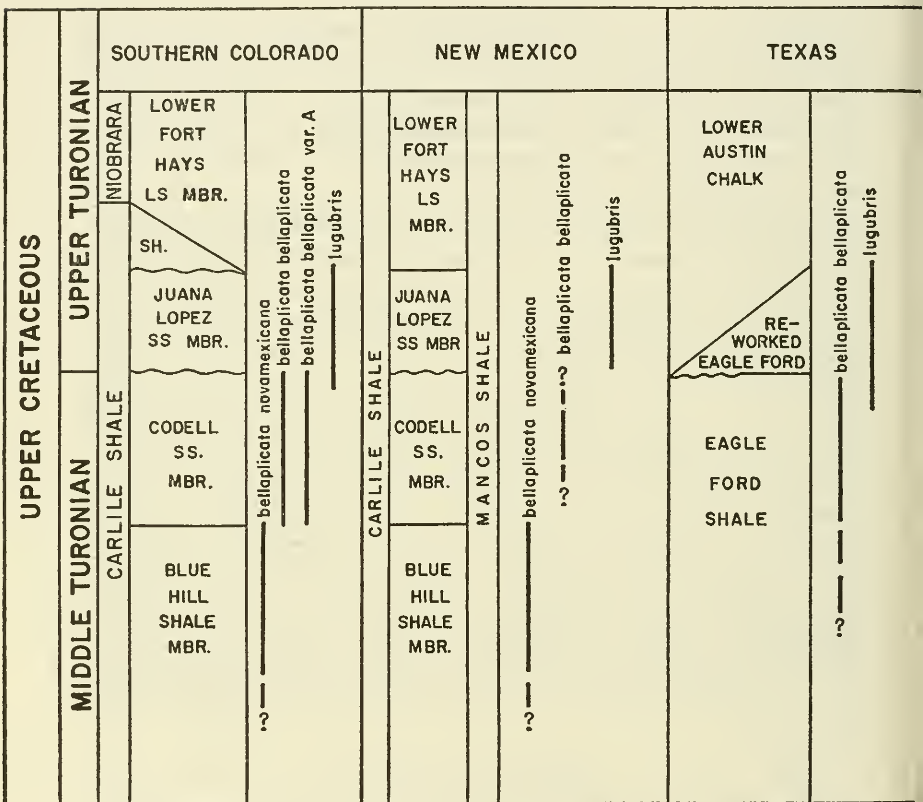


FIG. 1.—Stratigraphic range of oysters in the *Lopha lugubris* group from Colorado, New Mexico, and Texas, and proposed correlations. Colorado stratigraphy taken along the east flank of the Front Range (Cañon City, Pueblo, Huerfano Park areas). New Mexico section interpolated from Cerrillos and Carthage sections of Rankin (1944) and from stratigraphic data on collections made between Cerrillos, N. Mex., and Trinidad, Colo. Texas section generalized for central and northeast Texas.

the upper 2 or 3 feet of the Eagle Ford Shale. They are distinct in this zone of overlap, and do not intergrade. *L. lugubris* does not range below this level, as does *L. bellaplicata bellaplicata.* It ranges upward, however, above the range of *L. bellaplicata bellaplicata,* through the calcarenite bed between typical Eagle Ford Shale and Austin Chalk (fig. 1). A disconformity of unknown magnitude separates the Eagle Ford and the calcarenite at many places. Specimens of *L. lugubris* from this calcarenite are complete and do not exhibit signs of wear. They appear to have lived during deposition of the calcarenite rather than having been reworked from typical upper Eagle Ford Shale, as some workers have suggested. A similar situation exists in the Juana Lopez Member (Carlile Shale) of the Western Interior. The precise age of the "reworked Eagle Ford" calcarenite has not yet been established, but it appears to be lithologically and faunally the southern equivalent of the Juana Lopez.

Stratigraphic distribution in the Western Interior.—The stratigraphic distribution of the *Lopha lugubris* group in the Western Interior is the same as that observed in the Texas Cretaceous sequence (fig. 1), as are the general progression of ammonites and lithologies. The occurrence of *lugubris*-like oysters in Colorado, particularly in Huerfano Park, is of great importance, since it is only here that all members of the group have been found together geographically and their stratigraphic relationships accurately established. In this area, *Lopha bellaplicata novamexicana* occurs sporadically in septarian limestone concretions of the upper Blue Hill Shale Member (late Middle Turonian, lower part of the range of *Collignoniceras hyatti:* fig. 1). *L. bellaplicata bellaplicata* and the variety A are common throughout the Codell Sandstone Member ("Pugnellus Sandstone" of Stanton, 1893 [1894]: late Middle Turonian, upper part of the range of *C. hyatti*). *L. lugubris* questionably occurs in the uppermost Codell Sandstone (based on two poorly preserved specimens), and is common throughout the Juana Lopez Member (Juana Lopez Sandstone of Rankin, 1944; a calcarenite or limestone in Colorado) of the Carlile Shale. The upper and lower contacts of the Juana Lopez are disconformable throughout much of its geographic range in Colorado and northern New Mexico.

In northeastern and north-central New Mexico, and parts of the San Juan Basin, the Coloradoan sequence and distribution of the ostreid elements is similar to that in southern Colorado (fig. 1). The Juana Lopez Member is thicker in New Mexico, however, and locally consists of calcareous sandstone, or of interbedded calcarenites, shales, and sandy units. *Lopha lugubris* occurs throughout this member. Those from the base are possibly distinguishable from those occurring at the top of the sequence on the basis of relatively longer, coarser and less numerous radiating plicae on the older forms. Not enough specimens are available, however, to prove this statistically.

Elsewhere in New Mexico, where the Coloradoan sediments are more uniform (Mancos Shale of most authors), the distribution of members of the *L. lugubris* group is not as well established. *Lopha bellaplicata novamexicana* occurs in the middle Mancos, in the zone of *Collignoniceras hyatti* (late Middle Turonian). The range and position of *L. bellaplicata bellaplicata* is not precisely known, except that it occurs in the middle Mancos below the Juana Lopez calcarenites. *L. lugubris* occurs widely in the middle and basal upper Mancos, in calcarenites equivalent to the Juana Lopez Member. Here it is associated with *Prionocyclus wyomingensis wyomingensis* Meek, *P. macombi* Meek, and *Scaphites warreni* Meek and Hayden, a Juana Lopez assemblage. It has also been reported from slightly younger beds (zone of *P. wyomingensis elegans* Haas: middle Late Turonian).

Stratigraphic conclusions.—Comparison of the Texas, northeastern New Mexico, and south-central to southeastern Colorado Turonian sediments reveals a marked similarity in the sequence of ostreids, ammonites, sediment types (in part), and in the position of the Middle–Upper Turonian boundary, in many places marked by a disconformity. In these areas dark clay shale, locally sandy, silty, and containing lensing siltstones, silty limestones, and sandstones (upper Eagle Ford Shale; Codell Sandstone in many places) underlies this boundary. This unit contains *L. bellaplicata bellaplicata* and species of *Collignoniceras* (*C. hyatti, C.* sp.) in all areas and is locally underlain by sediments carrying *L. bellaplicata novamexicana.* Brown to rusty, sandy calcarenites and calcareous sandstones, locally containing fish tooth, bone, and phosphate pebble conglomerates overlie the boundary, especially where it is marked by a disconformity (Juana Lopez Member; "reworked Eagle Ford" zone), at many localities. This unit contains *L. lugubris* and species of *Prionocyclus* (*P. wyomingensis wyomingensis, P. macombi, P.* sp.) in the great majority of localities where it is found. In both Colorado (questionable occurrence) and Texas, *L. lugubris* is found rarely in the uppermost part of the lower unit (upper Eagle Ford equivalents), partially overlapping the range of *L. bellaplicata bellaplicata.*

I propose that the two sequences are correlative in the manner shown on figure 1, and that they may be correlated on the basis of lophid oysters as well as ammonites. Based on lithologic and faunal relationships, I suggest that the thin calcarenite locally present above the Middle–Upper Turonian boundary and disconformity in Texas should not be assigned to the Austin but rather to the Eagle Ford, forming the highest zone of that formation (zone of *Lopha lugubris*).

The Austin has been considered totally Coniacian in the past, although locally, the lowermost Austin chalks contain a Late Turonian fauna. The calcarenite unit is, without doubt, Late Turonian in age and faunally allied with pre-Austin sediments.

HISTORY

Attempts to treat the *Lopha lugubris* group in the past have encountered the many pitfalls inherent in taxonomic study of the Ostreidae. It has been treated as a single variable species (Stanton, 1893 [1894], pp. 58, 59) and as a series of related species, some of which appear valid, others merely environmental variants of described forms. The problems which have produced such inconsistency are those that have generally affected the taxonomy of ostreids in the past: Inability to distinguish environmental control on shell form from genetic shift; failure to define adequately the limits of specific variability through the study of small and geographically restricted samples rather than analysis of numerous, widely distributed "populations"; application of typologic paleontology; limited knowledge of modern representatives of the family; insufficient stratigraphic data; and others. It is not surprising that the group has a complex nomenclatural history in previously published studies.

Conrad's original description (1857, p. 156, pl. 10, figs. 5a, b) was based on a few small, densely plicate specimens with large attachment areas. These were obtained from calcarenites typical of the lower Juana Lopez member (upper Carlile Shale: zone of *Prionocyclus macombi* Meek and *P. wyomingensis wyomingensis*) in New Mexico and all belong to *Lopha lugubris* s. l. Shumard (1860, p. 608) later recognized a larger, more coarsely plicate, and somewhat older form, *Ostrea bellaplicata,* in the upper Eagle Ford Shale of Texas. White's *Ostrea blacki* (1880, p. 293, pl. 4, figs. 1, 2) appears to be erected on worn, smoother, ecologic variants of *L. bellaplicata bellaplicata.* The two forms occur in approximately time-equivalent strata.

These names were used by a number of authors without much change until Stanton (1893 [1894], pp. 58, 59) placed all members of the group into synonymy with *L. lugubris* Conrad, regarding them as ecologic variants of a single species. Stanton's concept has been generally perpetuated in this country, although the other names are used occasionally in fieldwork, on collection labels, and in unpublished faunal lists. In Mexico, however, Böse (1913, pp. 47, 48) recognized *L. lugubris, L. bellaplicata,* and *L. blacki* as distinct species, but overlooked the different stratigraphic ranges of the first two forms. Only mention has been made of the group since that time, and it has not been widely used in biostratigraphic work. The appearance of *L. lugubris* Conrad on most faunal lists compiled in this century has only limited stratigraphic value in that it is probably used in the concept of Stanton (1893) and indicates an age no more refined than Middle and Late Turonian.

STUDY OF FOSSIL OSTREIDAE

The Ostreidae, and in particular *Ostrea, Crassostrea,* and related genera, are among the most variable of shelled animals. The animal readily adapts to a number of environmental situations without significant change in morphology of the soft parts. Gross shell form, on the other hand, is greatly affected by the surrounding environment in many species. Long, narrow, straight shells are produced in strong currents; quiet water favors more rounded, broader shells; crowding produces elongate, irregular, laterally compressed forms; the depth and size of the mature shell is related in some groups to the amount of exposure in intertidal areas; high-energy shallow-water environments produce heavier-shelled, more prominently ribbed forms than do deep, quiet-water niches; some ostreids form imbricate frills to keep above soft mud and shifting sand bottoms, and so on. Many morphologic features of the shell, therefore, are highly variable within a single species, and must be analyzed with care. This is particularly true in regard to shell outline, convexity, and strength of surface ornamentation. Other structures, less affected by environmental variation (shell structure, prodissoconch, denticles, position and shape of muscle scar, cardinal area), form a more reliable basis for classification.

Finally, modern types of Ostreidae (*Ostrea, Crassostrea,* etc.) are generalized and successful animals, and have been exceptionally conservative in their evolution. They have undergone little basic change in shell form since they became established as an important group during the Mesozoic. Variants of living species are in many cases indistinguishable from certain Cretaceous forms when only a few shells are compared. Closely related species exhibit considerable morphologic overlap, and the differences between them are commonly subtle.

In studying the *Lopha lugubris* group, resolution of the problems inherent in biologic interpretation of the Ostreidae required analysis of large suites of specimens, including growth series, from many localities and sediment types, representing a broad range of environments. Only in this way could normal variation limits, ecologic control on shell form, and genetic shift be recognized. During the course of this study, I was fortunate to have at my disposal the large and well-documented collections of the U. S. National Museum, and Denver and Washington collections of the U. S. Geological Survey. These were supplemented by my own collections made over a period of 5 years in the Western Interior, and by small lots lent or donated for this study by various individuals. Several hundred measurable specimens, including ontogenetic series, form the basis for species descriptions and observations on stratigraphic distribution, variation, ecology, and evolution.

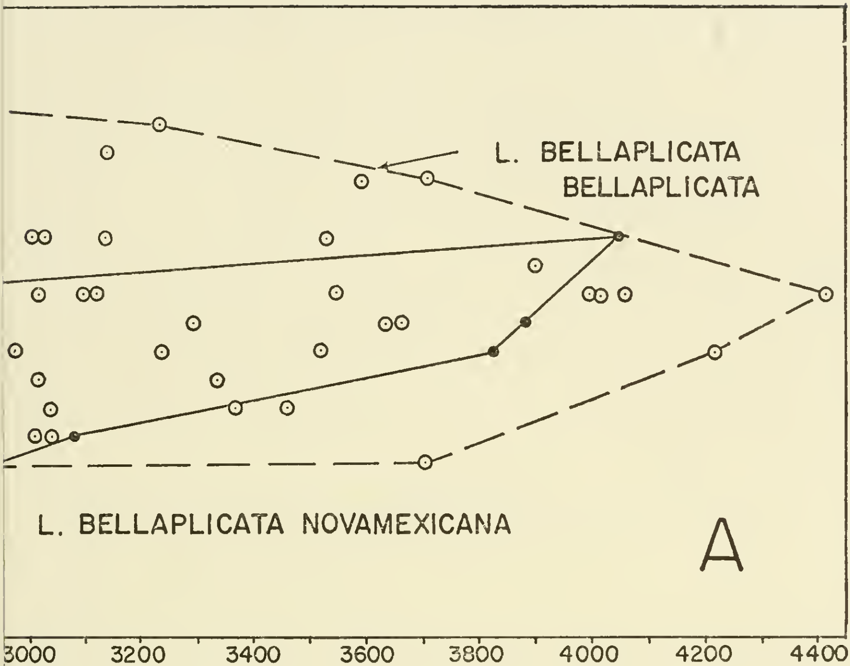
Time equivalency of the various fossil beds from one area to another was established on the basis of ammonites, species of *Inoceramus,* and widespread disconformities. The ammonite and inoceramid species used are widespread, well-established faunal indices occurring in a variety of sediment types (representing various environments) and apparently subject to minimal facies control.

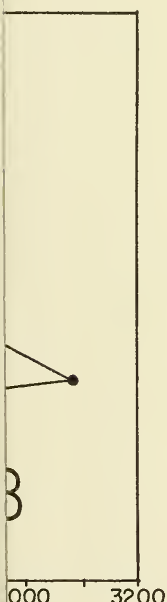
Simple biometric analysis of all available morphologic features, using graphs, charts, and simple ratios, indicated structures which might be useful in lophid taxonomy, and proved to be sufficient for the recognition of specific differences, ontogenetic development, and evolutionary trends within the *Lopha lugubris* group. Features that were employed in these aspects of the study are: Maximum adult size; basic ornament pattern; normal valve outline; the distribution of convexity on both valves; juvenile ornamentation; extent of valve covered with plicae; number, size, and bifurcation rates of the plicae at given intervals; plication density in a given area or distance; gross characteristics of the concentric ornamentation; differences between the ornamentation of the auricles and main body of the shell; relative development of the auricles and auricular sulci; angle of inclination of the beaks and umbones, and independently of the valve; curvature and position of the beaks and umbones; angle of the posterodorsal slope; relative size and development of various parts of the cardinal area; density and extent of the denticles on the dorsolateral valve margins; relative size and position of the muscle scar; and in some cases, the relative size, position, and inclination of the attachment scar. To this list might be added comparison of various ratios, such as length to height, length of the auricle to length of the shell, and others.

Although ontogenetic studies have not been attempted to any extent with fossil oysters, distinct and commonly abrupt changes in shell morphology with growth are common, especially in the more ornate groups, and can probably be tied to developmental phases of the animal. In this study the terminology of Hyatt (1894, pp. 349-647)—nepionic (babyhood), neanic (youth), ephebic (adult), and gerontic (senile)—is used to characterize growth periods between major morphologic changes in the shell. In oysters, and more specifically in the *Lopha lugubris* group, the nepionic stage is represented by the prodissoconch, the neanic (spat) stage by part or all of the umbo. The nepionic–neanic transition is marked by development of adult hinge characters, change in shell shape (usually from rounded to dorsoventrally elongate), and development of coarser concentric ornamentation. The ephebic stage is characterized by adult ornamentation (the plicae in *Lopha*), change in shell shape including development of auricles, folds, etc, well-defined denticles and muscle insertion areas, and further differentiation of the cardinal elements. The neanic–ephebic boundary is marked in some lophids by the abrupt appearance of plicae, development of auricular salients in the marginal outline, and differentiation of the resilifer and lateral cardinal plates on the hinge line. The gerontic stage is characterized by flattening and flaring of the ventral and lateral shell margins, deterioration of the ornament pattern, decrease in prominence of the radial ornament, crowding and increase in prominence of the concentric ornament, and decrease in prominence of structures related to sexual maturity and reproductive function.

Graphs and drawings depicting ontogenetic trends in members of the *Lopha lugubris* group are shown in figures 2-4, 6, 9, 11-18.

Geographic variation and environmental control on shell morphology were determined by comparing a number of "populations" from time equivalent but lithologically distinct sediments in different areas (fig. 14). Only *L. bellaplicata bellaplicata* exhibits significant variation in both respects. Comparison of related forms from a number of different stratigraphic levels, but from similar sediments (roughly representing similar environments) is the most satisfactory method of demonstrating evolutionary change in the lineage. Unfortunately, this method is not wholly applicable to the *L. lugubris* group, since there is little overlap of exact sediment type between faunal zones. Evolution of this group, therefore, is necessarily determined by comparing total variation plots of forms from different stratigraphic levels, irrespective of lithology (figs. 2-9). Such a system of separating evolutionary change from geographic or environmental variation is





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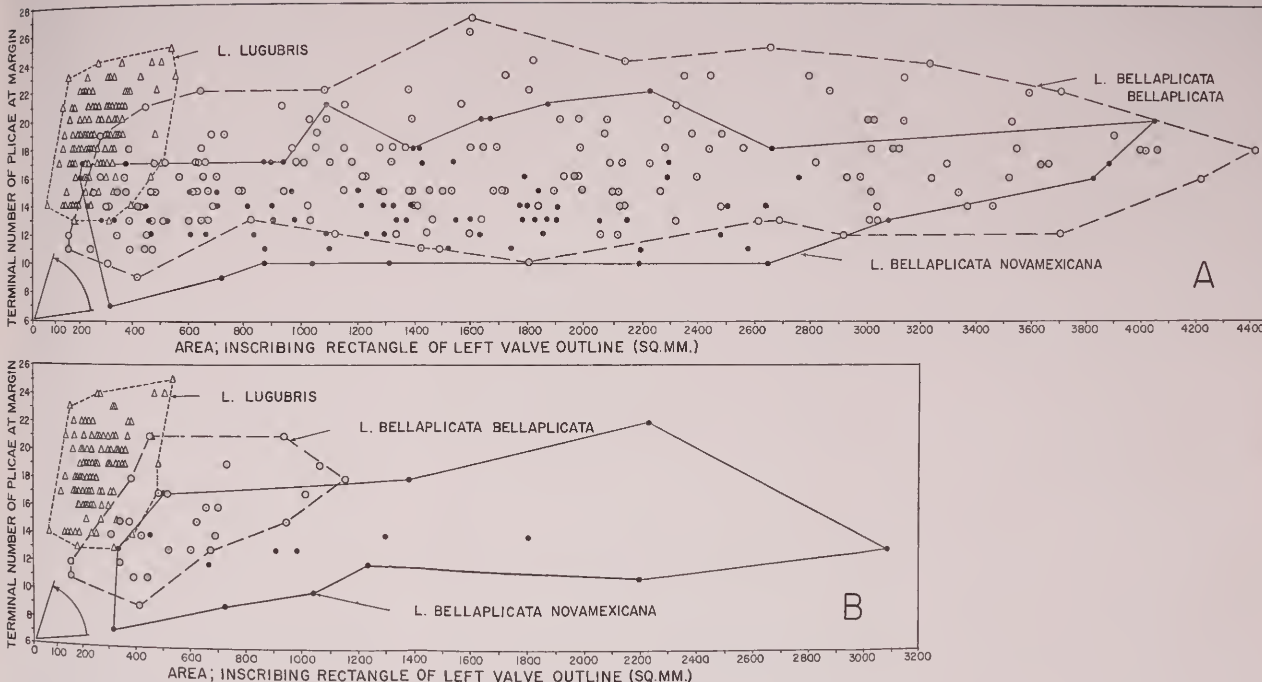

Fig. 2.—Evolution of the *Lopha lugubris* group. Increase in the density of the plicae, number per unit area, on left valves of progressively younger species. A, Scattergram for all specimens measured, from Colorado, New Mexico, Texas. B, Scattergram of Colorado sample only. Arrows in lower left-hand corner of each graph indicate direction of increasing plication density as shown by hypothetical regression lines visually fitted to plots of terminal species in group.

admittedly somewhat idealized. Obviously, it is not possible to evaluate properly all the environmental factors acting on these shells in different areas. The chemical environments of two very similar sandstones may have been entirely different and may have had a profound effect upon the type of shell produced in each area. Analysis of chemical aspects of the paleoenvironment is difficult or impossible in most coarse clastic sediments, and is well beyond the scope of this study. It should be understood that in dealing with environment here, I am dealing in generalities and am cognizant of the limitations this places on the accuracy of my interpretations.

Gross morphologic similarities in form, ornament pattern, development of the auricles, the cardinal area, and the muscle scar, in addition to detailed morphologic overlap in marginal variants of consecutive species clearly point out the close relationships of members in the *Lopha lugubris* group and suggest that they represent a continuous evolutionary sequence, without major break.

EVOLUTION

Several of the morphologic characters which are most important in the differentiation of species and subspecies of the *Lopha lugubris* group demonstrate significant evolutionary trends (figs. 2-9), most of them chronoclinal. These reflect, in part, gradual adaption of the lineage to a slowly changing regional environment characterized by regression and shallowing of the interior seas, increased wave and current action, and increased turbidity. The scope of these changes from one level to another is well beyond the normal ecologic variation caused by similar shallow water conditions in any member of the group during its existence.

In graphing evolutionary trends in the *Lopha lugubris* group, structures were compared wherever possible at equivalent ontogenetic stages on the three principal species and subspecies. Comparison of the terminal number of plicae at the margin of adult valves represents such a plot and can be analyzed irrespective of the differences in size range shown by *L. lugubris* when compared to subspecies of *L. bellaplicata.*

In addition to these plots, it seemed desirable to employ another type of comparison in which structures of adult valves from the three forms of *Lopha* were contrasted at equivalent sizes (i.e., at 20 mm. height) (figs. 6a, 7c). The purpose of this type of plot is twofold: (1) It provides a basis for morphologic comparison of the species and subspecies at equivalent sizes, and a test of their genetic

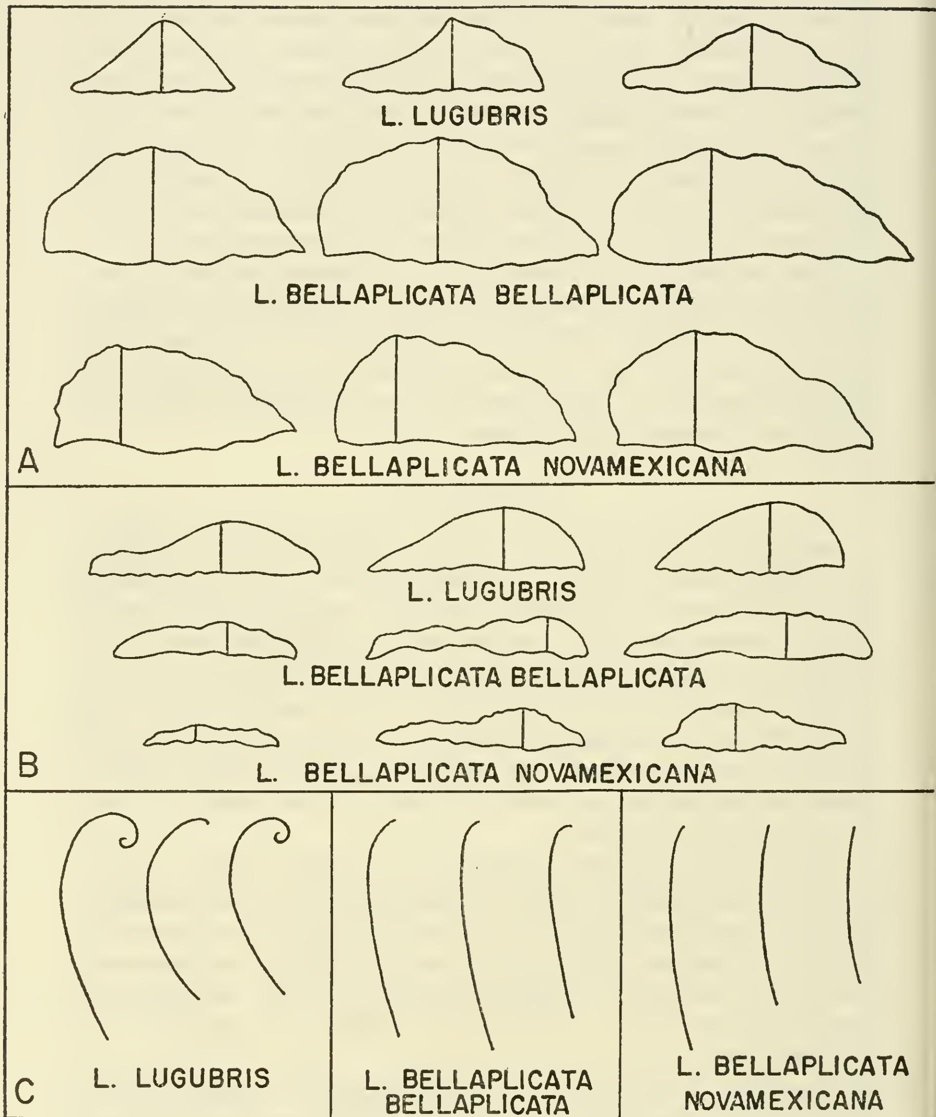

FIG. 3.—For explanation, see opposite page.

distinction. (2) At the same time it demonstrates evolutionary trends within the group in absolute measurements. These trends are not as well shown by this type of plot as they might be by comparing structures at the margins of adult shells, where morphologic differences are emphasized, but they are validly illustrated and significant because even this method essentially compares structures at an approximately equivalent stage of development.

Plots of structures comparing them at a constant height were made within the ephebic part of the shell for each species and subspecies; thus, only adult structures were compared. Ephebic development starts at about 10 to 15 mm. height on all forms, the difference in adult size between *L. lugubris* and *L. bellaplicata* (both subspecies) representing mainly differences in rate and amount of ephebic growth. Since *L. bellaplicata bellaplicata* and *L. bellaplicata novamexicana* have nearly equivalent size ranges, comparison of any structure at a given height on both is essentially a comparison made at equivalent ontogenetic stages. Because adult shells of *L. lugubris* attain a much smaller size, they theoretically should not be ontogenetically comparable with subspecies of *L. bellaplicata* at a given height. Such a comparison is valid however because the ephebic morphology of this species is strikingly constant. The plicae do not normally bifurcate (fig. 6b and c) and their number is relatively constant anywhere on the adult portion of the shell. In addition, beyond 20 mm. height, the width of the plicae and sulcae remains relatively constant. Since ephebic structures are so uniform in *L. lugubris,* and values obtained

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FIG. 3.—Evolutionary trends demonstrated by members of the *Lopha lugubris* group. A, Comparison of cross sections through normal left valves. Beak is to the left. Note general decrease in overall convexity, ventral migration of the high point of the valve (illustrated by vertical lines through cross sections) through time. B, Comparison of cross sections through right valves, beak to the right. Note increase in relative convexity and shift in high point of valve (illustrated by vertical lines through each cross section). C, Comparison of midline traces of typical left valves showing decrease in curvature of beaks, and in overall curvature of shell through time. Beaks dorsal in each case. Specimens: A, Top row, left to right, U.S.N.M. 132157, U.M.M.P. 43472, U.S.N.M. 132154; middle row, left to right, U.S.N.M. 132307, 132243, 8024b; bottom row, left to right, U.S.N.M. 132276, 132288, 132272. B, Top row, left to right, U.S.N.M. 132164, 132198, 132168; middle row, left to right, U.S.N.M. 132306, 132305, 132244; bottom row, left to right, U.S.N.M. 132265, 132286, 132287. C, *L. lugubris,* left to right, U.S.N.M. 132157, 132159, 132156; *L. bellaplicata bellaplicata,* left to right, U.S.N.M. 132225, 132224, 132222; *L. bellaplicata novamexicana,* left to right, U.S.N.M. 132275, 132267, 132263.

in measuring them do not vary significantly from one point to another, they are comparable at any given height with those of *L. bellaplicata* (either subspecies) regardless of whether or not they represent an equivalent stage of ephebic development.

The absolute height of the smooth stage increases in progressively younger species of the *L. lugubris* group (fig. 8), and its evolution is characterized by transgression of its ventral margin from the neanic to the ephebic part of the shell. The smooth stage terminates in the early to middle neanic stage of *L. bellaplicata novamexicana,* and in the middle to late ephebic stage of *L. lugubris.* Measurements of the height of the smooth stage used in plotting evolution are therefore not ontogenetically comparable for the three forms.

Correspondingly, the number of primary plicae arising at the edge of the smooth stage have also been measured at different ontogenetic stages. These are more readily comparable than the height of the smooth stage, however, because on many specimens of *L. bellaplicata* (both subspecies) and a few *L. lugubris* the number of primary plicae can be directly contrasted at the neanic–ephebic boundary. Although the plicae arise early in the ontogeny of the subspecies of *L. bellaplicata,* they do not undergo extensive bifurcation until the early ephebic stage. The number of plicae at the neanic–ephebic boundary therefore generally reflects the original number of primary plicae at the edge of the smooth stage. In *L. lugubris* the plicae normally arise at a later developmental stage, but on rare specimens with a small attachment scar, also arise near the neanic–ephebic boundary. In these specimens, the number of primary plicae is equal to the number found in specimens where the plicae arise at a later developmental stage. This indicates that the number of plicae is not ontogenetically controlled in *L. lugubris,* and relatively constant in number regardless of where they arise on the shell. Therefore, there is some validity in comparing the initial number of primary plicae on *L. lugubris* with subspecies of *L. bellaplicata,* despite the variation in ontogenetic stage at their first appearance.

Important evolutionary trends noted in progressively younger Turonian representatives of the *Lopha lugubris* lineage are:

1. Decrease in the maximum size attained by the species (fig. 2).

2. Slight decrease in the relative convexity of the left (lower, attached) valve, and ventral migration of the high point of the valve (figs. 3a, 4a, b).

3. Gradual increase in the relative convexity of the right (upper, free) valve, particularly in the umbonal region (fig. 3b).

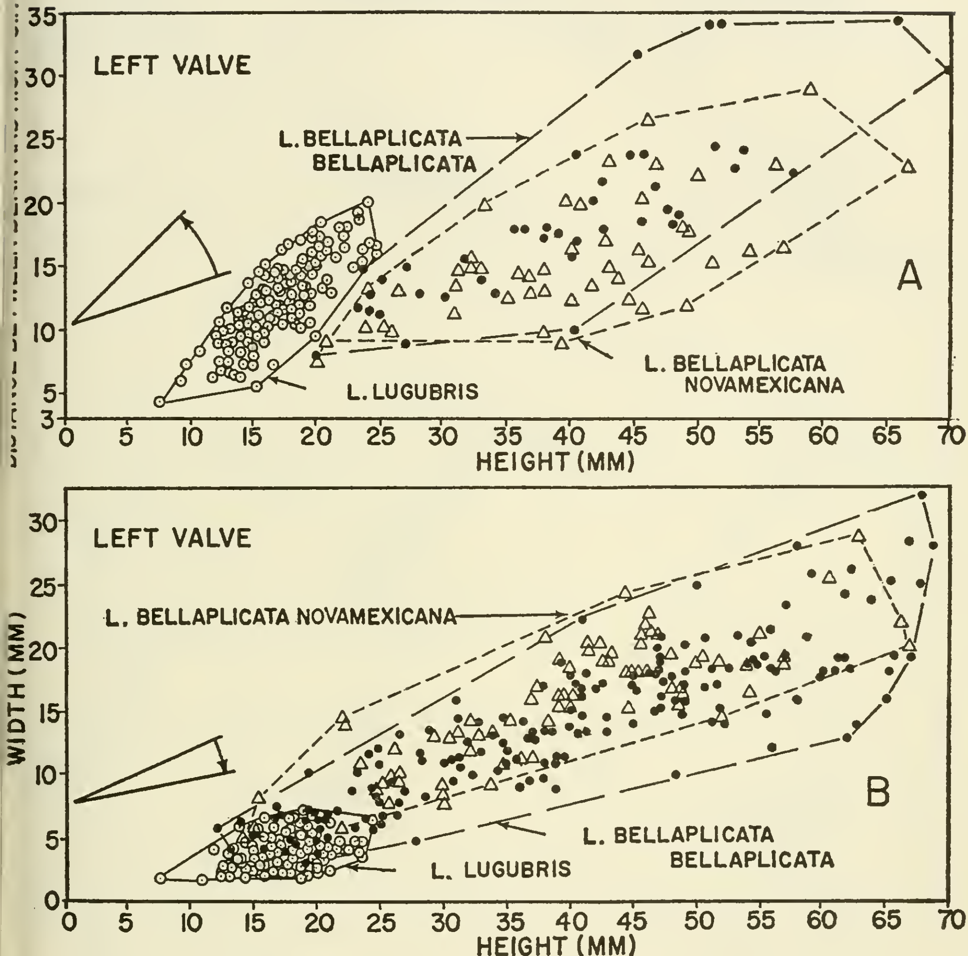

FIG. 4.—Evolution in the *Lopha lugubris* group. A, Scattergram showing relationship between valve height and the distance between the beak and high point of the left valve, measured parallel to height. Note ventral shift of the high point in progressively younger forms. Arrow in lower left-hand corner denotes direction of ventral migration of high point as illustrated by hypothetical regression lines fitted visually to plots of end members of group. B, Scattergram showing relationship between height and width of left valves. Note slight decrease in relative convexity of left valve in progressively younger forms. Arrow in lower left-hand corner denotes direction of decreasing convexity as illustrated by hypothetical regression lines fitted visually to plots of end members of lineage.

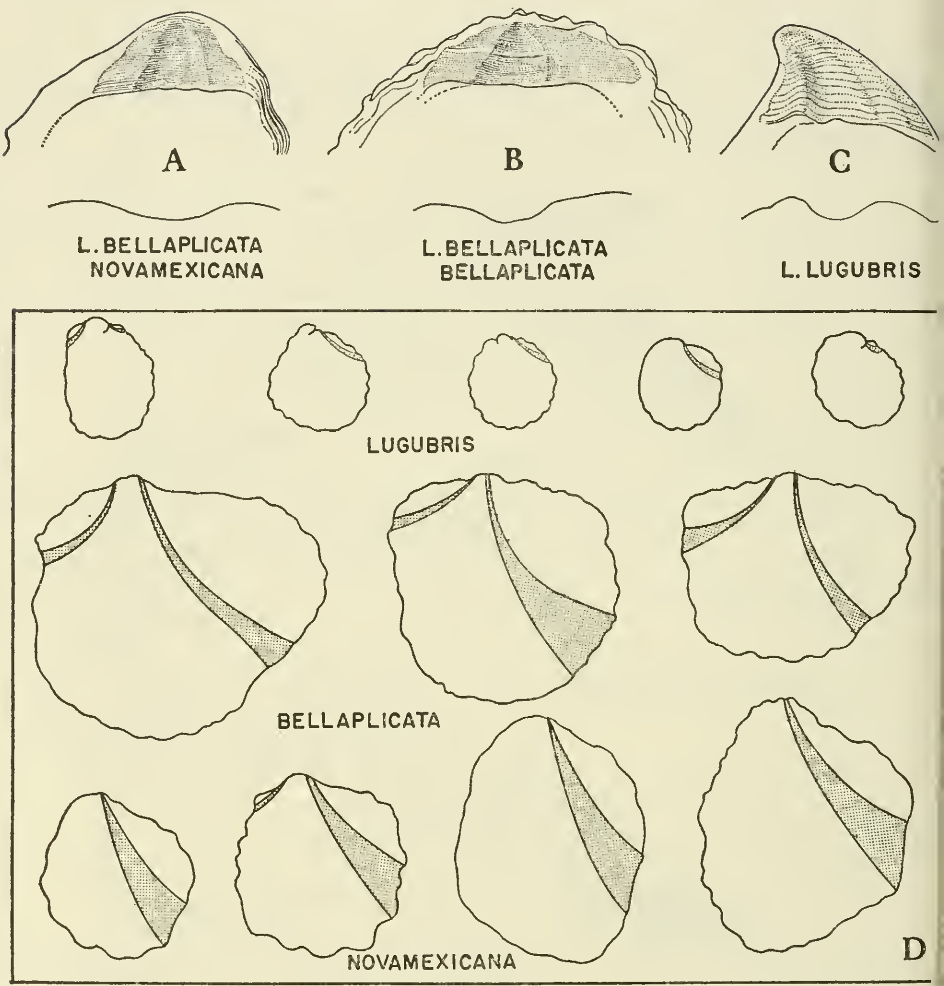

FIG. 5.—Evolution in the *Lopha lugubris* group. A, B, C, Drawings and cross sections of characteristic cardinal areas for species and subspecies within the group. Note gradual deepening, and increase in curvature of the resilifer in progressively younger forms. Also note increase in convexity of the lateral cardinal areas, from slightly arched lateral cardinal plates in the subspecies *novamexicana,* to distinct lateral cardinal folds in *L. lugubris.* D, Outline drawings of species and subspecies within the group, with the auricular sulci shaded. Note narrowing of the sulci in progressively younger forms, and variation in shape of the valves, of the posterior auricle, and in development of the anterior auricle. Specimens: A, U.S.N.M. 132263; B, U.S.N.M. 132243; C, U.S.N.M. 132167; D. Top row, left to right, U.S.N.M. 13274, 132154, U.M.M.P. 43472, 43464, U.S.N.M. 132157; middle row, left to right, U.S.N.M. 132229, 132225, 132308; bottom row, left to right, U.S.N.M. 132263, 132267, 132281, 132279.

4. Variation in the development of the auricles; a general trend toward reduction in size of the auricles, and elimination of the anterior auricle (fig. 5d). The size of the auricles increases from the subspecies *novamexicana* to subspecies *bellaplicata,* and decreases considerably in *L. lugubris.*

5. Reduction in the size (width, depth) of the auricular sulci, relative to shell size (figs. 5d, 6a).

6. Increase in the number of radiating plicae, including an increase in the number of primary plicae at the edge of the smooth stage, increase in number at any given distance below the beak, increase in total number developed at the margin of adult shells, and increase in the plication density (number per unit area) (figs. 2, 7).

7. Decrease in the average width of the radiating plicae, measured at a uniform distance below the beak in all species (fig. 7c).

8. Variation in the amount of bifurcation of primary plicae, with an overall trend toward decrease in bifurcation rate (figs. 6b, c). The bifurcation rate increases slightly from subspecies *novamexicana* to subspecies *bellaplicata,* then sharply decreases with the evolution of *L. lugubris.*

9. Increase in the absolute height and relative extent of the smooth stage on the early shell, particularly in left valves. This is the distance between the beak and the first abrupt appearance of plicae (fig. 8).

10. Some posterior migration of the beaks and umbos along the dorsal margin, and increase in the amount of curvature of these structures (figs. 3c, 5d, 9b).

11. Changes in the nature of the cardinal area: general, though not chronoclinal, increase in the size of the resilifer relative to the lateral cardinal areas; increase in the convexity and prominence of the lateral cardinal folds; development and accentuation of the marginal cardinal troughs between the lateral folds and the valve margin (figs. 5a-c).

12. Increase in the density of the denticles on the inner dorsolateral margins (fig. 9a).

Many of these trends are interpreted as adaptations to widespread environmental changes through Middle and Late Turonian time, established in the lineage through natural selection. They are adaptations shown by many living and fossil, shallow-water, epifaunal pelecypods. In the *Lopha lugubris* lineage they gradually evolved with the steady change from quiet-water, mud-bottom conditions (Blue Hill and lower to middle Mancos Shales), through near-shore,

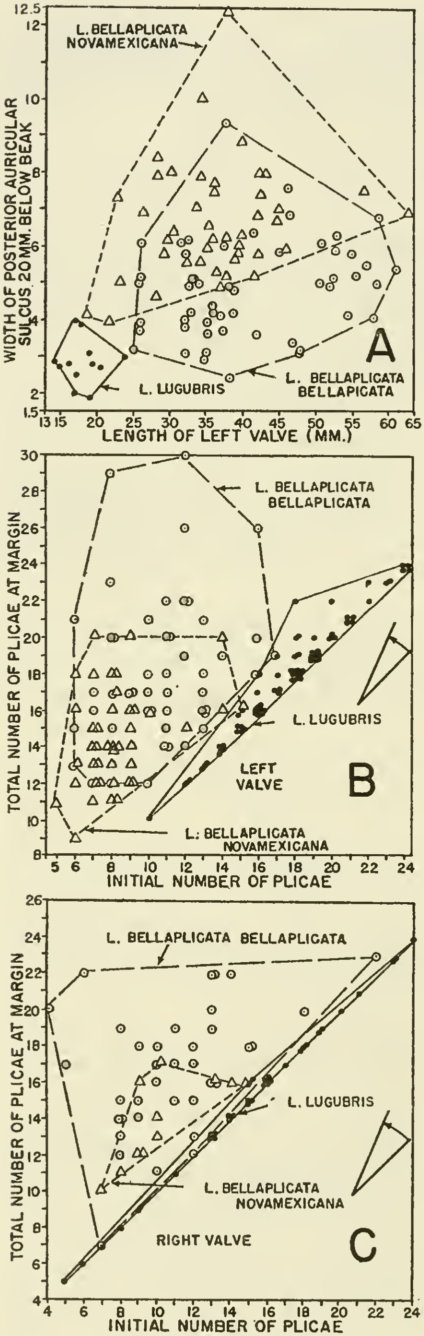

FIG. 6.—Evolution in the *Lopha lugubris* group. A, Variation plot showing relationship between the width of the posterior auricular sulcus 20 mm. below the beak and the length of the left valve, the most variable linear measurement. Note variation within each form and good separation of variation plots, lack of correlation between width and valve length, and decrease in the relative width of the sulcus at this point in progressively younger species and subspecies (the latter defined by differences in the vertical range of the individual variation plots). B, C, Comparison of the bifurcation rates of the radiating plicae on various members of the group, showing an increase in bifurcation of the plicae from *L. bellaplicata novamexicana* to the younger *L. bellaplicata bellaplicata* and then an abrupt decrease in bifurcation rate with the evolution of *L. lugubris,* in which the majority of specimens lack bifurcating plicae. Arrows on right central portion of B and C denote direction of increasing bifurcation rate as illustrated by hypothetical regression lines visually fitted to plots of terminal members of group.

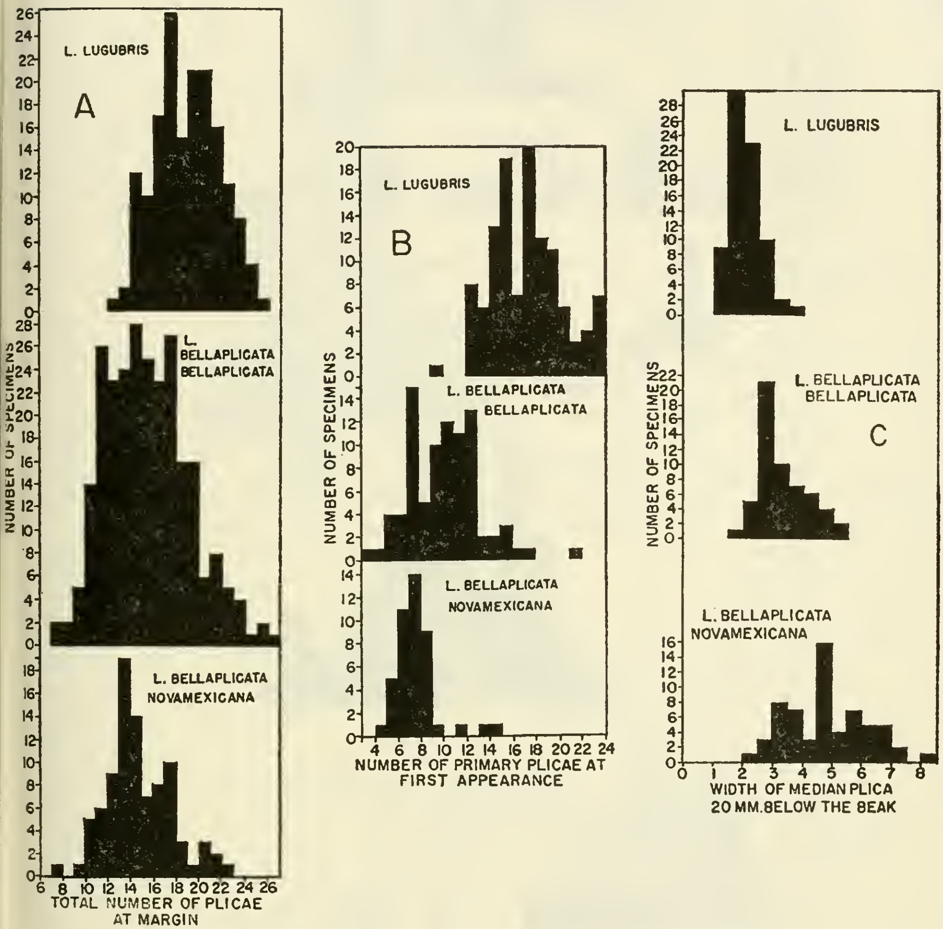

FIG. 7.—Evolution in the *Lopha lugubris* group. A, Increase in total number of radiating plicae developed at the margin of adult shells in progressively younger species of the lineage. B, Increase in the total number of primary plicae first appearing at the margin of the smooth stage on progressively younger species. C, Decrease in the width of the median plica measured 20 mm. below the beak on progressively younger species of the group. All measurements made on left valves.

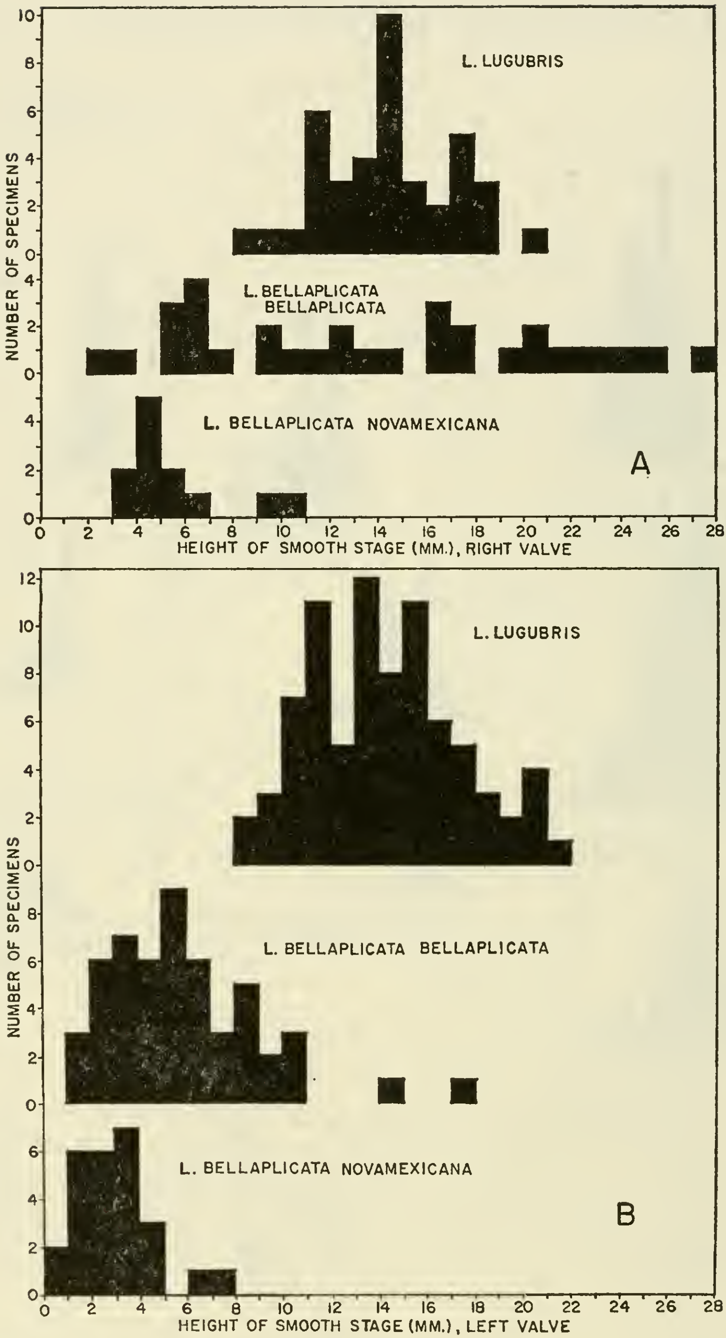

FIG. 8.—Evolution in the *Lopha lugubris* group. Increase in the actual height of the smooth umbonal area, dorsal to the abrupt appearance of radiating plicae, in successively younger species and subspecies. A, Right valve. B, Left (attached) valve, on which the trend is best observed.

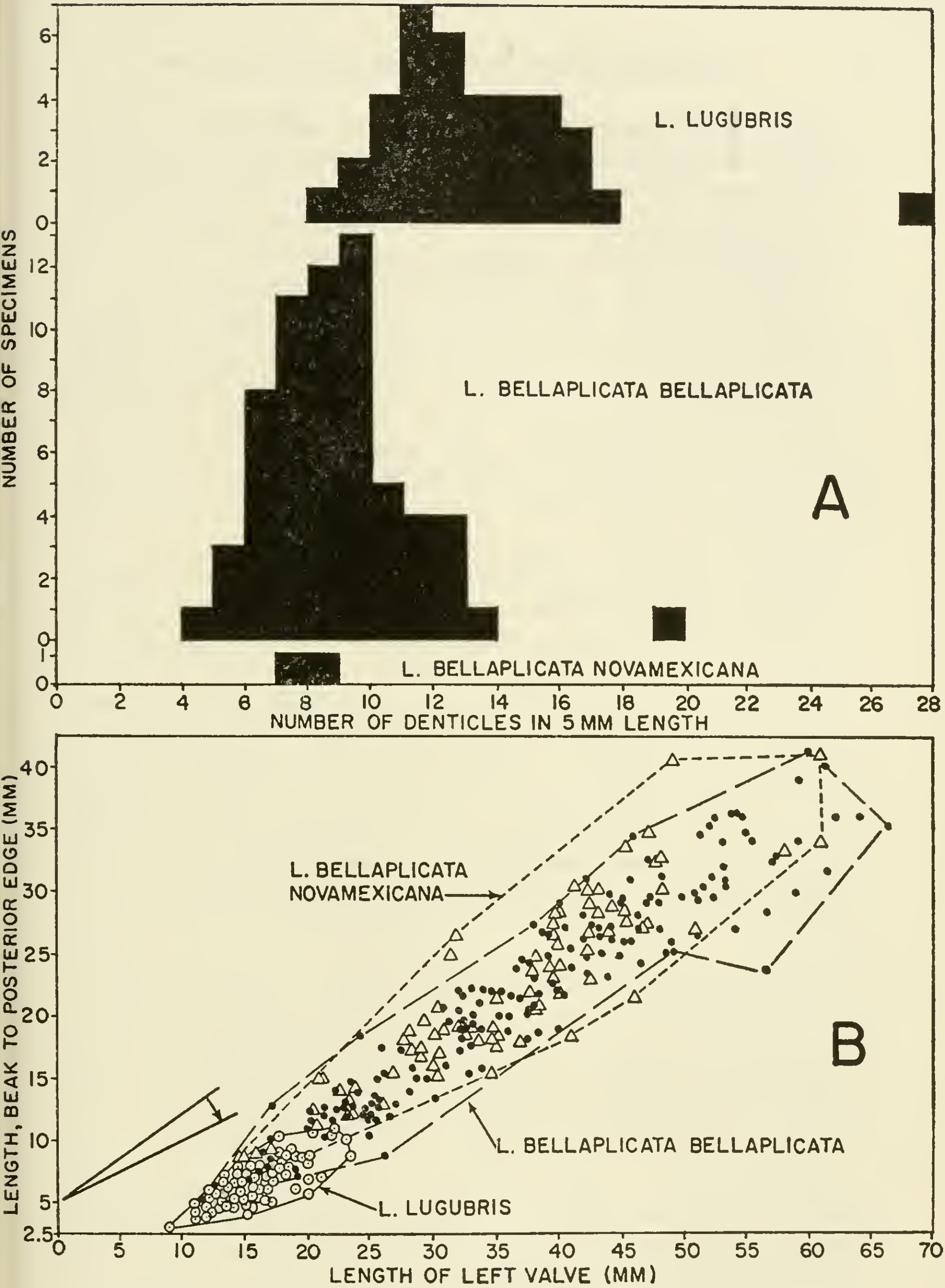

FIG. 9.—Evolution in the *Lopha lugubris* group. A, Increase in the density of the denticles along the inner lateral and dorsolateral margins in successively younger species. B, Ventral shifting of the beaks along the dorsal margin in successively younger species and subspecies, and decrease in the length of the posterior auricle. Arrow in lower left-hand corner denotes direction of central shifting of beak along dorsal margin as shown by hypothetical regression lines visually fitted to plots of terminal species in lineage.

moderate- to shallow-water environments with active currents (upper Eagle Ford Shale, Codell Sandstone, parts of the middle Mancos), to shallow-water, inner-sublittoral, high-energy conditions, including wave action, a great deal of reworking, and periods of nondeposition (Juana Lopez Member, "Reworked Eagle Ford zone").

Most of the trends thought to be selected for environmental changes concern themselves with improving the hydrodynamic stability, strength, and anchorage of the shell. Hydrodynamic stability of the shell in the face of increased current and wave activity was probably improved by the overall decrease in shell convexity, ventral migration of the high point, reduction of projecting surfaces such as the auricles, increase in relative symmetry of the shell, and evening of the overall shell surface by a great reduction in the prominence of the auricular sulci, interplical sulci, and plicae. Reduction in shell size may also have affected stability of the shell, though it is more likely tied to the restricted amount of available feeding time in active shallow-water environments as compared to that available in deeper, nonagitated waters.

The development of smaller and more numerous plicae by shallow-water ostreids in this lineage appears to be a twofold adaptation to a near-shore environment. Most obviously this results in strengthening of the shell, necessary for life in the presence of waves, strong currents, and continued buffeting, while at the same time eliminating coarse projections from the shell surface, producing a more even, less resistant surface over which water can flow. Even more important may be the role of plications as an adaptation to feeding in a turbid, high-energy environment. Development of extensively plicate and crenulate commissures in marine bivalves allows the animal to reduce considerably the gape of the valves during feeding over that required by forms with smooth margins, without greatly altering the total amount of open area between the valves for the influx of water. The advantages of reducing the gape while maintaining normal water intake in a turbid environment are apparent, since there is a corresponding reduction in the size and possibly the amount of foreign particles able to filter between the valves, and consequently a greater degree of protection against clogging of the feeding mechanisms and agitation of the mantle. This helps to offset the abundance of mobile detritus found in near-shore, high-energy environments, and allows the oyster to feed for longer periods of time, and tolerate greater turbidity, than nonplicate species subject to the same conditions.

Progressively younger members of the lineage display a gradual increase in the relative size of the attachment area, the general size and inclination of the area being unusually consistent within species and subspecies. Increase in the size of the attachment area, and decrease in the angle between the area and the commissure both appear to be adaptations to high-energy, near-shore conditions, providing a firmer anchor and lower, hydrodynamically more stable shell in the face of strong current and wave action. There is evidence in the *Lopha lugubris* group that these may be genetically controlled features of the shell as well as adaptive variations of individual members of the lineage.

Evidence favoring genetic control of inclination and size of the attachment area is found in the end members of the lineage. All observed specimens of *L. bellaplicata novamexicana* have a very small attachment area. The size of the area relative to the size of the adult shell possibly indicates early detachment of the shell from the substrate and a free-living adult stage. Were this purely an adaptive feature, one would expect it only in quiet-water environments, since a free-living shell of the *novamexicana* type in normal living position (convex left valve downward) would be highly unstable in the face of strong currents or wave action, and easily overturned and buried. Although sediments containing most *L. bellaplicata novamexicana* indicate quiet or slightly agitated water conditions, a few specimens occur in coarse-grained, coarse-bedded sandstones of high-energy environments. These maintain the small attachment area. Further, no adaptive counterpart of the subspecies having a large attachment scar is developed in the near-shore facies. Scar size thus appears to be independent of environment in this case.

Similarly, *L. lugubris* has an exceptionally large, gently inclined attachment area regardless of associated sediment type and inferred environment. These features indicate attachment throughout life, and are adapted to high-energy conditions. Sediments containing most specimens of *L. lugubris* reflect such an environment. The species is most common in cross-bedded, ripple-marked calcarenites and calcareous sandstones. A number of examples from thinly laminated shales and fine sandstones and siltstones, however, maintain the large, gently inclined scar, even though it was probably not necessary for firm anchorage in the more quiet water environments.

The change in inferred living habit from partially free to wholly attached, and the consistency in the character of the attachment area on these two forms, regardless of associated environment, suggest genetic control on the size and inclination of the area.

The middle member of the lineage, *L. bellaplicata bellaplicata,* exhibits more variation in scar size (pl. 3), with individuals that probably lived free during part of their adult life, and others that could well have been attached throughout life. These two forms coexist in the great variety of environments from which the species is known, but there is a notable increase in the relative percentage of individuals with large attachment areas in shallow-water sediments deposited under high-energy wave and current conditions (Codell Sandstone). Scar size thus appears to be largely adaptive and environmentally controlled in this subspecies.

Small shell size is considered by some ecologists as an adaptation to turbid, near-shore environmental conditions. This may be the case in the *L. lugubris* lineage where there is a distinct trend toward reduction in the average adult dimensions with the onset of shallow-water conditions during the Late Turonian. Shallow-water epifaunal elements are able to spend less time feeding than their counterparts in deeper, quieter waters. Long periods during which little feeding takes place are imposed on them by extended times of high turbulence and water agitation. This restriction on food intake has been related to the below average size of many shallow-water epifaunal pelecypod species which develop to normal proportions in quiet, offshore waters. This, of course, is purely an ecologic control on shell form. In the many cases, however, where the smaller of two closely related species or subspecies of epifaunal pelecypods lives closest to the inner sublittoral zones of constant water agitation and turbidity, small size seems to be a genetic adaptation to the environment. The smaller species, requiring less food, are better able to survive in environments presenting shorter and more irregular feeding opportunities.

The changes of other structures through time are well defined and easily recognized, but based on my present knowledge of the zoological characteristics of the group and of the Turonian environment, it is difficult to explain them in terms of adaptive features.

SHELL MORPHOLOGY

Standard terminology has been used wherever possible in describing species and subspecies of the *Lopha lugubris* group (see Newell 1937, 1942, Shrock and Twenhofel, 1953, for definitions of standard terms). A few new or rarely used terms are employed here for features not generally considered in ostreid description. It is desirable to briefly define these. In most cases this is simply accomplished by means of an illustration (fig. 10a, b, c, d), especially in regard to spacial divisions of the valve (fig. 10c; see explanation). Discussions are presented below for new terms employed, as a key to abbreviated ratios (tables 1-5) or where it seems possible that misunderstandings may arise in interpretation of a term in the descriptions as it is applied to the Ostreidae. The letters arranged alphabetically below refer to fig. 12, and tables 1-5.

A: AATS—The ratio of the approximate area of the left (lower) valve to the approximate area of the attachment scar, as determined by their inscribing rectangles, oriented with their sides paralleling height and length.

AA—Anterior auricle, or ear (fig. 10a); rarely developed and generally poorly defined flattening and projection of the dorsoanterior margin, generally separated from the main body of the shell by a small auricular furrow or sulcus.

ANS—Anterior slope of the valve (includes lower part of the anterior auricle, where developed); the portion of the shell between the dorsal and anteroventral slopes, and the crest (fig. 10c).

A: P—The ratio of the area of a rectangle inscribing the valve to the number of plications present at the valve margin.

AS—Auricular sulcus (figs. 10a-c); an external furrow or depression which separates the anterior and posterior auricles from the main body of the shell. In this group it is commonly expressed as a relatively deep, slightly enlarged interplical sulcus.

AVS—Anteroventral slope of the shell, between the median plication, crest, and anterior slope (fig. 10c).

CCP—Central cardinal plate. On the right valve, a flat surface developed in the central cardinal area, in place of a shallow resilifer.

CR—Crest of the valve; the highest area of the valve, either slightly convex or nearly flat, situated dorsocentrally (fig. 10c).

D—Denticles; small raised nodes, rounded to elongate, on the inner dorsolateral margins of the valves (fig. 10d).

DS—Dorsal slope of the valves (includes the attachment scar where present; fig. 10c).

HA—Hinge axis (cardinal axis), the axis of rotation of the valves (fig. 10d). The ligament lies dorsal, the main part of the resilium ventral. The only parts of the two shells always in contact. When the hinge line is straight, it may parallel this axis.

H: L—Ratio of valve height to valve length.

HP—High point of the valve (fig. 10c), marking the point of greatest convexity. This is usually within the crest on the median plication, and is a good reference point for delineating the various flanks of the valves.

H:DPAS—The ratio of the valve height to the greatest diameter of the posterior adductor muscle scar.

H: HATS—The ratio of the valve height to the height of the attachment scar, as measured on the left valve.

H: HD—The ratio of the valve height to the height of that part of the valve bearing denticles along the inner lateral margins.

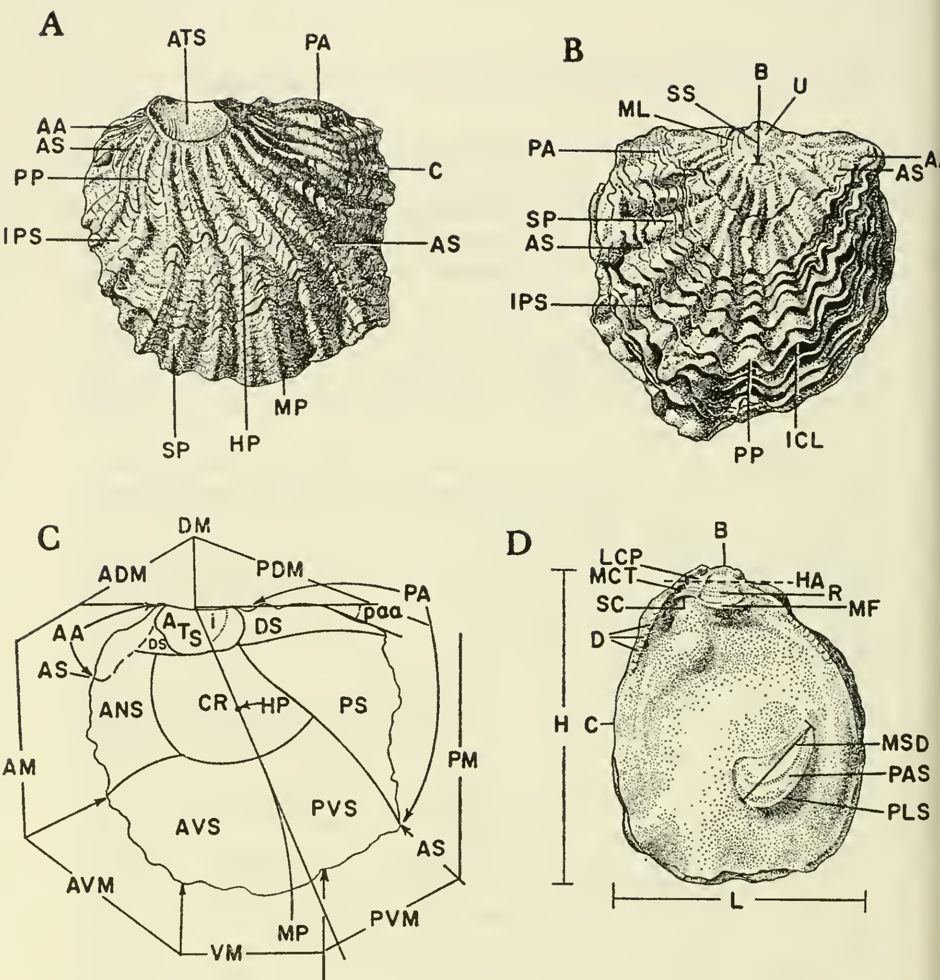

Fig. 10.—Morphology of oysters in the *Lopha lugubris* group, using specimens of *L. bellaplicata bellaplicata* for illustration (A, C, U.S.N.M. 132222; B, U.S.N.M. 132239; D, U.S.N.M. 8024d). A, External shell morphology of left valve. B, External shell morphology of right valve. C, Spatial divisions of valve referred to in text. D, Interior morphology of right valve. Symbols explained in detail under "Shell Morphology." AA, Anterior auricle. ADM, Anterodorsal margin. AM, Anterior margin. ANS, Anterior slope. AS, Auricular sulcus. ATS, Attachment scar. AVM, Anteroventral margin. AVS, Anteroventral slope. B, Beak. C, Commissure. CR, Crest of valve. D, Denticles. DM, Dorsal margin. DS, Dorsal slope. H, Height of valve. HA, Hinge axis. HP, High point of valve. *i*, Angle of inclination. ICL, Imbricating concentric lamellae. IPS, Interplical sulcus. L, Length of valve. LCP, Lateral cardinal plate. MCT, Marginal cardinal trough. MF, Midcardinal fold. ML, Microlamellae. MP, Median plica. MSD, Maximum diameter of posterior adductor muscle scar. PA, Posterior auricle. *paa*, Posterior auricular angle. PAS, Posterior adductor muscle scar. PDM, Posterodorsal margin. PLS, Posteroventral lip of the muscle scar. PM, Posterior margin. PP, Primary plica. PS, Posterior slope. PVM, Posteroventral margin. PVS, Posteroventral slope. R, Resilifer. SC, Subcardinal cavity. SP, Secondary plica. SS, Smooth stage of umbo. U, Umbo. VM, Ventral margin. All figures ×1.

H : HSS—The ratio of the valve height to the height of the smooth stage on the early portion of the valve.

i—The angle of inclination of the valve (fig. 10c); the angle between the plane of the hinge line (horizontal) and a line connecting the beak (or center of the attachment scar) with the most distant edge of the shell. This line generally roughly bisects the shell.

ICL—Imbricating concentric lamellae; the major concentric features of the ornamentation (fig. 10b).

IPS—Interplical sulcus; the trough between any two plicae. The auricular sulci are enlarged interplical sulci separating the auricles from the main body of the shell (figs. 10a, b).

LCP—Lateral cardinal plates (fig. 10d, 5a-c); triangular flat areas for ligament attachment on either side of the resilifer and midcardinal fold (right valve). These are highly variable in size, and commonly bordered laterally by a shallow groove (marginal cardinal trough).

L :LHL—Ratio of the length of the valve to the length of the hinge line.

L : LPA—Ratio of the length of the valve to the length of the posterior auricle.

MCT—Marginal cardinal trough. A shallow, narrow groove or trough on the cardinal area between the lateral cardinal plate and upturned lateral margin of the valve (fig. 10d).

MF—Midcardinal fold. The raised convex portion of the central cardinal area on the right (upper) valve, below the resilifer (where present). It occupies from one-fourth to the whole of the area.

ML—Microlamellae; very fine overlapping sheets of lamellar calcite. The major ornament on the smooth stage of the shell and between imbricating concentric lamellae over the rest of the shell (fig. 10b). They appear as simple growth lines in many cases.

MP—Median plica (figs. 10a, c); the major primary plication that runs down the approximate center of the valve, passing through its high point. It is usually the most prominent plica on the shell, and is a useful reference line for defining the various flanks.

MSD—Maximum scar diameter (fig. 10d); the longest diameter of the posterior adductor muscle scar, the least variable parameter of the scar to measure; useful in ontogenetic study.

PA—Posterior auricle (figs. 10a-c), or wing of the shell (in the sense of Newell, 1942, p. 22 as applied to the Mytilacea). This is a prominent, flattened, projecting salient of the posterior and dorsoposterior flanks of the shell, in some cases separated from the main body of the shell by an auricular sulcus.

paa—Posterior auricular angle (fig. 10c); the angle between the dorsoposterior margin of the posterior auricle and the plane of the hinge line (horizontal reference line).

PD—Plication density. The number of plications per unit approximate shell area ($H \times L$).

PLS—Posteroventral lip of the adductor muscle scar (fig. 10d). A raised ridge that bounds the scar posteriorly and ventrally in many species.

PP—Primary plica; one of the initial plications of the shell, arising at the edge of the smooth stage and extending to the shell margin. It may or may not give rise to other plicae by bifurcation (fig. 10a, b).

PS—Posterior slope of the shell, including the posterior auricle (fig. 10c).

PVS—Posteroventral slope of the valves, bounded by the median plica, crest, and posterior slope of the valve (fig. 10c).

SC—Subcardinal cavities; shallow re-entrants of the valve floor beneath structures of the cardinal area, predominantly below the midcardinal fold or lateral cardinal plates.

SP—Secondary plica; one that arises through bifurcation from a primary plication (figs. 10a, b).

SS—Smooth stage; that portion of the beak, umbo (in many cases the whole umbo), and adjacent parts of the valve that lack radiating plications (fig. 10b). This probably represents part or all of the shell of the spat.

T—Thickness; valve thickness is employed in this study as the actual thickness of the shell material. This is naturally variable in a single valve. Valve thickness should not be confused with shell or valve width.

W—Shell width; here defined as the broadest diameter of coattached valves when viewed along the plane of the commissure. It is the length of a diameter joining the high points of each valve and perpendicular to the plane of symmetry. The width of a single valve is measured similarly—between the high point of the valve and the commissure plane (or if the beak is overhanging, the plane passing along its most projecting edge).

SYSTEMATIC PALEONTOLOGY

Genus LOPHA Bolten, J. F.: Emended Kauffman, 1964

1798. Bolten, J. F. (=Roeding, P. F.), Museum Boltenianum sive catalogus cimeliorum e tribus regnis naturae, pt. 2, pp. 168, 169.

1898. Dall, W. H., Contributions to the Tertiary Fauna of Florida. Trans. Wagner Free Inst. Sci. Philadelphia, vol. 3, pt. 4, p. 672.

1936. Maury, C. J., Brazil Servico Geol. e Mineralog., Mon. 11, p. 157.

1937. Arkell, W. J., A monograph of British Corallian Lamellibranchia. Paleont. Soc., p. 180.

1940. Cox, L. R., The Jurassic Lamellibranch fauna of Kuchh (Cutch). Mem. Geol. Surv. India, ser. 9, vol. 3, p. 95.

Type species.—Ostrea crista-galli Linné, by subsequent designation, Dall, 1898, p. 672.

Diagnosis.—Shell normally small to moderate size, subequilateral to moderately inequilateral, slightly to moderately inequivalve, left valve slightly larger and more convex than right. Outline ovate, subround, or subquadrate; posterior auricle commonly developed. Beak opisthogyre to suberect. External ornament subequally developed on both valves, consisting of strong radiating plicae originating at the umbone and extending to the commissure, increasing by bifurcation and intercalation. Commissure trace undulating, more rarely zigzag. Shell structure predominantly lamellate (subnacreous layer), adjacent layers of gently inclined lamellae commonly with opposed dips.

Cardinal area of both valves consisting of central triangular resilifer and triangular, subequally developed, lateral cardinal plates. Resilifer of right valve commonly bounded ventrally by a low lip or partial midcardinal fold. Subcardinal cavities commonly absent. Dorsolateral inner valve margins subequally denticulate; denticles small, simple, ovoid to elliptical, their long axis perpendicular to commissure. Posterior adductor muscle attachment area posterocentral; outline comma-shaped; well defined.

Remarks.—Many recent workers have included *Lopha* (=*Alectryonia*) in synonymy with *Ostrea,* or considered it a subgenus or section of *Ostrea.* Modern representatives of *Lopha* lack a promyal chamber and are monoecious as are species of *Ostrea.* Ranson (1942, 1948) has demonstrated that the prodissoconch features of *Ostrea* and *Lopha* are similar as well. Paleontologists have continued to use the name however, since *Lopha* is quite distinct from *Ostrea* in shell sculpture, and the two do not intergrade. *Ostrea* rarely develops plications, and in cases where they are present, they do not approach those of *Lopha* in size or development. In addition, species of *Ostrea* are more equivalve, generally lack curved beaks and umbos, and have a flat commissure.

Perhaps the most important distinction between *Lopha* and *Ostrea* is in the shape of the muscle scar—comma-shaped in *Lopha,* consistently laterally elongate, ovate to kidney-shaped, and larger in *Ostrea.* This reflects basic differences in the anatomy of the muscle itself. In combination, these distinctions are sufficient to consider *Lopha* and *Ostrea* separate genera. Their similarities probably reflect a common ancestry somewhere in the Mesozoic.

The name *Alectryonia* has commonly been applied to oysters with the characteristics of *Lopha,* and the two are objective synonyms, having the same type species. The popularity attained by *Alectryonia* in recent years stems from Stenzel's acceptance of the name in place of *Lopha* (1947, p. 169, 177) under the rules of the International Commission of Zoological Nomenclature that existed at the time of his work. *Lopha* originally appeared in Bolten's Catalogue without description or definition other than "Lopha Der Hahnenkamm" (Lopha the cock's comb: Stenzel, 1947, p. 177). A list of several valid species followed, but with no indication as to which was the type. *Ostrea crista-galli* Linné, now considered the type species of *Lopha,* headed the list. Subsequently, *Alectryonia* Fischer de Waldheim was validly proposed in 1807 before *Lopha* was validated with formal description. The new rules of the Commission, however, published in 1961, do not demand formal description of a new genus as long as it is accompanied by listing of a valid species. Thus *Lopha* can be considered validly proposed as of 1798, and *Alectryonia,* proposed later with the same type species, becomes a junior objective synonym.

The restricted usage of *Lopha* here does not incorporate many groups that have previously been assigned to the genus because of their plicate shell, but which probably belong to distinct groups. Among these are the plicate *Pycnodonte,* which have vesicular shells, *Arctostrea,* a distinct lineage since the Jurassic, *Agerostrea,* a modification of the *Arctostrea* branch, and the narrow elongate "tree oysters" with their clasping shelly processes.

In published descriptions of *Lopha* or *Alectryonia,* certain morphologic features are given as diagnostic of the group which I do not consider significant at this taxonomic level. Curvature of the adult hinge line is too easily distorted by variation in direction of adult growth to be useful, especially for oysters growing in crowded conditions. The divaricate pattern of radiating ornamentation attributed to *Alectryonia* and *Lopha* is not characteristic of the genus but rather of *Arctostrea* and some *Rastellum.* The use of this as a diagnostic generic character reflects the time when these groups were all placed under *Lopha.* Clasping shelly processes are rarely developed around the attachment area of *Lopha* and are not diagnostic. They are more typical of the so-called tree oysters, which probably constitute a distinct group.

Characters of the shell which appear to be useful in distinguishing *Lopha* from similar forms, and in separating the genera of plicate oysters, are: General shell form; basic ornament pattern; relative development of component parts of the cardinal area; presence, morphology, and distribution of the denticles; presence or absence of subcardinal cavities; depth of the valves (especially the left valve); position, size, and shape of the posterior adductor muscle scar; shell structure; and in some cases juvenile ornamentation and nature of the commissure.

LOPHA LUGUBRIS Conrad

Plate 1, figures 1-18; plate 2, figures 1-17; plate 8, figure 12

Ostrea lugubris Conrad, U. S. Mex. Boundary Rep., vol. 1, p. 156, pl. 10, figs. 5a, b, 1857.—Coquand, Mon. Genre Ostrea Terr. Cret., p. 66, pl. 36, figs. 22, 23, 1869.—MEEK, Macomb's Expl. Exped. from Santa Fe to Junction Grand and Green Rivers, p. 123, pl. 1, figs. 1a-d, 1876.—WHITE, 4th Ann. Rep. U. S. Geol. Surv., p. 297, pl. 41, fig. 3, 1884.—CRAGIN, 4th Ann. Rep. Geol. Surv. Texas, p. 204 (in part), 1893.—STANTON, U. S. Geol. Surv. Bull. 106, pp. 58, 59 (in part), pl. 4, figs. 1-5, *non* figs. 6-10, 1893 [1894].—LOGAN, The Univ. Geol. Surv. Kansas, vol. 4, pt. 1, p. 455 (in part), pl. 91, figs. 1-5, *non* figs. 6-10, 1898.—HERRICK and JOHNSON, Bull. Denison Univ. Sci. Lab., vol. 40, p. 202 (in part), 1900.—JOHNSON, School of Mines Quart., vol. 24, No. 2, pp. 186, 187, 1903a; Columbia Univ. Contr. Geol. Dept., vol. 10, No. 90, pp. 114, 115 (in part), 1903b.—SHIMER and BLODGETT, Amer. Journ. Sci. Arts, 4th ser., vol. 25, p. 61 (in part), 1908.

Ostrea (*Alectryonia*) *lugubris* CONRAD, BÖSE, Bol. Inst. Geol. Mexico, No. 30, Algunas faunas del Cret. de Coahuila, pp. 47, 48, pl. 8, figs. 4-6, 1913.—SHIMER and SHROCK, Index foss. N. Amer., p. 395, pl. 154, figs. 4, 5, 1955.

Alectryonia lugubris (Conrad) ADKINS, Handbk. Texas Cret. Foss., p. 104 (in part), 1928.

DESCRIPTION

Material.—Approximately 350 well-preserved specimens (measured) and an additional 200 to 300 poorly preserved valves from various localities in Texas, New Mexico, and Colorado, including most illustrated types of the species. Ontogenetic series and large variation suites are available from several New Mexico and Colorado localities.

General form.—Summary of measurements presented in table 1. Shell small, inequivalve, left (lower) valve slightly larger, much more convex than right valve. Valves slightly to moderately inequilateral, normally prosocline; beaks, umbos typically opisthogyre (exogyroid) (pl. 1, fig. 5). Left valves commonly round, subround, or broadly subovate, rarely subelliptical; right valves subovate to elliptical, slightly curved (pl. 1, figs. 1-6; pl. 2, figs. 1-3, 5-12 typical of species). Height normally greater than length. Anterior and ventral margins slightly to moderately and unevenly rounded, posteroventral corner narrowly rounded, posterior margin slightly concave to nearly straight on valves with posterior auricle, otherwise moderately curved. Dorsal margins short, rounded, moderately inclined anteriorly, gently sloping posteriorly over auricle, recessed posteriorly adjacent to beak, umbo.

Convexity.—Left valve moderately to highly convex, rarely flattened; high point subcentral, on ventral edge of attachment scar. Anterior, posterior, ventral, ventrolateral flanks moderately to steeply sloping; dorsal and dorsolateral flanks, including attachment scar, gently sloping. Right valve flat to moderately convex, normally slightly arched, with umbo more inflated (pl. 2, figs. 2, 6); rarely concave. Some right valves with upturned margins and submarginal trough.

TABLE 1.—*Summary of measurements on specimens of* Lopha lugubris (Conrad)

Character	Valve	No. of specimens	Range	Average
Height (H)	L	175	7.6-41.2 mm.	17.3 mm.
	R	161	7.4-23.9 mm.	15.2 mm.
Length (L)	L	173	7.5-23.3 mm.	14.9 mm.
	R	161	4.6-23.0 mm.	12.8 mm.
Width (W)	L	169	1.5-9.6 mm.	3.7 mm.
	R	160	1.0-6.2 mm.	2.7 mm.
Percent valves with H > L	LR	303		90.7%
Percent valves with L > H	LR	303		7.9%
Percent valves with H = L	LR	303		1.4%
Area, inscribing rectangle of valve (H × L)	L	133	118.8-564.0 mm.	272.5 mm.
Length, beak to posterior margin (LBP)	L	163	2.5-11.0 mm.	6.5 mm.
Ratio, LBP : L	L	94	0.31-0.55 mm.	0.43 :1 mm.
Angle of inclination (i)	L	80	43°-97°	73.4°
	R	65	40°-93°	72.3°
Height of attachment scar (HATS)	L	157	4.4-20.0 mm.	12.3 mm.
Length of attachment scar (LATS)	L	157	4.0-17.5 mm.	9.5 mm.
Area, inscribing rectangle of attachment scar (HATS × LATS)	L	100	17.6-285.4 mm.^{2}	121.9 mm.^{2}
Ratio, area of scar (inscribing rectangle) : area of valve (inscribing rectangle)	L	100	0.13 : 1-0.78 : 1	0.46 : 1
Percentage of valves with plicate exterior surface (not including those with only the margin plicate or crenulate)	L	175		81.7%
	R	161		23.0%
Height, smooth young stage (HSS), on dorsal part of plicate valves	R	40	9.4-21.1 mm.	15.0 mm.
	L	79	7.1-21.1 mm.	14.2 mm.
HSS on left valves with HSS > HATS	L	24	9.0-20.2 mm.	13.7 mm.
Ratio, HHS : H	L	80	0.60 : 1-1 : 1	0.80 : 1
	R	64	0.62 : 1-1 : 1	0.92 : 1
Number of primary plicae at first appearance	L	78	10-24	18.1
	R	38	13-24	16.9
Number of plicae at 10 mm. H (on shells where HSS < 10 mm.)	L	6	10-18	14.7
	R	3	13-16	14.7
Number of plicae at 20 mm. H	L	47	15-24	19.6
	R	16	14-24	18.8
Total number of plicae (marginal count)	L	130	10-24	18.8
	R	38	13-25	17.0
Number plicae in 20 mm. L at 20 mm. H (median plica central)	L	44	5.75-11.0	7.32
	R	19	5.25-8.5	6.8

Table 1.—*Summary of measurements on specimens of* Lopha lugubris (Conrad)—*continued*

Character	Valve	No. of specimens	Range	Average
Width of median plica at 20 mm. H..	L	50	1.2-3.5 mm.	2.1 mm.
	R	24	1.1-3.1 mm.	2.1 mm.
Percentage of plicate valves with bifurcating plicae	L	130		23.8%
	R	32		18.8%
Percentage increase in plicae by bifurcation (measured only on valves with bifurcating plicae)....	L	13	4.5-22.2%	9.22%
	R	2	6.7%	6.7%
Percentage of specimens with opisthogyre beaks and umbones........	L	157		78.9%
	R	161		72.7%
Percentage of specimens with orthogyre beaks and umbones........	L	157		3.3%
	R	161		3.7%
Percentage of specimens with prosogyre beaks and umbones...........	L	157		17.8%
	R	161		23.6%
Length of hinge line (LHL)........	L	33	2.3-8.5 mm.	5.1 mm.
	R	26	2.8-8.1 mm.	4.4 mm.
Ratio, LHL:L	L	34	0.15:1-0.55:1	0.33:1
	R	26	0.17:1-0.43:1	0.28:1
Extent of denticles on inner margins (in terms of valve height; HD)....	L	32	2.2-9.6 mm.	4.7 mm.
	R	25	1.2-10.2 mm.	4.6 mm.
Ratio, HD:H.....................	L	32	0.12:1-0.41:1	0.26:1
	R	25	0.08:1-0.51:1	0.26:1
Number of denticles in 5 mm. length along dorsolateral margins, just below cardinal area...............	L	18	9-17	13.2
	R	18	11-29	14.3
Maximum diameter of muscle scar (MDS)	L	32	3.0-7.8 mm.	5.1 mm.
	R	18	3.3-8.6 mm.	5.3 mm.

Auricles.—Anterior auricle rarely developed, most common on right valve. Auricle small, rounded, flattened salient of dorsoanterior margin (pl. 2, fig. 5), in some cases separated from shell by shallow, broad anterior auricular sulcus. Posterior auricle present on 59 percent of measured specimens; small to medium size, subtriangular, elongate, flattened, margin rounded, position dorsoposterior (pl. 1, fig. 4). Auricle rarely separated from main body of shell by shallow, broad auricular sulcus. Auricular sulci corresponding to enlarged interplical sulci on plicate valves.

Beaks, umbones.—Typically opisthogyre, rarely erect, more commonly prosogyre, predominantly exogyroid on left valves, attaining three-quarters to one and one-half volutions (pl. 1, fig. 5, text fig. 3c) on both prosogyre and opisthogyre shells; strongly curved where not exogyroid, Beaks, umbos moderately curved posteriorly on most right valves. Beak pointed (right valve) to narrowly rounded (left valve), situated centrodorsally or just posterior to midline. Prodissoconch rarely preserved, smooth, flat, separated from umbo by single prominent growth line or concentric constriction. Beak, umbo flat to concave on left valve, deformed on attachment scar; slightly to moderately inflated on right valve, in some cases separated from rest of valve by prominent constriction and/or abrupt change in ornament (pl. 2, figs. 2, 5, 6).

Attachment area.—Situated on dorsoposterior flank, large on most left valves (pl. 1, figs. 1-14), equal to one-half area of shell, flat to concave, gently inclined to plane of commissure (average angle 24°), outline rounded to subovate, similar to ultimate shape of valve. Ornament of attachment area reflects surface to which attached, normally *Ostrea* and *Inoceramus* shells; area marked with concentric lines and folds. No clasping processes developed. Attachment area commonly obscures beak, umbo.

Ornamentation, left valve.—Beak smooth; early part of umbo smooth, central and ventral portions covered with fine growth lines, small concentric undulations. Free surfaces of most valves covered with coarse, simple (primary), radiating plicae (pl. 1, figs. 1, 2, 4-6), originating abruptly at or near margin of attachment area and extending to commissure, rarely bifurcating; rare valves smooth, with plicae reflected as marginal crenulations, or with plicae greatly reduced in prominence (pl. 1, figs. 3, 11-14). All gradations known between smooth and fully plicate forms. Primary plicae straight to slightly curved, slightly broader than high, crests rounded, flanks steep, more prominent centrally than laterally, becoming higher, more angular, broader, more prominent with age. Secondary plicae smaller, lower than primaries, more rapidly expanding in size (pl. 1, fig. 4). Interplical sulci deep, steep-walled, narrower than plicae, angular to narrowly rounded at base. Commissure strongly undulating, rarely zigzag, at intersection with plicae.

Concentric ornament between edge of attachment area and plicate portion of valve with faint growth lines, microlamellae, more rarely with crowded, coarse, flat, major overlapping lamellae. Plicate portion of valve characterized by moderately spaced to crowded overlapping lamellae separated by very fine growth lines. Lamellae irregularly spaced, normally flat, terminally in contact with succeeding ones; rarely raised. Plicae rugose at intersection with lamellae.

Ornamentation, right valve.—Ornament of right valve distinct from that of left valve. Beak and early umbonal area smooth; central, ventral portions of umbo marked with faint growth lines, less commonly with small, low undulations and microlamellae, rarely with scattered coarse lamellae or undulations on ventral umbo. Majority of specimens lack radiating sculpture over rest of valve, but many of these have marginal crenulations near commissure (pl. 2, figs. 1, 8). Plicae variously developed on minority of specimens (pl. 2, figs. 2-7), never covering more than half of valve, commonly confined to marginal 5 mm. Plicae originate abruptly, on strongly plicate valves at edge of inflated umbonal area (pl. 2, fig. 5); plicae prominent, rounded, with steep flanks, becoming coarser with age, rarely bifurcating; secondary plicae smaller, more rapidly expanding than primaries. Plicae rugose at intersection with concentric lamellae; plicae of right valve more prominent, sharper, than those of left. Interplical sulci deep, narrow, sharp-based, steep-walled.

Concentric ornament variable, depending on extent of plicae. Low, evenly convex valves lacking plicae covered with faint concentric growth lines, microlamellae, low, broad undulations (pl. 2, fig. 11) except at margin where coarse, crowded lamellae occur. Valves with inflated, smooth umbo and flat flanks (pl. 2, fig. 2) exhibit coarse, crowded, major lamellae, raised growth lines, small prominent undulations on flanks; ornament more prominent near commissure. On plicate valves, prominent lamellae and/or concentric constrictions occur at inner margin of point of origin for plicae (pl. 2, figs. 5, 6). Growth lines and lamellae occur throughout plicate portion of valve.

Cardinal area.—Composed of subcentral resilifer and/or midcardinal fold (right valve), bounded laterally by flat to moderately arched lateral cardinal plates or folds for ligament attachment. Resilifer of left valve shallow to moderately concave, elongate-triangular with twisted apex, higher than long, slightly flared ventrally, equal to or larger than lateral cardinal plates or folds (pl. 1, fig. 16). Lateral plates, folds subequal, variable in relative size, flat to arched, obscure to prominent, triangular with curved dorsal apices, in some valves separated from lateral margins by narrow lateral cardinal grooves (pl. 2, fig. 17), otherwise merging with margin. Lateral cardinal areas of right valve similar, less commonly arched.

Central part of cardinal area variable in right valves, ranging from flat midcardinal plate to shallow concave resilifer with raised ventral lip or partial midcardinal fold (pl. 2, fig. 17). Rarely, entire midcardinal fold developed (pl. 2, fig. 14), slightly to moderately convex. Cardinal area of both valves marked by moderately strong, irregularly spaced, crowded, raised horizontal lines transected by finer, more crowded, more evenly spaced, raised vertical lines, forming reticulate pattern. Hinge line short, straight to slightly curved (concave ventrally), situated ventral to hinge axis.

Denticles.—Denticles present on inner dorsolateral margins of all valves, rarely extending below upper one-third of margin; small, simple, elongate perpendicular to shell margin, subround to ovate, crowded, distributed along commissure and in shallow trough just inside it; color whitish, lighter than surrounding shell.

Inner valve surface.—Commissure undulating, more rarely zigzag. Plicae reflected internally as rounded, low folds and sulci, nearly equal in extent to external trace of plicae, more prominent toward commissure. Fine, irregularly spaced, sinuous, pallial or vascular grooves transgress most of inner shell surface (pl. 1, fig. 17).

Muscle scar.—Monomyarian, posterior adductor muscle insertion area (scar) subcentral, slightly posterior to midline, comma-shaped to subcrescentic, moderately curved, slightly to moderately concave, prominent. Surface of area marked with faint concentric lines and microlamellae, crowded near ventral and posterior margins, their trace conforming to growth lines. Posterior and ventral part of area bordered by low, raised, lip; dorsal and dorsoanterior margins overlapped by inner shell layers.

Shell structure.—Valves of medium thickness, variation in thickness moderate. Shell thickest at cardinal area, moderately thick over attachment area, thinning laterally, posteriorly. Thickness of average left valve: at cardinal area 0.9 mm.; middle of attachment area 0.6 mm.; high point 0.5 mm.; 2 mm. from ventral margin, 0.5 mm. Periostracum, prismatic layer, hypostracum not observed on sectioned valves. Subnacreous layer forms greatest part of shell, consisting of flat to gently curved calcite lamellae, parallel to one another on free flanks of valve, and curved, slightly inclined plates in distinct sets or layers over attachment scar. Inclination of plates in one layer commonly opposed to those of adjacent layers (pl. 8, fig. 12). Cardinal area composed of slightly curved, subparallel, thin lamellae of calcite.

ONTOGENY

Lopha lugubris is the species least suited for ontogenetic study in this group owing to the size of the attachment scar, which obscures the nepionic and neanic development of many left valves, the lack of immature shells in the collections, and the limited size range of the species. Ontogenetic trends can be studied in the following structures, which are graphed or illustrated in figures 2-4, 6b, c, 9, 11-13.

Concentric ornament.—Nepionic shell smooth, transition to neanic marked by single growth line or small constriction. *Neanic* stage with fine growth lines, becoming coarser, more crowded, mixed with microlamellae ventrally. *Neanic–ephebic* boundary poorly defined. *Ephebic* stage with coarse growth lines, microlamellae and scattered macrolamellae, faint undulations, on left valve. Right valve with faint growth lines during *early ephebic* stage (ventral umbo), abrupt constriction of shell at *midephebic* stage, marking cessation of major growth in body size, prominent lamellae, growth lines in *late ephebic*. *Gerontic* stage characterized by crowded, coarse major lamellae, small undulations near margin, marking great reduction in rate of shell growth, sharp change in concentric ornament marks *ephebic—gerontic* boundary.

Radiating ornament.—Plicae appear abruptly in *middle* to *late ephebic* (most left, some right valves), rarely earlier, marking point where shell begins to grow free of substrate; plicae becoming higher, broader, sharper, and rarely bifurcating through *late ephebic, gerontic* stages.

Marginal outline.—(See fig. 11.) *Nepionic:* Prodissoconch subround. *Neanic:* Ventral growth exceeds lateral, outline vertically ovate, slight expansion of posterior flank. *Ephebic:* Ventral and posterior growth exceed that anteriorly and are nearly equal. Auricles form in *early ephebic* stage, expand with age. Relationship between expansion rate of auricle and overall lateral ephebic growth constant (fig. 12a). *Gerontic:* Outline remains essentially the same, slight flaring of ventral, ventrolateral margins.

Curvature of midline axis.—Nepionic: Slight, poorly known. *Neanic:* Moderate to great (fig. 3c), gradually decreasing in late *neanic* stage and through *ephebic* and *gerontic* stages, becoming slight.

Convexity.—On right valve (fig. 3b), gradual increase in degree of outward curvature from *nepionic* through *early neanic,* greatest in *late neanic, early ephebic,* gradually to abruptly decreasing through *late ephebic*. *Gerontic* stage marked by abrupt flattening, upturning of margin.

Internal structures.—Rate of expansion of muscle scar, hinge line, constant, and less than rate of shell growth during *neanic* and *early ephebic* stages, tapered off gradually during *late ephebic,* and *gerontic* stages (figs. 13b, c). Elements of cardinal area poorly differentiated in *neanic* stage, becoming well defined at later stages. Extent of denticles relative to height of shell, and density of denticles, greatest during *neanic, early ephebic* stages, gradually decreasing in later growth stages (fig. 13a).

Attachment scar.—Rate of size increase relative to total size of shell constant throughout *neanic, ephebic* stages, demonstrating continued growth of attachment area throughout life.

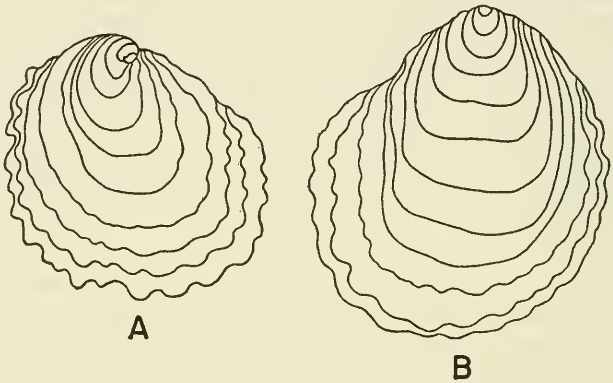

FIG. 11.—Ontogeny of *Lopha lugubris* (Conrad). Growth line traces at approximately 1.25 mm. intervals on representative left (A) and right (B) valves of the species, showing developmental history of the marginal outline. Drawings ×2. A, U.S.N.M. 132156; B, U.S.N.M. 132164.

REMARKS

Lopha lugubris (Conrad) is the most distinct member of the group and easily differentiated from related older species. In the Western Interior, it is the terminal member of the lineage known. On the Gulf Coast, however, *Lopha panda* (Morton) (Campanian, Lower Maestrichtian) possibly represents a stratigraphic extension of the lineage. Forms definitely connecting the two are presently unknown in this country.

Lopha lugubris may be distinguished from *L. bellaplicata bellaplicata* (Shumard) and *L. bellaplicata novamexicana* n. subsp. by its smaller size, greater relative height, much-reduced posterior auricle, general absence of an anterior auricle, subovate to subelliptical marginal outline, shorter, more inclined dorsolateral margins, subcentral and strongly curved to exogyroid beak and umbo, much larger and more gently inclined attachment scar, less convex left valves and relatively more convex right valves, relatively larger muscle scar, a less inflated midcardinal fold (where present), and in having the resilifer relatively larger than either lateral cardinal plate or fold. It may be further distinguished from older species by the external ornamentation of the valves. In *L. lugubris,* the majority of right valves lack plicae, and smooth left valves are common. Plicate valves may be distinguished from those of older species in the follow-

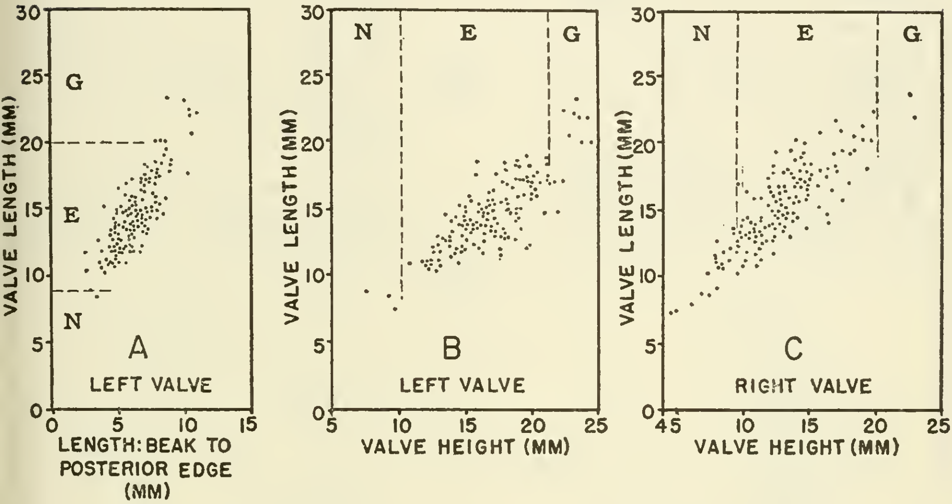

FIG. 12.—Ontogeny in *Lopha lugubris* (Conrad). A, Relationship between length of the left valve and the distance between the beak and posterior edge, measured parallel to the length. B, C, Relationship between height and length of the left and right valves, respectively. Approximate boundaries between ontogenetic stages marked by dashed lines. N = Neanic; E = Ephebic; G = Gerontic.

ing manner: The plicae appear at a later stage of development, rarely bifurcate, and then only in the ephebic stage, and are smaller, narrower, and more numerous than those of other species. The auricular plicae are similar to those of the main body of the shell. *L. lugubris* is further distinct in generally lacking coarse concentric sculpture, and in having the plicae well defined on part of the valve interior.

No species of oysters known to me are closely comparable to *L. lugubris,* although marginal variants of some North American and foreign species resemble it. Notable among these are *"Ostrea" semiplana* Sowerby, *L. bellaplicata bellaplicata,* and *L. panda* Morton.

No consistent ecologic control on any morphologic feature was

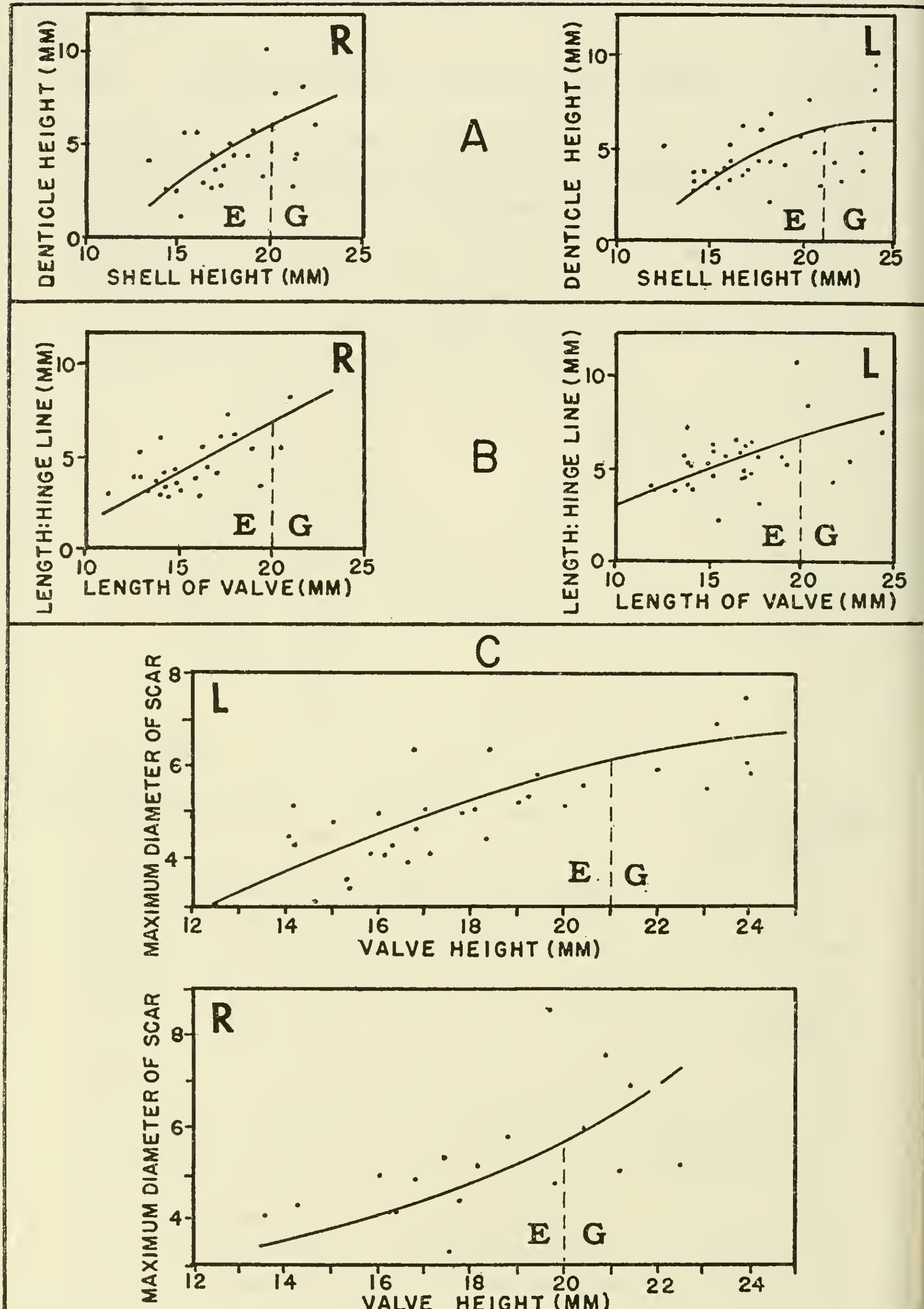

FIG. 13.—Ontogeny in *Lopha lugubris* (Conrad). A, Relationship between valve height and the amount of dorsal and lateral margin covered with denticles, measured parallel to valve height. B, Relationship between the length of the hinge line and the length of the valve. C, Relationship between the maximum diameter of the muscle scar and the height of the valve. All lines fitted visually. Approximate boundaries between ontogenetic stages marked by dashed lines. E = Ephebic; G = Gerontic; R = Right valve; L = Left valve.

noted in comparing suites of specimens from calcarenite, calcareous sandstone, dark shale, and conglomeratic calcarenite facies. The species is amazingly consistent in form for an ostreid. Similarly, there appears to be no recognizable geographic variation between Texas and northern Colorado. There is, however, some suggestion of stratigraphic variation which, when studied with large suites of specimens, may prove to be of subspecific importance. In Colorado and New Mexico, the species ranges through the Juana Lopez Member and its equivalents. In New Mexico, where the Juana Lopez includes a relatively thick series of calcarenites, shales, and calcarous sandstones, specimens of *L. lugubris* (particularly left valves) from the base of the section appear to be covered to a greater extent with radiating plicae than those from the top, which typically have the plicae limited to the valve margins. The younger specimens also have denser plication. Similar trends were noted at scattered localities in southern Colorado. The proper interpretation of these apparent trends must await larger collections, with better stratigraphic data, than are now available.

Specimens of *Lopha lugubris* commonly occur in great numbers in basal Upper Turonian calcarenites of the Juana Lopez Member and its equivalents. The valves are typically unbroken, separated, and oriented with the convex surface upward. They do not occur in beds or "colonies," and very few show any evidence of deformation due to crowding. In many cases, they are the only well-preserved, complete shells in the sediment.

Of particular interest is the commonly developed reverse curvature of the valves, and the development of exogyroid beaks in either direction. In most species of oysters that develop tightly coiled or exogyroid beaks and umbones, the direction of coiling is relatively constant and appears to be genetically controlled. Exceptions to the rule are deformed specimens growing in crowded living conditions. There are examples of reverse curvature in many of these species, but it is rare in almost all of them. The unusual coiling behavior of *L. lugubris* therefore provoked an investigation to see whether it was due to a breakdown in normal genetic control over coiling direction, or whether the species was capable of attachment by either valve.

Well-developed reverse beak curvature is found in 17.8 percent of all left valves and 23.6 percent of all right valves of *L. lugubris*. In most of these, the coiling is exogyroid. In all cases of reverse curvature the muscle scar retains its position just posterior to the midline and there is no alteration in the structure of the cardinal areas on either valve. I conclude from this that the direction of curvature is variable and not rigidly controlled genetically in this species (although posterior curvature dominates). Consistency in the position of the muscle scar and cardinal characters on both valves, irrespective of coiling direction, indicates attachment is always by the left valve, as in other ostreids.

Stratigraphic and geographic occurrence.—Lopha lugubris ranges through the Juana Lopez Member and its equivalents (zones of *Prionocyclus wyomingensis wyomingensis:* early Late Turonian, and *P. wyomingensis elegans:* middle Late Turonian) in central, south-central, and eastern Colorado, western Kansas, and northern New Mexico. The primary types were reported to have come from beds containing *P. macombi* (*P. wyomingensis wyomingensis* zone). It has been found at an equivalent level in the Mancos Shale of western Colorado and New Mexico. In Huerfano Park, Colo., fragments questionably referable to this species were collected in the upper part of the "Pugnellus Sandstone" (Codell Sandstone Member, Carlile Shale; upper part of zone of *Collignoniceras hyatti)* associated with *L. bellaplicata bellaplicata.* The ranges of these species overlap slightly in Texas also, where *L. lugubris* is found in the upper 3 feet of the Eagle Ford Shale (late Middle Turonian, upper part of *L. bellaplicata bellaplicata* zone) and in the overlying conglomeratic calcarenite bed between typical Eagle Ford Shale and Austin Chalk. Hattin's report of this species from the Blue Hill Shale Member in Kansas (lower part of zone of *Collignoniceras hyatti;* 1962, p. 84) is based on a typical specimen of *L. lugubris* collected by J. B. Reeside, Jr. Pieces of matrix adhering to the specimen are rusty-brown calcarenite characteristic of the Juana Lopez Member in Colorado and at scattered Kansas localities, and the specimen probably came from a higher level than Reeside assumed. I have also examined specimens from the Fairport Chalk Member which Hattin assigned to this species (1962, p. 54). These belong to a distinct lineage and appear most closely related to the younger *"Ostrea" tecticosta* Gabb.

Specimens of *Lopha lugubris* used in this study were obtained from localities 1 through 39 and 48, described in detail at the end of this report.

Illustrated and measured specimens.—Lectotype, selected by Stanton (1894), U.S.N.M. 9822, the original of Conrad's plate 10, figure 5b (1857); Stanton's hypotypes, reillustrated (1893, pl. 4), U.S.N.M. 22859a (Stanton's fig. 5) 22859b (Stanton's fig. 3), 22860a (Stanton's fig. 2); Meek's hypotype (1876, pl. 1, fig. 1a), U.S.N.M. 20255; new hypotypes, U.S.N.M. 8354, 22008a, b, 22210a, b, 22211, 132154-132168 inclusive, 132174, 132198, 132258, 132285; U.M.M.P. 43463-43465 inclusive, 43470-43472, inclusive, 43476, 43484, 43486, 43487. Measured specimens, unfigured, U.S.N.M. 22210c, 132169-132173 inclusive, 132175-132197 inclusive, 132199-132210 inclusive: U.M.M.P. 43460-43462 inclusive, 43467-43469 inclusive, 43473-43475 inclusive, 43477, 43488, 43489, 43491. Specimens from the upper Codell Sandstone questionably referred to this species, U.S.N.M. 132211, 132212.

LOPHA BELLAPLICATA BELLAPLICATA (Shumard)

Plate 3, figures 1-18; plate 4, figures 1-8; plate 5, figures 1-15; plate 6, figures 7-24; plate 8, figures 10, 11

Ostrea bellaplicata SHUMARD, Trans. St. Louis Acad. Sci., vol. 1, p. 608, 1860.—WHITE, 4th Ann. Rep. U. S. Geol. Surv., p. 292, pl. 47, figs. 1, 2, 3, 1884.—CRAGIN, 4th Ann. Rep. Geol. Surv. Texas, p. 199, 1893.—BÖSE, Algunas faunas del Cret. Sup. Coahuila, p. 48, 1913.—WINTON, Univ. Texas Bull. 2544, p. 62, pl. 8, fig. 5, 1925.

Ostrea (*Alectryonia*) *bellaplicata* WHITE, 11th Ann. Rep. U. S. Geol. Geogr. Surv. Terr. Idaho and Wyoming, pp. 276, 277, pl. 4, figs. 3a, b; pl. 8, figs. 2a, b, 1879.

Ostrea (*Alectryonia*) *blackii* WHITE, Proc. U. S. Nat. Mus., vol. 2, p. 293, pl. 4, figs. 1, 2, 1880; 12th Ann. Rep. U. S. Geol. Geogr. Surv. Terr. Wyoming and Idaho, pt. 1, pp. 11, 12, pl. 14, figs. 1a, b; pl. 17, fig. 5a, 1883.

Ostrea blackii WHITE, 4th Ann. Rep. U. S. Geol. Surv., p. 292, pl. 45, fig. 1; pl. 46, fig. 2, 1884.

Ostrea lugubris Conrad, STANTON, U. S. Geol. Surv. Bull. 106, pp. 58, 59, pl. 4, figs. 6-10, *non* figs. 1-5, 1893 [1894].—LOGAN, The Univ. Geol. Surv. Kansas, vol. 4, pt. 1, pp. 445, 446, pl. 91, figs. 6-10, 1898.—HILL, 21st Ann. Rep. U. S. Geol. Surv., pl. 40, fig. 9, 1901.—HERRICK and JOHNSON, Bull. Denison Univ. Sci. Lab., vol. 40, p. 202 (in part), 1900.—JOHNSON, School of Mines Quart., vol. 24, No. 2, pp. 186, 187 (in part), 1903a; Columbia Univ. Contr. Geol. Dept., vol. 10, No. 90, Geol. of the Cerrillos Hills, New Mexico, p. 114 (in part), 1903b.—SHIMER and BLODGETT, Amer. Journ. Sci. Arts, 4th ser., vol. 25, p. 61 (in part), 1908.—HOPKINS, POWERS, ROBINSON, U. S. Geol. Surv. Bull. 736, pl. 3, figs. 1, 2, 1923.—ADKINS and LOZO, Stratigraphy of the Woodbine and Eagle Ford, Waco Area, Texas, pl. 5, fig. 1, 1951.

Alectryonia lugubris, ADKINS, Handbk. Texas Cret. Foss., p. 104 (in part), pl. 16, fig. 5; pl. 24, figs. 8, 9, 1928. Listed on pls. 16, 24, as *A. lugubris* (*bellaplicata*).

DESCRIPTION

Material.—Approximately 400 well-preserved specimens (measured) from localities in Texas, New Mexico, and Colorado, including large variation and ontogenetic series, fossil "populations," and most North American types of the species. Numerous additional fragments.

General form.—Summary of measurements presented in table 2. Shell attaining moderate size, average size decreasing from south (Texas) to north (Colorado) (fig. 14a, c); inequivalve, left valve slightly larger, much more convex than right; slightly to moderately inequilateral, prosocline to acline. Outline commonly round to ovate, subquadrate, rarely triangular (pls. 3-6; pl. 3, figs. 1, 3, 5, 9-15 typical); height slightly greater than length on majority of specimens. Anterior, ventral margins straight to slightly curved; ventrolateral margins moderately curved; posterior margin with moderately convex curvature in absence of auricle, moderately concave beneath auricle when developed. Dorsolateral margins normally straight to slightly curved, gently inclined (pl. 3, fig. 3), posterodorsal margin longest, equaling two-thirds to slightly over one-half total length of shell.

TABLE 2.—*Summary of measurements for* Lopha bellaplicata bellaplicata (Shumard)

Character	Valve	No. of specimens	Range	Average
Height (H)	L	171	12.2-69.0 mm.	38.7 mm.
	R	112	4.4-63.8 mm.	37.3 mm.
Length (L)	L	173	6.3-66.1 mm.	37.5 mm.
	R	112	4.0-58.9 mm.	34.6 mm.
Width (W)	L	162	3.0-28.5 mm.	13.4 mm.
	R	109	1.0-17.2 mm.	7.4 mm.
Percent valves with H > L	LR	186/265		70%
Percent valves with H = L	LR	13/265		5%
Percent valves with H < L	LR	66/265		25%
Area, inscribing rectangle of valve	L	171	153-4416 mm.^{2}	1670.5 mm.^{2}
	R	51	235-3637 mm.^{2}	1782.1 mm.^{2}
Length, beak to posterior margin (LBP)	L	172	5.2-40.4 mm.	22.1 mm.
	R	109	1.5-37.8 mm.	19.2 mm.
Ratio, LBP : L	L	150	0.33:1-0.76:1	0.58:1
Angle between dorsal and dorso-posterior margins	L	56	5-47°	23.1°
Angle of inclination (i)	LR	249	62-95°	79°
Percent of specimens with observable attachment scar	L	138/173		80%
Height of attachment scar (HATS)	L	123	1.0-42.6 mm.	7.8 mm.
Length of attachment scar (LATS)	L	137	1.1-36.0 mm.	10.1 mm.
Area, inscribing rectangle of attachment scar (HATS × LATS)	L	124	2-1367.5 mm.^{2}	111.9 mm.^{2}
Height of smooth portion of shell dorsad to plicate ornamentation	L	50	1.5-17.4 mm.	5.9 mm.
	R	36	0-36.8 mm.	24.7 mm.

Table 2.—*Summary of measurements for* Lopha bellaplicata bellaplicata (Shumard)—*continued*

Character	Valve	No. of specimens	Range	Average
Number of primary plicae at first appearance	L	50	6-17	10.6
	R	36	4-22	13.4
Total number of plicae (plicate valves only)—				
At 10 mm. height	L	44	8-19	14
	R	13	6-16	11.6
At 20 mm. height	L	48	10-21	15.8
	R	28	7-22	14.8
At 30 mm. height	L	37	12-27	17.9
	R	26	8-22	19
At 40 mm. height	L	18	13-22	18.4
	R	21	8-23	15.8
At 50 mm. height	L	6	14-23	18
	R	13	11-22	17.9
Total number of plicae at margin	L	173	9-27	16.4
	R	104	1-26	15.9
Number of plicae in 20 mm. length at 20 mm. height	L	78	3-8.5	5.6
	R	28	4-7	5.9
Percentage increase in plicae by bifurcation	L	50	12-263%	79.6%
	R	34	0-400%	72.1%
Width of posterior auricular sulcus, 20 mm. below beak	L	53	2.4-9.4 mm.	4.9 mm.
Width of median plica 20 mm. below beak	L	78	2.0-7.3 mm.	3.7 mm.
Inclination of beak, umbo:				
Percent opisthogyre	L	115/173		66.5%
	R	68/112		60.7%
Percent orthogyre	L	44/173		25.4%
	R	27/112		24.1%
Percent prosogyre	L	14/173		8.1%
	R	17/112		15.2%
Length of hinge line (LHL)	L	50	4.2-29.0 mm.	14.5 mm.
	R	43	5.1-28.5 mm.	15.0 mm.
Ratio, LHL:L	L	50	0.21:1-0.75:1	0.37:1
	R	43	0.16:1-0.60:1	0.37:1
Height of denticulate portion of margins (HD)	L	32	5.1-30.0 mm.	10 mm.
	R	41	1.8-33.0 mm.	12.8 mm.
Number of denticles in 5 mm. distance along margin	L	28	5-13	9
	R	34	6-20	9.7
Ratio, HD:H	L	32	0.15:1-0.69:1	0.30:1
	R	40	0.09:1-0.79:1	0.28:1
Maximum diameter of muscle scar (MDS)	L	63	5.2-20.3 mm.	14.0 mm.
	R	45	7.2-20.1 mm.	14.2 mm.
Ratio, MDS:H	L	63	0.23:1-0.42:1	0.31:1
	R	45	0.24:1-0.41:1	0.32:1

Rarely, dorsolateral margins moderately rounded or steeply inclined (pl. 5, figs. 7, 10). Left valve typically moderately to highly convex, rarely flattened (pl. 5, figs. 1, 2 typical). High point dorsocentral, commonly on crest of median plica. Slope of anterior, ventral flanks moderate, dorsal slope steep, posterior slope gentle, flattened on auricle. Right valves slightly concave, flat, or gently arched, in rare cases gently and irregularly undulating. High point of right valve on umbone.

Auricles.—Anterior auricle a flattened dorsoanterior expansion of margin and first few plicae; auricle small, rounded, semicircular, commonly absent, in most cases separated from body of shell by an enlarged interplical sulcus, the anterior auricular sulcus (pl. 3, fig. 15). Posterior auricle variable, normally well developed, ranging from indistinct, small, flattened area on dorsoposterior flank (pl. 3, fig. 13) to prominent, flattened, projecting dorsoposterior salient (pl. 4, fig. 2), straight dorsally, narrowly rounded posteriorly, slightly curved to concave ventrally, delineated by concave midposterior notch in valve outline. All gradations noted between the two forms. Auricle separated from body of shell by faint and shallow, to deep and prominent auricular sulcus, an enlarged interplical sulcus (pl. 3, figs. 11, 15), connecting umbo and midposterior notch.

Beaks, umbos.—Opisthogyre, rarely exogyroid (one volution). Beak of left valve flat, small, bluntly pointed to moderately rounded, commonly obscured by attachment scar. On right valve, posterior curvature of beak, umbo, greater than on left, rarely orthogyre or exogyroid, moderately convex, smooth or with faint growth lines (pl. 5, fig. 7). Left and right umbones typically moderately to highly inflated, rarely flat, right valve with greatest umbonal convexity. Umbonal axes moderately curved, opisthocline medially, acline ventrally on umbo. Beaks situated anterior to midline, about one-third the length from the anterior margin, slightly elevated above dorsal margin but not projecting.

Attachment scar.—Predominantly small, commonly minute or apparently missing, rarely large (pl. 3, fig. 17), position middorsal on early part of umbone; highly variable in shape, normally round to subovate, slightly concave, steeply inclined to plane of commissure. Attachment commonly to small, smooth oyster shells, other *Lopha,* elongate objects (sticks, etc., but without clasping processes) gastropods, and large pelecypods. Shell thin in area of scar, apparently reinforced with secondary calcite layers in some specimens. Shape, size of scar unrelated to that of adult valve, or to plication density.

Ornamentation, left valve.—Beak smooth or with fine growth lines; first 3-8 mm. of umbo with fine growth lines, flat microlamellae, faint concentric undulations, rarely faint radiating undulations (pl. 3, fig. 3). Majority of shell marked with coarse radiating plicae transected by prominent concentric lamellae (pl. 3, fig. 15). Plicae arise abruptly on early part of umbo, extend to commissure, increasing in number irregularly through bifurcation, especially on early plicate portion of valve, posterior auricle, and on ventral and lateral margins of large shells. Plicae high, rounded, steep-flanked, broader than angular interplical sulci between them, becoming coarser but lower, more rounded with age, faint or absent near margins of largest valves. Secondary plicae smaller, lower, narrower than primaries but more rapidly expanding, commonly equal to primary plicae in size at valve margin. Posterior auricular plicae smaller, narrower, more divergent, more extensively bifurcating, more curved than those of main body of shell (pl. 3, fig. 11). Plicae most prominent centrally and ventrally on valve; spinose, subnodose, fluted on rare left valves where intersected by coarse, raised concentric lamellae (pl. 3, fig. 6; pl. 4, fig. 4). Rare adult shells smooth, or with plicae faintly developed throughout (*L. blacki* types), expressed mainly as marginal crenulations.

Development of plicae preceded by formation of a few coarse, crowded lamellae on umbone. Concentric sculpture on plicate portion of valve consisting of prominent, moderately to widely spaced, concentric lamellae separated by numerous, very fine, crowded, irregularly spaced, growth lines and microlamellae (pl. 3, fig. 15). Major lamellae terminally in contact with succeeding ones, or raised above valve surface, forming flutes over plicae.

Ornamentation, right valve.—Right valve distinct from left in detail of ornament. Beak smooth or with faint growth lines. Umbo almost totally devoid of plicae; smooth stage higher than that of left valve (pl. 5, fig. 7). Umbo smooth or with very fine, crowded, growth lines and microlamellae; commonly with narrow zone of crowded, coarse lamellae ventrally, near point of origin of plicae. Plicate portion of valve marked by numerous, raised, closely spaced, major concentric lamellae (pl. 5, fig. 8), becoming crowded near margin of adult valves, much coarser than on left valve.

Plicae originate abruptly on ventral portion of umbo or below it; plicae very prominent, high, steep-sided, with sharp to narrowly rounded crests, fluted and spinose at intersection with major concentric lamellae. Interplical sulci narrower than plicae, deep, angular at base, more prominent than those of left valve. Radial elements most prominent at valve margin, becoming coarser with age.

Cardinal area.—Composed of central resilifer bounded laterally by flat to slightly arched, striated, triangular lateral cardinal plates. Resilifer of left valve shallow (most common) to moderately concave, triangular to subtriangular with bent dorsal apex, slightly flared base; moderately narrow (common) to broad (rare). Lateral cardinal plates subequal to moderately unequal (on shells with prominent posterior auricle), posterior plate largest; each plate larger than resilifer in most valves. Narrow marginal cardinal troughs commonly developed between lateral cardinal plates and margin of valve, most common on left valves. Cardinal area of right valve similar to left except for resilifer, which is commonly shallow (concave), flat, or rarely raised into a low midcardinal fold. Majority of right valves with shallow resilifer bounded ventrally by a raised lip (partial midcardinal fold).

Cardinal area marked with moderately strong, crowded, irregularly spaced, horizontal striae, raised lines, and narrow ridges of various sizes. Horizontal elements transected by faint, crowded, vertical lines. Ornament most strongly developed in adult shells, on lateral cardinal plates. Cardinal area color-banded on some specimens, with narrow, dark horizontal lines on lighter background. Hinge line short to moderately long (in presence of well-developed posterior auricle), straight to slightly curved (common), concave toward center of valve except below resilifer, where slightly convex (pl. 5, fig. 13).

Denticles.—Present on inner dorsolateral margins of both valves; small, simple, subround to elongate perpendicular to margin, in some valves their trace visible on lateral margin of shell, crossing lamellae. Interspaces equal to or slightly wider than denticles. Denticles situated on commissure and in narrow trough just inside it, generally restricted to dorsolateral margins, rarely extending well down margin, generally faint on young shells, best developed on adults, becoming indistinct on large old valves.

Commissure, interior surface.—Commissure situated at margin of left valve, just inside margin of right valve; normally undulating, rarely zigzag or flattened (old specimens). Plicae faintly expressed on interior of left valves near margins, more prominent on interiors of right valve, extending to center as rounded folds, sulci. Scattered, sinuous, pallial grooves faintly developed on a few valves.

Muscle scar.—Monomyarian, insertion area of moderate size, well defined, subcrescentic to comma-shaped if not worn (pl. 5, fig. 13), slightly concave, bordered ventrally, posteroventrally by low raised lip, overlapped dorsally and anteriorly by inner shell layers; position subcentral, in posteroventral quadrant of valve on corner nearest center. Surface of area coarsely striated with flat, crowded microlamellae, scattered raised ridges, their trace conforming to the growth lines; rare muscle scars exhibit faint radiating lines.

Shell structure.—Thickness moderately variable in single valve; greatest in cardinal area and vicinity of beak and umbone, thinning ventrally and laterally. Crest of left valve commonly thinner than shell immediately around it. Shell thickness of average left valve: cardinal area, 4.1 mm.; crest, 2.9 mm.; 10 mm. above ventral margin, 1.8 mm. Right valve: Cardinal area, 6 mm., center of valve 2.3 mm.; 10 mm. above ventral margin, 1.4 mm. Only subnacreous layer preserved, forming bulk of shell, consisting of subhorizontal to gently curved and inclined plates of calcite arranged en echelon in distinct to roughly defined layers. Inclination of plates in each layer opposed to that in every other, or every third layer adjacent to it (pl. 8, fig. 11). Individual calcite plates thin, moderately short, of irregular thickness, with irregular terminations. Layered arrangement of plates, and opposed inclination of units well defined over most of shell, less distinct in cardinal–umbonal area, where orientation of plates more uniform, not commonly with opposed inclination.

ONTOGENY

Numerous well-preserved specimens of *Lopha bellaplicata bellaplicata* in the collections used for this study retain the morphologic detail of the early ontogenetic stages. The small size, or apparent absence, of the attachment scar on many left valves is of additional help in ontogenetic study since it allows observation of even the earliest stages of the attached valve, an opportunity not afforded by many species of oysters. Graphs and figures depicting the ontogenetic development of *L. bellaplicata bellaplicata* are presented in figures 2-4, 6b, c, 9b, 14-17. Ontogenetic changes were observed in the following structures.

Concentric sculpture.—*Nepionic* shell smooth or with faint growth lines; *nepionic–neanic boundary* marked by a prominent growth line. Fine growth lines characterize *early neanic* development; *middle* and *late neanic* marked with more crowded growth lines, microlamellae, small folds and undulations, becoming progressively coarser. Abrupt appearance of plicae during *neanic* preceded by a few, closely spaced, moderately coarse lamellae or growth lines. *Ephebic* stage characterized by scattered coarse lamellae on left valve, some raised above shell surface, and by numerous, closely spaced, very prominent raised lamellae on right valve. Growth lines, microlamellae crowded between major lamellae. *Neanic–ephebic boundary* marked on many

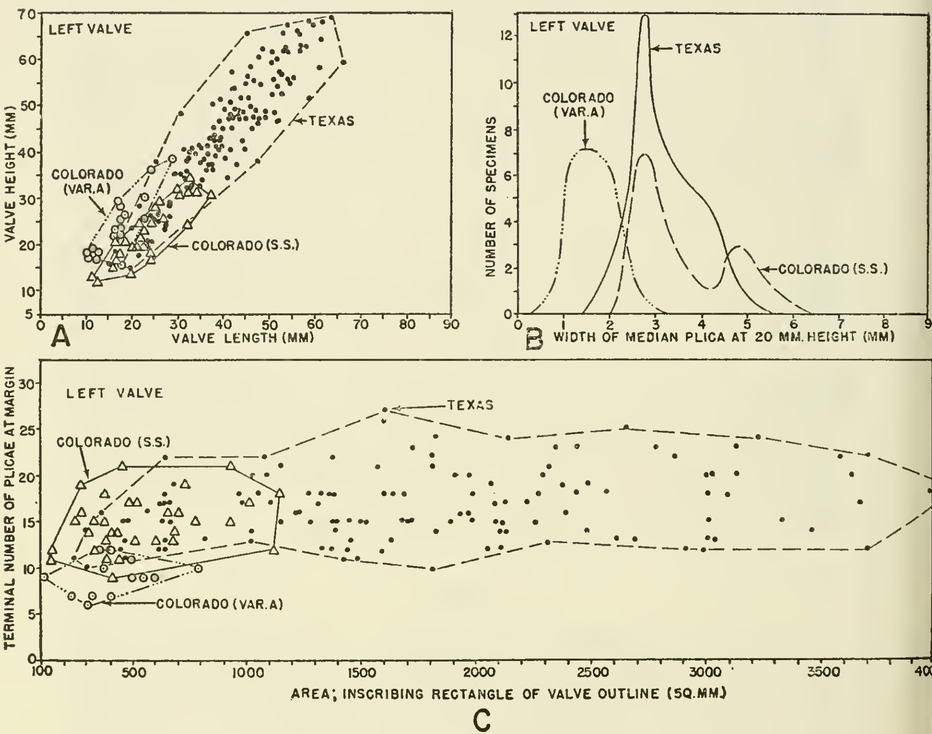

FIG. 14.—Geographic variation in *Lopha bellaplicata bellaplicata;* comparison of Texas and Colorado specimens of the typical form of the subspecies, and Colorado representatives of *L. bellaplicata bellaplicata* variety A. A, Variation in height to length relationship and size range. B, Variation in width of the median plica 20 mm. below the beak. C, Variation in size range, and in number of plicae relative to area of an inscribing rectangle of valve.

shells by first common occurrence of major lamellae. Lamellae become gradually coarser, more elevated, more crowded through *ephebic* development, probably recording a decrease in growth rate and increase in the length of resting periods with increasing age. *Gerontic* stage characterized by numerous, coarse, crowded lamellae and coarse growth lines near margin of old shells.

Radiating sculpture.—*Neanic* stage marks first abrupt appearance of plicae, anywhere from *earliest* to *late neanic* in left valves, at or near beginning of *ephebic* development in right valves. Plicae become gradually coarser with age to *late ephebic* stage on left valves (about 40 mm. height); beyond this they become fainter, broad, low folds, many of which disappear with continued deterioration of ornamentation during *gerontic* development. Plicae of right valve become coarser with age through at least *early gerontic* stage. Plicae bifurcate throughout development; bifurcation greatest in *late neanic* or *early ephebic* stage, again at *late ephebic* development, the former possibly marking a period of accelerated growth.

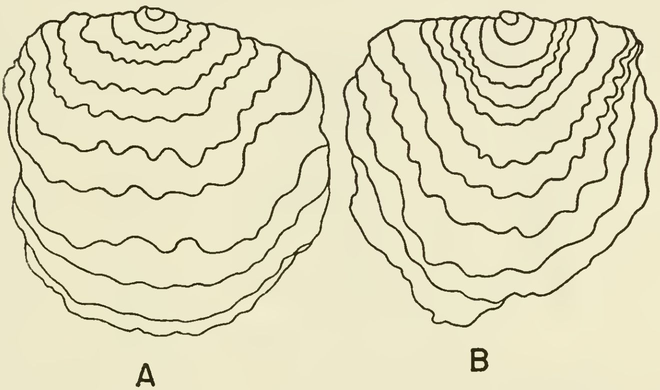

FIG. 15.—Ontogeny of *Lopha bellaplicata bellaplicata* (Shumard). Growth line traces at approximately 2.5 mm. intervals on representative left (A) and right (B) valves of the species. Traces show developmental history of the valve outline and the auricles. Drawings ×1. A, U.S.N.M. 132225; B, U.S.N.M. 132239.

Convexity.—Outward curvature of valves (convexity) slight in *nepionic* shell, on the left valve (fig. 3a) becoming moderate to great during *neanic* and *early ephebic* development, decreasing through *late ephebic* stage. Relatively abrupt flattening, flaring of flanks characterizes *gerontic* development. On right valves (fig. 3b), moderate outward curvature characterizes *neanic, earliest ephebic* stages; gradual to abrupt flattening occurs during most of *ephebic* stage, Upturning of valve margin and flaring are common *gerontic* characters.

Valve outline and auricles.—(Based on fig. 15.) *Nepionic* shell subround. *Neanic* shell ovate, with ventral growth exceeding lateral growth. Auricles appear as faint salients of dorsolateral margins in

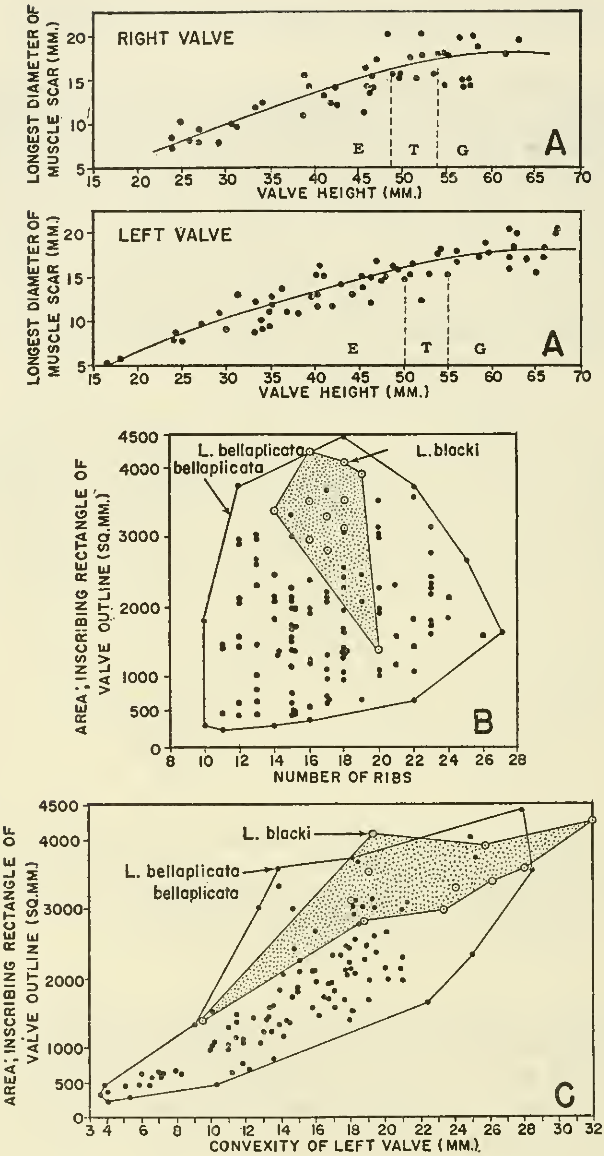

FIG. 16.—A, Ontogeny of the muscle scar in *Lopha bellaplicata bellaplicata* (Shumard), showing relationship between maximum diameter of the posterior adductor muscle scar and the height of the valve. Note the decline and virtual cessation of scar growth with increased size and age. Approximate boundaries between ontogenetic stages marked by dashed lines. E = Ephebic; T = Ephebic-Gerontic transition; G = Gerontic. B, Comparison of the plication density of *Lopha bellaplicata bellaplicata* with that of *L. blacki* (White), showing total overlap of the two forms. C, Comparison of the relative convexity of *L. bellaplicata bellaplicata* and *L. blacki*, showing nearly total overlap between the two forms.

late neanic or *early ephebic* stage, corresponding to development of plicae. During *ephebic* and *gerontic* development ventral and posterior growth exceeded that anteriorly and the auricles continued to expand at a constant, but greater, rate than normal lateral expansion.

Curvature of growth axis (midline).—(See fig. 3c.) Axis slightly curved in *nepionic* shell, more moderately curved during *neanic* and *early ephebic* development, slightly curved, becoming nearly straight through *ephebic* and *gerontic* stages. Inclination of *neanic* shell possibly opisthocline. *Ephebic, gerontic* shells prosocline.

Muscle scar.—Scar growth constant through *neanic, ephebic* stages, at a rate less than overall growth of shell; growth rate tapers off during *latest ephebic* stage (40 to 45 mm.), corresponding to decrease in rate of shell growth, and ceases altogether in *gerontic* stage (fig. 16a), after animal reaches maximum size. Muscle scar migrates ventrally through *neanic, ephebic* stages, with increase in shell size.

Cardinal area.—Elements of cardinal area distinct in *early ephebic* stage, becoming thicker, broader, better defined at a diminishing rate through life of animal. Length of hinge line gradually increasing through *middle ephebic* stage at a rate slightly less than overall lateral expansion of valve; during *late ephebic* and *gerontic* stages growth of hinge line continues, but at a rate greater than that of lateral expansion of valve (fig. 17c).

Denticles.—Present in all observed stages, forming throughout life and gradually extending farther down commissure with age. Rate of transgression of denticles down margin (denticle height vs. valve height at various growth stages) uniform and less than rate of ventral shell expansion during *neanic* through *mid-ephebic* stages (20-43 mm. height), accelerating and eventually exceeding rate of ventral shell growth in *late ephebic* and *gerontic* stages (fig. 19b). Density of denticles decreased at a variable rate throughout growth of shell to *gerontic* stage (fig. 17a), where it remained stable.

REMARKS

Lopha bellaplicata bellaplicata is the best-known species in the *L. lugubris* group. It is represented by a greater number of individuals, from more localities, and from a broader geographic range than any other member of the group. This is primarily due to its extensive occurrence in the upper Eagle Ford Shale of Texas, and the numerous collections available from that area.

L. bellaplicata bellaplicata may be distinguished from the morphologically similar subspecies *novamexicana* by its more rounded or

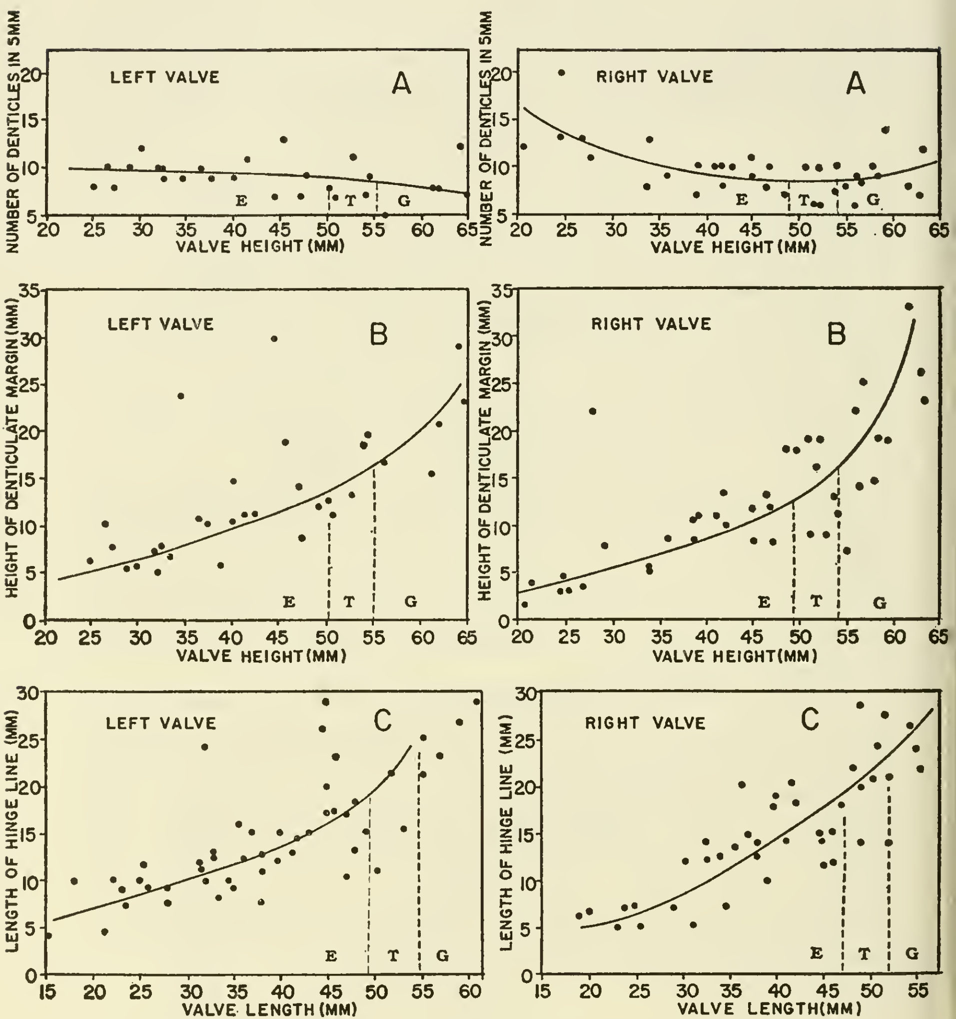

FIG. 17.—Ontogenetic development of *Lopha bellaplicata bellaplicata* (Shumard). A, Relationship between number of denticles in 5 mm. length (measured along margin) and valve height, showing decrease in density with age, and with increase in size. B, Relationship between the height of the valve and the extent of the denticulate portion of the margin, measured in terms of height, showing increase in extent of denticles with age and size. C, Relationship between length of hinge line and valve length, showing increase in size of hinge line relative to lateral expansion with age and size. All lines fitted visually. Approximate boundaries between ontogenetic stages marked by dashed lines. E = Ephebic; T = Ephebic–Gerontic transition; G = Gerontic.

subquadrate outline, less oblique shell, gently sloping posterodorsal margin, more projecting dorsoanterior margin and auricle, larger and better-defined posterior auricle, which is dorsoposterior rather than centroposterior in position, and by its less convex left valve, especially in the umbonal area. In the subspecies *bellaplicata,* the plicae originate at a later developmental stage, especially on the right valve, and are smaller, narrower, more numerous, more extensively bifurcating, and differentially developed on the auricles and main body of the valve. The posterior auricular sulcus is narrow and composed of a single, accentuated interplical sulcus.

The differences between *L. bellaplicata bellaplicata* and *L. lugubris* have previously been discussed under "Remarks" for the latter species. *L. bellaplicata bellaplicata* is easily distinguished from its variety A by being broader, rounder, less erect, auriculate, and in having better defined, much more numerous plicae.

Among foreign species of *Lopha, L. bellaplicata bellaplicata* is most closely comparable to *Lopha syphax* (Coquand), a Lower Cenomanian species which is larger, more coarsely and irregularly ribbed, and has a more pronounced anterior auricle. It further differs from the North American species in being proportionately higher, having a larger posterior auricle, and a more twisted umbone. This form may well be ancestral to the North American group of *L. lugubris.*

White (1880, p. 293; 1883, p. 12) gave the name *Ostrea* (*Alectryonia*) *blacki* (a *Lopha*) to a variant of *L. bellaplicata bellaplicata* which he considered distinct on the basis of its greater size, flatter valve, coarser and less numerous plicae, proportionately broader ventral dimension of the valves, and longer, more oblique dorsal margin. He evidently did not recognize the apparent age equivalency of the two forms. Cragin (1893, p. 199) and later writers have established that the two species both came from the upper Eagle Ford Shale of Texas. The present study validates this observation.

White's syntype lot of *L. blacki* consists of 26 specimens, most of them large, displaying late ephebic or gerontic ornament, and obviously worn. Among these latter specimens are the ones White illustrated (1880, pl. 4, figs. 1, 2; 1883, pl. 14, figs. 1a, b, pl. 17, fig. 5a; 1884, pl. 45, fig. 1, pl. 46, fig. 2). His collection also includes, however, specimens identical to *Lopha bellaplicata bellaplicata,* and a complete morphologic gradation exists between the two forms in this and other collections from the upper Eagle Ford Shale.

Differences between the species cited by White break down under simple biometric comparison. The syntype lot of *L. blacki* contains predominantly large individuals, but all fall within the size limits of *L. bellaplicata bellaplicata* populations (fig. 16b). The plicae are not less numerous than those of *L. bellaplicata bellaplicata* (fig. 16c). They appear broader owing to the great amount of wear on certain valves. The valves are neither flatter (fig. 16b), nor broader ventrally than typical examples of *L. bellaplicata bellaplicata,* and there is total overlap in the inclination of the dorsal margin. Slight differences existing between these forms are probably the product of environmental control. Examples of *L. blacki* are from a relatively coarse argillaceous sandstone, while forms typical of *L. bellaplicata bellaplicata* occur in finer clastic and mud facies.

Lopha bellaplicata bellaplicata occurs in a number of different sediments over a broad area and provides a good basis for the study of environmental control on shell form. This opportunity is not presented by other members of the group, which occur in more uniform lithologies. Large collections of *L. bellaplicata bellaplicata* were obtained from buff calcarenitic chalk, gray carbonaceous and calcareous shale with numerous shell fragments, shaly calcarenite, sandy shale, and in argillaceous to calcareous quartz sandstone (Colorado). A single specimen from New Mexico was found in dark clay shale.

In collections from Texas, oysters from the calcarenitic marl units are thinner shelled, less convex, less inclined, and have less prominent posterior auricles than those from calcarenitic, sandy, or clay shale, and from thin calcarenites. Specimens from the latter lithology have the largest, thickest shells. These differences are probably related to differences in the energy conditions of the environment. Current and wave action was probably much stronger in the shallow-water environment where the calcarenites were formed than it was in the quieter, presumably deeper marl-forming areas. Thickening of the shell appears to be an adaption to this more active environment, its chief function being to strengthen the valves.

Specimens from New Mexico, found as gypsum replacements in dark clay shale, are typical of the species. The Colorado sample, however, shows significant environmental, and possibly geographic variation. Specimens from the Codell Sandstone Member ("Pugnellus Sandstone") of south-central Colorado attain a much smaller size than those from Texas and show a somewhat greater variation in marginal outline. The majority of specimens from Colorado, though smaller, are typical of the species and closely comparable morphologically to the Texas forms (compare pl. 3, figs. 1-15, with pl. 6, figs. 7-15).

Marginal variants of the Colorado sample, however, show structural features that are not within the range of variation observed for the Texas specimens. The most notable variant, here termed variety A, is a narrow, high form with relatively few plicae and no auricles (pl. 6, figs. 1-6, 19), possibly but not definitely a product of crowded growth conditions. This form is treated separately on subsequent pages.

A second unusual variant of Colorado *L. bellaplicata bellaplicata* assemblages is exceptionally long, with abnormally produced anterior and posterior auricles and, in some cases, very broad, rounded, plicae (pl. 6, figs. 11, 15). This form is also represented by a single specimen in the upper Blue Hill Shale, where it is probably a marginal variant of *L. bellaplicata novamexicana,* gradational into the younger *L. bellaplicata bellaplicata.*

Finally, rare specimens of *L. bellaplicata bellaplicata* from Colorado are nearly smooth, and lack well-developed plicae (pl. 6, figs. 17, 18, 21, 24), a condition not attained by Texas representatives of the species. This is most commonly expressed on right valves.

Analysis of these differences between Texas and Colorado representatives of *L. bellaplicata bellaplicata* is difficult, since it is not possible here to separate geographic variance from environmental variance. The shallow-water, high-energy environment indicated by the Codell Sandstone lithology and sedimentary structures is not duplicated in Texas, so there is no basis for comparison of environmental influences. I would not consider any of the unique variation in morphology shown by the Colorado sample as being particularly adaptive to the shallower, more turbid, active Codell environment. Modern oysters do not show such structural adaptations in similar niches. This is the only argument that can be presented in favor of the differences being geographic, and thus genetically controlled. Even if this were the case, I would not consider the differences between the Texas and Colorado samples to be of subspecific magnitude, especially since they are shown by a very small percentage of the specimens examined.

Stratigraphic and geographic occurrence.—In Texas, *L. bellaplicata bellaplicata* occurs in the upper 50 to 70 feet of the Eagle Ford Shale, being most common in the upper 15 to 25 feet, and forming prominent beds in the upper 2 to 5 feet at various localities. The species has been found in New Mexico at only one locality, in the dark shale of the Benton Subgroup (Mancos), on the Zuni Indian Reservation. In Colorado, the species is restricted to the "Pugnellus Sandstone"

(Codell Sandstone Member) of the Carlile Shale, where it is found in limestone and calcareous sandstone lenses throughout the unit.

In Colorado, the species has been found at localities 40-43, 55, and 58-61; in New Mexico, at locality 45; in Texas, at localities 15, 44, 46-54, 56, and 57, described in detail at the end of this report.

Illustrated and measured specimens.—The holotype is presumed to have been lost in the fire at the St. Louis Academy of Science. Neotype, here selected, a mature left valve (pl. 3, fig. 11), U.S.N.M. 132222. White's hypotypes, paired valves (1879; 1884), illustrated on plate 3, figure 13, U.S.N.M. 12383; White's "paratype" of *O.* (*A.*) *blacki* (1884, pl. 46, fig. 2), U.S.N.M. 8024b. Stanton's hypotypes (1893 [1894], pl. 4), U.S.N.M. 11822a (Stanton's fig. 8), U.S.N.M. 22860b, c, d (Stanton's figs. 9, 6, 4, respectively), 22861 (Stanton's fig. 7). New hypotypes, U.S.N.M. 8024a, c. d; U.S.N.M. 11882b; U.S.N.M. 22009a, b; U.S.N.M. 22011b; U.S.N.M. 132213-132221, inclusive, U.S.N.M. 132223-132244, inclusive; U.S.N.M. 132250, 132251, 132283, 132284, 132305-132308; U.M.M.P. (University of Michigan Museum of Paleontology) 38038, 38039, 38041, 43466, 43478, 43482, 43483. Measured specimens, unfigured: U.S.N.M. 8024e, U.S.N.M. 11882c, U.S.N.M. 22009; U.S.N.M 22011c; U.S.N.M. 22860e, U.S.N.M. 132245-132249, inclusive; U.S.N.M. 132291-132300, inclusive, 132304.

LOPHA BELLAPLICATA BELLAPLICATA var. A

Plate 6, figures 1-6, 19

DESCRIPTION

Material.—36 left and right valves, moderately well preserved, from the Codell Sandstone Member. ("Pugnellus Sandstone"), Carlile Shale, at a number of localities in Huerfano Park, Colorado. The collection includes mostly small individuals, forming a partial growth series.

General form.—Summary of measurements presented in tables 3, 4. Shell small, inequivalve, left (lower, attached) valve much more convex, slightly larger, less curved dorsally than right; most valves slightly inequilateral, prosocline to erect. Highly variable in outline: typically elongate-ovate along midline axis (pl. 6, figs. 1, 2, 5) less commonly broadly subovate due to lateral flaring of posterior or posteroventral margins (pl. 6, figs. 6, 19), or irregularly elongate due to crowded growing conditions. Height greater than length. Anterior margin steeply inclined, straight to slightly and irregularly curved, without anterior auricle. Ventral margin moderately to narrowly rounded, regular to irregular. Posterior margin with irregular outline, slightly concave (outward) dorsally, moderately to

TABLE 3.—*Summary of measurements on left valves of* Lopha bellaplicata bellaplicata *var. A*

Character	No. of specimens	Range	Average
Height (H)	21	15.4-38.4 mm.	23.4 mm.
Length (L)	22	10.1-29 mm.	17.0 mm.
Ratio, L:H	17	0.56:1-1.20:1	0.73:1
Width (W)	23	3.0-12.9 mm.	7.7 mm.
Area, inscribing rectangle of valve (A)	20	179.6-1128.1 mm.^{2}	432.9 mm.^{2}
Length; beak to posterior margin (LBP)	22	3.9-14.4 mm.	9.4 mm.
Ratio, LBP:L	21	0.39:1-0.71:1	0.53:1
Angle of inclination (i)	20	67-101°	82.3°
Height of attachment scar (HATS):			
Maximum vertical diameter	20	2.6-21.9 mm.	9.8 mm.
In plane of commissure	20	1.4-21.9 mm.	8.4 mm.
Length of attachment scar (LATS)	20	2.3-17.2 mm.	9.5 mm.
Area, inscribing rectangle of attachment scar (HATS × LATS)	20	6-354.8 mm.^{2}	110.6 mm.^{2}
Height, smooth young stage (HSS), dorsal part of valve	22	2.3-23.4 mm.	9.98 mm.
Height, plicate portion of valve	20	4.9-26.5 mm.	13.6 mm.
Ratio, H:HSS	20	0.108:1-0.777:1	0.432:1
Number of plicae at first appearance	22	4-12	8
Number of plicae at 10 mm. height	14	4-12	8.5
Number of plicae at 20 mm. height	16	5-12	9.6
Total number of plicae	22	4-14	9.3
Number of plicae in 10 mm. distance (length) 10 mm. below beak	13	3-6.75	4.8
Width of median plica at 10 mm. height	21	0.8-2.6 mm.	1.7 mm.
Percentage of plicate valves with bifurcating plicae	23		78.3%
Percentage increase in number of plicae by bifurcation	18	9.1-41.7%	17.9%
Curvature of beaks and umbones:	21		
Opisthogyre			81%
Orthogyre			9.5%
Prosogyre			9.5%

slightly convex ventrally (pl. 6, figs. 2, 6, 19). Dorsal margin short, straight to moderately curved, generally equal to width of attachment scar. On rare specimens, ventroposterior margin flared outward, considerably flattened, forming small, rounded, semicircular, posterior auricle separated from main body of shell by a broad, shallow, indistinct auricular sulcus, generally a broadened interplical sulcus or 2 sulci with the intermediate plication greatly reduced.

Right valve flat to slightly arched; convexity greatest in umbonal region; flanks flat, rarely concave near margin when ventral edge upturned. Left valve moderately to highly convex, convexity greatest at upper edge of attachment scar where prominent; otherwise crest and high point situated medially on lower third of valves. Anterior slope typically steep, ventral slope shallow, posterior slope steep dorsally, moderate to gentle or irregular ventrally, depending on development of posterior auricle.

TABLE 4.—*Representative measurements of right valves associated with* Lopha bellaplicata bellaplicata *var. A and possibly belonging to this form.*

Character	U.M.M.P. 43406	U.M.M.P. 43413
Height (H)	19.1 mm.	16.7 mm.
Length (L)	9.6 mm.	15.8 mm.
Width (W)	3.5 mm.	4.8 mm.
Height, cardinal area	2.2 mm.	
Length, hinge line	3.9 mm.	
Width, midcardinal fold	1.9 mm.	
Height, denticulate margin	7.1 mm.	
Number of denticles in 5 mm. distance	11	
Maximum diameter of muscle scar	6.9 mm.	
Minimum diameter of muscle scar	3.6 mm.	
Distance (height), dorsal edge of muscle scar to beak	8.1 mm.	
Angle of inclination (i)	82°	61°
Number of major lamellae in 5 mm. height (midvalve)		3

Beaks and umbos.—Beak, umbo unknown on left valve, obscured by attachment scar, apparently slightly recurved, orthogyre to slightly opisthogyre. Beak of right valve known from numerous, nearly smooth, associated upper valves; pointed to narrowly rounded, smooth, normally opisthogyre, moderately recurved. Umbone gently arched, in some valves separated from main body of shell by a constriction or large lamella.

Attachment scar.—Area of attachment terminal, small to medium size, round to subovate, flat to slightly concave, steeply inclined or vertical relative to plane of commissure, rarely moderately inclined. Scar surface smooth or with faint concentric markings of shell to which oyster attached; attachment to other *Ostrea* and *Inoceramus* shells. In some specimens scar area appears secondarily thickened by additional layers of lamellar calcite.

Ornamentation, left valve.—Variable: Beak and early umbo smooth, or with fine concentric ornamentation. Lower umbo and portion of valve between attachment scar and plicate flanks marked by numerous fine, crowded, overlapping lamellae, fine growth lines, and scattered concentric undulations or moderate size lamellae. All lamellae terminally in contact with succeeding ones.

Plicae commonly arise abruptly at or slightly below ventral edge of attachment scar (pl. 6, fig. 2). Plicae large, coarse, rounded, broader than interspaces between them, their width greater than their height, subequally developed to irregular (compare pl. 6, fig. 1, with fig. 2), bifurcating irregularly over entire valve; rate of bifurcation greatest dorsally. Secondary plicae rapidly expanding, rarely attaining size of primaries near commissure. Plicae become broader, lower, more rounded, indistinct near ventral and ventrolateral margins of a few valves, rarely disappearing altogether (pl. 6, figs. 2, 4). Interplical sulci narrow, sharp to narrowly rounded at base.

Concentric ornamentation on plicate portion of valve consisting of numerous crowded, subequally to irregularly spaced, fine to medium size, overlapping lamellae, most terminally in contact with succeeding lamellae, and scattered coarse, raised lamellae; latter particularly common near margin. Plicae finely fluted at intersection with major lamellae. Radial and concentric ornamentation of posterior auricle, where developed, more irregular than that of main body of shell; plicae smaller, more curved and sinuous, more extensively bifurcating. Concentric elements coarser on auricle.

Ornamentation, right valve.—Beak smooth; umbone with scattered fine growth lines and faint concentric undulations. Remainder of valve covered with numerous fine growth lines, scattered flat lamellae of several sizes, and low concentric undulations, irregularly spaced and unequally developed, becoming coarser toward valve margins. Some valves with several coarse lamellae crowded near margins.

Majority of specimens lack radiating ornamentation. A few right valves have traces of plicae near and on margins. Rare valves exhibit well-developed plicae similar to those of left valve; plicae arise abruptly near ventral and ventrolateral margins and extend to the edge. Variants of these associated right valves illustrated on plate 6, figures 3, 4.

REMARKS

The collections contain no valves with the interior preserved, and the thin, fragile nature of the shell makes it difficult to excavate one successfully. Presumably, the internal structures are the same as those on *L. bellaplicata bellaplicata* forma typica. Right valves were not found coattached with left valves. Their description is based on numerous smooth valves occurring in the same sediment and conforming in shape and size to typical left valves.

It seems advisable to describe separately this marginal variant of *L. bellaplicata bellaplicata* for two reasons. First, a continuous morphologic series cannot be established between the typical form of the species and variety A. The specimens illustrated on plate 6, figures 6 and 19, are the only ones that approach the typical form, and these show significant differences. Graphs and charts comparing structures of the two forms invariably show a bimodal distribution with little overlap (figs. 14a-c). There is a possibility, therefore, that the differences between the two forms are not totally environmental, but genetic, and that they were related and coexisting subspecies or species.

This possibility is further evident considering the apparent environment of deposition of the Codell Sandstone Member. The Codell contains a diverse normal marine, shallow-water invertebrate fauna. The deposit has all the characteristics of a shallow-water, inner sublittoral sand sheet formed under moderate- to high-energy conditions of current and wave action. Variety A and the typical form of the species occur together, represented by numerous well-preserved shells, in the same lenses of fossils. They appear to have lived together and were probably subject to the same environmental influences. *L. bellaplicata bellaplicata* var. A occurs characteristically in clusters, where the elongate form of the shell appears to be, in part, a product of crowding. But free-growing examples are also known, and these are equally elongate. The form, convexity, and ornamentation are more regular on the free-growing specimens. The differences between the two forms therefore do not appear to be ecologic, or wholly a product of growth habit, indicating that *L. bellaplicata bellaplicata* var. A may be genetically distinct from the typical form of the species. The small number of specimens available for study, their limited size range, and lack of knowledge concerning the shell interior do not permit verification of these differences, or formal description of a new species or subspecies. Based on modern observations, it seems more likely that a single variable ostreid species would occupy such a well-defined ecologic niche than that two closely related species or subspecies would be living together and competing for the same niche.

Recognition of the variety is of additional importance since it may be the source from which contemporary and younger species of *Lopha,* having generally similar features, originated. Such ostreids, mostly undescribed, occur at various localities and stratigraphic levels in the Western Interior and will be the object of future study. They are not found in older sediments.

The morphologic distinctions between *L. bellaplicata bellaplicata* and variety A have been previously discussed under "Remarks" for the former subspecies.

Stratigraphic and geographic occurrence.—The variety occurs throughout the Middle Turonian "Pugnellus Sandstone" (Codell Sandstone member) of the Carlile Shale at localities 41, 58, 59, 60, and 61 in Huerfano Park, Colo. Rare marginal variants of the Texas and Colorado collections of *L. bellaplicata bellaplicata* approach this form, but none attain it.

Illustrated specimens.—Left valves: U.S.N.M. 22011a, d; 132249; U.M.M.P. 38051, 38052; associated right valves, illustrated; U.S.N.M. 132259, U.M.M.P. 43413; hypotypes. Measured specimens, not illustrated: U.S.N.M. 132301-132303; U.M.M.P. 43406.

LOPHA BELLAPLICATA NOVAMEXICANA new subspecies

Plate 7, figures 1-19; plate 8, figures 1-9

DESCRIPTION

Material.—About 100 well-preserved specimens (measured), predominantly left valves, from 4 localities in New Mexico and 8 localities in Colorado, including ontogenetic series and 2 large suites of specimens from single localities.

General form.—Summary of measurements presented in table 5. Shell attaining moderate size; inequivalve, left (lower, attached) valve slightly larger, much more convex than right valve; slightly to moderately inequilateral, prosocline. Valves close-fitting, outline moderately variable; typically subovate, commonly subquadrate or elongate-ovate parallel to axis of inclination, rarely rounded (pl. 7, figs. 1-5, 10-12, 14-19; pl. 8, figs. 7-9 typical of subspecies). Height greater than length in most specimens. Anterior margin slightly curved dorsally and ventrally, moderately rounded medially. Ventral margin moderately and evenly rounded; ventroposterior corner more narrowly

TABLE 5.—*Summary of measurements for* Lopha bellaplicata novamexicana

Character	Valve	No. of specimens	Range	Average
Height (H)	L	67	14.2-90 mm.	39.5 mm.
	R	8	18.3-53.6 mm.	36.3 mm.
Length (L)	L	67	13.4-61 mm.	35.9 mm.
	R	8	20.7-51.5 mm.	32.5 mm.
Width (W)	L	67	5.0-28.9 mm.	15.7 mm.
	R	6	3-18.3 mm.	8.7 mm.
Percent valves with H > L	LR	59/75		78.6%
Percent valves with H < L	LR	16/75		21.4%
Percent valves with H = L	LR	0		0
Area, inscribing rectangle of valve (A = H × L)	L	66	201-4050.4 mm.²	1550 mm.²
	R	8	379-2760 mm.²	1125 mm.²
Length, beak to posterior margin (LBP)	L	67	5.4-41.0 mm.	22.5 mm.
	R	8	11.2-34.0 mm.	19.2 mm.
Ratio, LBP : L	L	50	0.40:1-0.83:1	0.63:1
	R	8	0.53:1-0.66:1	0.58:1
Angle of inclination (i)	LR	64	59°-89°	76.5°
Percent of specimens with observable attachment scar	L	84		20.2%
Height of attachment scar (HATS)	L	13	1.0-12.1 mm.	4.7 mm.
Length of attachment scar (LATS)	L	17	2.1-22.3 mm.	7.3 mm.
Area, inscribing rectangle of attachment scar (HATS × LATS)	L	24	2.1-265.0 mm.²	39.3 mm.²
Ratio, area, inscribing rectangle of scar : area, inscribing rectangle of valve	L	24	0.002:1-0.24:1	0.04:1
Height of smooth portion of valves dorsad to plicae (HSS)	L	26	1.0-7.3 mm.	2.7 mm.
	R	11	4.0-11.1 mm.	6.3 mm.
Ratio, HSS : H	L	26	0.03:1-0.18:1	0.08:1
	R	11	0.15:1-0.35:1	0.25:1
Number of plicae (total): Primary plicae at first appearance	L	44	5-15	8.1
	R	11	7-15	10.4
Number of plicae at 10 mm. height	L	50	7-19	11.5
	R	11	8-15	12.0
Number of plicae at 20 mm. height	L	48	9-18	15.0
	R	10	10-17	13.4
Number of plicae at 30 mm. height	L	40	9-20	13.8
	R	4	10-15	12
Number of plicae at 40 mm. height	L	22	9-21	14.8
	R	0	0	0
Number of plicae at 50 mm. height	L	3	13-19	16.0
	R	0	0	0
Total number of plicae at margin	L	52	9-21	14.4
	R	11	10-17	13.9

Table 5.—*Summary of measurements for* Lopha bellaplicata novamexicana—*continued*

Character	Valve	No. of specimens	Range	Average
Number of plicae in 20 mm. length at 20 mm. height	L	64	3-8	4.75
	R	15	4-6	4.43
Width of median plica 20 mm. below beak	L	63	2.2-8.3 mm.	4.9 mm.
Percent increase in plicae by bifurcation	L	44	7-200%	84%
	R	11	6-77%	37%
Width of posterior auricular sulcus 20 mm. below beak	L	43	3.9-12.4 mm.	6.6 mm.
Inclination of beak, umbo (67 left valves, 8 right valves):				
Percent opisthogyre	L	41		61.2%
	R	3		37.5%
Percent orthogyre	L	14		20.9%
	R	5		62.5%
Percent prosogyre	L	12		17.9%
	R	0		0
Length of hinge line (LHL)	L	1		14.6 mm.
	R	1		10.7 mm.
Ratio, LHL:L	L	1		0.43:1
	R	1		0.33:1
Number of denticles in 5 mm. length	L	1		8
	R	1		9
Maximum diameter of muscle scar (MDS)	L	1		12.9 mm.
	R	1		12.8 mm.
Ratio, MDS:H	L	1		0.37:1
Ratio, area of scar : area of valve	L	1		0.08:1

rounded. Posterior margin straight to gently curved except in valves with prominent posterior auricle, where concave notch developed in outline at intersection with posterior auricular sulcus. Dorsolateral margins straight to slightly curved; dorsolateral corners narrowly rounded over auricles. Anterodorsal margin steeply to moderately inclined; inclination least in presence of auricle. Posterodorsal margin longest, moderately inclined with or without auricle.

Left valve moderately to highly convex (pl. 8, figs. 1-3); high point dorsocentral, just anterior to midline, on median plica. Anterior and dorsal flanks steeply sloping; ventral, posteroventral, posterodorsal flanks moderately sloping; posterior flank slopes steeply into auricular sulcus, becomes flat beyond this. Right valve flat to slightly concave dorsally and centrally, slightly convex ventrally, ventrolaterally, rarely with margins upturned, forming shallow submarginal trough. High point central to posterocentral.

Auricles.—Anterior auricle not commonly developed (20 percent of left valves, 5 percent of right valves), dorsoanterior in position, small, flat, subtriangular, terminally rounded, bearing 1 or 2 flattened primary plicae. Anterior auricular sulcus prominent, deeper, broader than adjacent interplical sulci (pl. 7, figs. 10, 11). Posterior auricle small to large, typically of moderate size, flat to slightly convex; outline subtriangular, with posterior apex situated centrally on posterior margin (pl. 7, figs. 3, 4, 10, 11). Auricular sulcus very prominent, composed of single broad interplical sulcus, or 2 adjacent interplical sulci with intermediate plica greatly reduced or absent (pl. 7, figs. 10, 11). Auricle smaller, less distinct on right valves than on left valves; rarely absent.

Beaks and umbos.—Normally slightly opisthogyre, rarely prosogyre, orthogyre, or with strong posterior curvature; slightly projecting, incurved, commonly extending inward beyond plane of commissure on left valve. Beaks small, narrowly to broadly rounded, flat to slightly convex, smooth, situated one-third to slightly less than one-half the length from the anterior margin, commonly obscured on attachment scar. Umbo of left valve highly arched, prominent, plicate. Umbone of right valve flat, smooth to partially plicate. Curvature of umbonal axis gentle, dorsally orthocline to slightly opisthocline, ventrally prosocline.

Attachment scar.—Small, indistinct, commonly not visible or absent; round to subovate, flat to slightly concave, steeply inclined to plane of commissure; terminal and central in position, or on posterior slope of early umbo. Attachment to smooth, slightly convex surfaces, predominantly other oysters, smooth clams. Shell moderately thick over attachment area.

Ornamentation, left valve.—Beak smooth, earliest umbo bearing growth lines, fine concentric lamellae. Plicae originate abruptly on early umbo, at edge of attachment scar (where present), or rarely on middle umbo. Primary plicae typically large, narrow in early stages, broader than high on adult part of shell, becoming broader, more rounded, lower with age, extending to margin on largest valves. Crests of plicae moderately to narrowly rounded, flanks moderately inclined. Plicae bifurcate over entire valve; bifurcation rate high on umbonal and subumbonal areas, low and irregular over rest of valve. Secondary plicae smaller, narrower, more rapidly expanding than primaries, some attaining size equal to primaries near margin. Rare valves with sharp, narrow plicae over entire valve (pl. 7, fig. 11). Plicae of posterior auricle smaller, more curved, more irregular, and more extensively bifurcating than those of main body of shell.

Concentric sculpture over plicate portion of valve consisting of fine, crowded, irregularly spaced growth lines and flat microlamellae dorsally, becoming gradually coarser ventrally. Coarse, raised, major lamellae appear at midvalve (pl. 7, figs. 10, 18), and are scattered singly, or in groups of 2 or 3, over ventral half of valve, intercalated with growth lines and microlamellae. Major lamellae coarsest, most crowded near commissure. Plicae fluted at intersections with major raised lamellae.

Ornamentation, right valve.—Right valve distinct from left in detail of ornamentation. Beak smooth; umbo with fine growth lines, microlamellae, faint undulations, becoming coarser ventrally. Plicae arise abruptly at edge of umbo, preceded by a few coarse, crowded major lamellae and/or concentric ridges. 75 to 80 percent of valve plicate. Plicae coarse, higher than wide initially, becoming broader with age but remaining prominent; crests narrowly rounded to angular, flanks steep; plicae sparsely bifurcating throughout, generally near margins, much less than on left valve. Interplical sulci narrow, with angular to narrowly rounded bases. Concentric ornament of plicate flanks consisting of numerous, prominent, raised lamellae, moderately and unevenly spaced centrally, crowded ventrally, commonly marking major constrictions or change in slope of shell surface, more prominent on right than on left valve. Major lamellae intercalated with numerous crowded, growth lines and microlamellae. Plicae spinose, fluted at intersection with major lamellae. Typical right valves illustrated on plate 7, figures 8, 9.

Cardinal area.—Known from single right and single left valves; on left valve consisting of subcentral, broad, shallow, triangular resilifer, and equally large, flat, subequal (posterior largest), subtriangular, lateral cardinal plates. Surface of cardinal area marked with closely spaced, moderately strong horizontal lines of various sizes and by fine, crowded, subequally spaced, raised vertical lines. Cardinal area of right valve similar, but with ventral half of resilifer convexly folded, forming a low lip.

Denticles.—Denticles present on inner dorsolateral margins of both valves; small, simple, rounded to ovate, crowded, moderately convex, situated on commissure, rarely reflected on thick lateral edges of auricles.

Commissure.—Commissure at edge of right valve, just within edge of left valve; flat dorsolaterally, undulating at intersection with major plicae elsewhere. Internal expression of plicae variable, typically developed as low, rounded folds and sulci confined to valve margins, less commonly extending to center of shell, becoming more subtle inward. Thick-shelled specimens commonly with lamellate lateral edges of shell flattened in plane of commissure (pl. 7, fig. 5).

Muscle scar.—Monomyarian; posterior adductor scar large, situated centroposteriorly, or in upper part of posteroventral quadrant of valve (pl. 7, fig. 5); comma-shaped, arcuate, slightly concave, well defined, overlapped dorsally, anteriorly by inner shell layers, bordered ventrally by a low, raised lip. Surface striated, covered with fine, crowded, microlamellae and raised lines, irregularly spaced, conforming to trace of growth lines.

Shell structure.—Periostracum, prismatic layer, and hypostracum not observed. Subnacreous layer forms bulk of shell, consisting of several layers of slightly curved, inclined calcite plates arranged en echelon within each layer. Inclination of plates in each layer may be opposed to that of adjacent layers. Individual plates and layers flatter, more conformable around cardinal area and at ventral edge. Nacreous layer thin, composed of flat calcite lamellae. Shell thick; thickness of a typical left valve (height 38 mm., length 34 mm.) through the hinge area, 4.5 mm.; thickness at crest, 3.4 mm.; thickness 5 mm. above ventral margin, 2.3 mm.

ONTOGENY

A few significant ontogenetic trends regarding the external features of the shell are worthy of note. Internal structures of the valves are virtually unknown in this respect.

Concentric sculpture.—*Nepionic* stage smooth. *Neanic* stage with fine growth lines, microlamellae initially, becoming coarser toward *late neanic*. *Early* to *middle neanic* in left valve marked by a few, coarse, crowded growth lines, lamellae, and ridges just before abrupt development of plicae. *Ephebic* stage marked by development of scattered (left valve) to moderately spaced (right valve) major concentric lamellae in addition to fine ornament, possibly marking growth rests, and becoming somewhat more crowded in *late ephebic* as growth slowed. *Gerontic* stage marked by crowded, coarse lamellae and growth lines near margin.

Radiating sculpture.—Plicae abruptly appear in *early,* rarely *middle neanic* stage on left valves, at the beginning of *ephebic* development on right valves, becoming coarser, more prominent, broader, more rounded with age through the *middle ephebic* stage; becoming lower, more subtle during *late ephebic* and *gerontic* stages, especially on left valves. Bifurcation rate highest during *neanic,* low and irregular at later stages.

Convexity.—Outward curvature of shell growth moderate to great through *neanic* and *early ephebic* development, gradually decreasing in later growth (fig. 3a), becoming moderate to slight. No flattening and flaring noted in late growth stages.

Marginal outline; auricles.—(Based on fig. 18.) *Nepionic* shell subround, *Neanic* shell ovate, longer than high; lateral growth exceeded

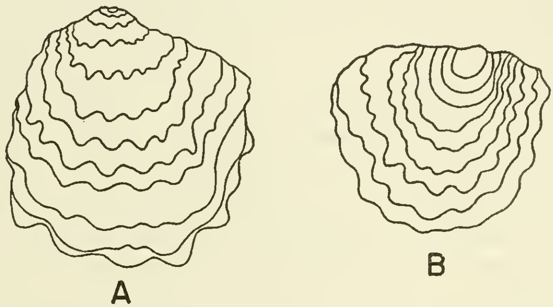

FIG. 18.—Ontogeny of *Lopha bellaplicata novamexicana* new subspecies. Growth line traces at approximately 2.5 mm. intervals on representative left (A) and right (B) valves of the subspecies, showing developmental history of the marginal outline and the auricles. Drawings ×1. A, U.S.N.M. 132267, B, U.S.N.M. 132265.

ventral growth during *neanic* and *early ephebic* stages. *Ephebic* stage marked by ventral growth exceeding lateral expansion and the latter becoming irregular. Auricles appear in *early ephebic* as more rapidly expanding salients of lateral margins, continue to grow at a more accelerated rate throughout life. *Gerontic* growth similar to that of *ephebic* stage.

Curvature of growth axis (midline).—Curvature slight during *nepionic, neanic, early ephebic* stages, decreasing uniformly through *ephebic* and *gerontic* stages, becoming nearly straight (fig. 3c).

REMARKS

The distinction between *L. bellapliata novamexicana* and its most closely comparable relative, *L. bellaplicata bellaplicata* has been discussed in detail under the "Remarks" section of the latter subspecies. Basically, *L. bellaplicata novamexicana* is distinguished by its more oblique marginal outline, greater convexity of the umbonal region, larger, broader, less numerous plicae, reduced and more centrally situated auricles, much larger posterior auricular sulcus, and more inclined posterodorsal margin. The plicae arise at an earlier developmental stage than in *L. bellaplicata bellaplicata.* No other Cretaceous species of *Lopha* are closely comparable. Young shells of these two subspecies are nearly identical (compare pl. 3, figs. 1-9, with pl. 7, figs. 1-3), but average adult shells are readily distinguished. Marginal variants of the subspecies show overlap of many structures.

Shells of this subspecies are typically found complete, with both valves intact and well preserved. Although they are common at some localities, they have not been observed living gregariously in beds or "oyster reefs," and show no evidence of crowding. The small size of the attachment scar (in some cases too small to be observed, or preserved, on the beak) possibly indicates early detachment from the substrate and predominantly a free life.

Lopha bellaplicata novamexicana is known from three lithofacies: Fine- to medium-grained, well-sorted, cross-bedded marly sandstone; similar sandstone with an argillaceous cement and abundant carbonaceous debris; and sandy, argillaceous, limestone concretions or lenses (septarian) in a sandy shale matrix. The first two types are from New Mexico, and the concretions mark its occurrence in Colorado. The only observable morphologic differences between forms from the two States which may be environmentally controlled are (1) the sharper plicae on many Colorado examples (pl. 7, fig. 11), and (2) the tendency for some Colorado specimens to have a ventral "hump," or sharp break in slope about one-third the height from the ventral margin. On the steep slope below this break, the plicae on certain specimens show greater bifurcation than is normal for the subspecies. No such structure was noted on New Mexico specimens. These differences are difficult to evaluate in light of the sparse knowledge concerning the paleoenvironment to which this form was subjected. Similar irregularities in growth form are produced in some oysters exposed to abrupt changes in rate of sedimentation, in others periodically exposed in intertidal zones. This structure is genetically produced in certain species of *Inoceramus,* irrespective of environment. It is a gerontic feature of other pelecypods.

Stratigraphic and geographic distribution.—*Lopha bellaplicata novamexicana* is the oldest known member of the *L. lugubris* group. It is commonly found in the middle Mancos Shale of New Mexico, in the zone of *Collignoniceras hyatti* (Stanton) (late Middle Turonian), well below the occurrence of *L. lugubris.* Its position relative to *L. bellaplicata bellaplicata* in New Mexico is uncertain, however, since the latter is rare in this area, and the two have not yet been found associated.

The stratigraphic relationship between *L. bellaplicata bellaplicata* and the subspecies *novamexicana* can be established in Huerfano Park, Colo. Here, typical examples of *L. bellaplicata bellaplicata* are found throughout the Codell Sandstone Member ("Pugnellus Sandstone") (pl. 6, figs. 7-9, 12). Below this unit, in the upper part of the Blue Hill Shale Member, septarian limestone concretions contain scattered but characteristic examples of the subspecies *novamexicana* (pl. 7, fig. 11). The two forms do not have overlapping ranges in this area, although rare individuals transitional between them occur as marginal variants of each form. This occurrence suggests, therefore, that *L. bellaplicata novamexicana* is characteristic of the lower part of the *Collignoniceras hyatti* zone (Blue Hill Shale Member equivalents) and *L. bellaplicata bellaplicata* marks the upper part of the *C. hyatti* zone (Codell Sandstone Member: "Pugnellus Sandstone" of older authors). If future collections prove this to be true over a broad area in the Western Interior, these ostreids will have particular importance as stratigraphic markers, since the faunas of these two units overlap in almost every other respect. The subspecies *novamexicana* occurs at localities 62 through 73, described in detail at the end of this report.

Illustrated and measured specimens.—Holotype, a typical left valve with the interior excavated, U.S.N.M. 132267 (pl. 7, fig. 10). Figured paratypes, left and right valves, U.S.N.M. 22012; U.S.N.M. 132260-132266 inclusive; U.S.N.M. 132268-132282 inclusive; U.S.N.M. 132286-132288 inclusive. Measured, unfigured paratypes, U.S.N.M. 132252-132257 inclusive, 132290. University of Michigan Museum of Paleontology (U.M.M.P.) 43480, 43481. Sectioned specimen, discussed, U.S.N.M. 132289.

COLLECTING LOCALITIES

Collecting localities and stratigraphic information are cited as they appear in the Mesozoic catalogs of the U. S. Geological Survey and U. S. National Museum. In many cases, data available for older collections are brief and generalized. Many such collections have been omitted from this study for this reason. Others have been incorporated because it is obvious from the locality data and from associated matrix at what stratigraphic level they were obtained. Localities cited for the latter collections contain, in parentheses, stratigraphic data which is not listed in our catalogs and which represents my own interpretation, based on experience in the areas in question. For localities that I have not actually visited, this information is followed, in parentheses, by a question mark. I have collected from all other areas in the past 6 years, and feel certain of the stratigraphic assignments.

Lopha lugubris (Conrad)

1. U.S.G.S. 513—"Colorado Formation" (Juana Lopez equivalent ?), hills 6 miles each of Mexican settlements on road from Jemez to Copper City, N. Mex. 100 feet above massive gray sandstone standing on edge. Collected by J. W. Powell, 1887.
2. U.S.G.S. 747—"Colorado Formation" (Juana Lopez Member of the Carlile Shale), Rattlesnake Buttes, 18 miles east of Walsenburg Post Office, Colo. Collected by T. W. Stanton, 1890.
3. U.S.G.S. 827—"Colorado Formation" (Juana Lopez Member, Carlile Shale), near Malachite, Huerfano County, Colo. Collected by T. W. Stanton, 1891.
4. U.S.G.S. 833—100 to 600 feet above base of Colorado Shale (Juana Lopez equivalent ?), near Mancos, Colo. Collected by T. W. Stanton, 1891.
5. U.S.G.S. 1306—Benton (Subgroup: Juana Lopez Member, Carlile Shale), 12 miles northwest of Pueblo, Colo., lat. 38°25′, long. 104°47′. Collected by G. K. Gilbert, 1893.
6. U.S.G.S. 1380—Upper Benton (Subgroup: Juana Lopez equivalent ?), mesa 5 miles west of Drip Springs, lat. 37°38′, long. 104°30′, Colo. Collected by G. K. Gilbert, 1894.
7. U.S.G.S. 2005—Colorado (Group: Juana Lopez equivalent ?), about 150 feet above top of Dakota Sandstone, railroad cut north of Thompson Park, Colo. Collected by A. C. Spencer, 1897.
8. U.S.G.S. 2009—Colorado (Group), Mancos Shale (Juana Lopez equivalent ?), near F—down corral on middle Mancos (River ?), La Plata Quad., Colo. Collected by W. T. Lee.
9. U.S.G.S. 2015—Colorado (Group: Juana Lopez equivalent ?), west fork of Mancos (River ?), 10,700 feet elevation, Colo. Collected by W. Cross.
10. U.S.G.S. 2019—Colorado (Group: Juana Lopez equivalent in Mancos Shale), second fossil layer exposed northwest of Mancos, Colo. Collected by Mr. Cane, 1895.
11. U.S.G.S. 3673—(Colorado Group, Juana Lopez equivalent), *"Ostrea" lugubris* zone, Rio Puerco, about 5 miles above San Ygnacio, Albuquerque Quad., N. Mex. Collected by T. W. Stanton, 1906.
12. U.S.G.S. 4358—Benton (Subgroup), fine brown sandstone ledges 400 feet above Dakota Sandstone (Juana Lopez equivalent), Willow Creek at the old wagon road south of Blue Mountain, sec. 12, T. 3 N., R. 102 W., coal fields of northwest Colorado and adjacent territory. Collected by H. S. Gale, 1907.

13. U.S.G.S. 4456—Benton (Subgroup: Juana Lopez equivalent ?), horizon No. 2 (J. H. Gardner: unpublished), about 60 feet below main massive sandstone of Coloradoan age, 5 miles below Arnold's store, 10 miles northeast of Gallup, N. Mex. Collected by J. H. Gardner, 1907.
14. U.S.G.S. 6516—Upper part of the Benton (Subgroup: Juana Lopez equivalent), 150 to 200 feet above the Greenhorn Limestone, branch of Vermejo Creek, about 12 miles northwest of Vermejo Park Post Office, N. Mex. Collected by T. W. Stanton, 1910.
15. U.S.G.S. 7539—Eagle Ford Shale, layer No. 1, quarry of the Texas Portland Cement Co., 2.5 miles due east of Eagle Ford, Dallas County, and 3 miles west of Trinity River at Dallas, Tex. Collected by L. W. Stephenson, 1911.
16. U.S.G.S. 7579—Basal bed of the Austin Chalk, on Walnut Creek, about 1 mile east of Watters' Station, Travis County, Tex. Collected by L. W. Stephenson, 1911.
17. U.S.G.S. 7993—Colorado (Group: Juana Lopez equivalent), in 50 feet of yellow calcareous shaly sandstone, zone of *Prionocyclus wyomingensis* and *Scaphites warreni,* about 3.5 miles south of Casa Salazar, Mt. Taylor Quad., N. Mex. Collected by W. T. Lee and T. W. Stanton, 1912.
18. U.S.G.S. 9250—Mancos Shale, 300 to 400 feet above the base, near Delta, Colo. Collected by G. H. Stone, 1915.
19. U.S.G.S. 10368—Colorado (Group: Juana Lopez equivalent ?), 14 miles S. 20° W. from Shiprock Mt. (Wilson Peak), sec. 5 or 8, T. 9 N., R. 4 W., Navajo Meridian, near the base of Beautiful Mt., San Juan Basin, N. Mex. Collected by W. E. Bryant, Dobbin, and J. B. Reeside, Jr., 1920.
20. U.S.G.S. 10506—Mancos Shale, 300 feet above Dakota Sandstone, *Scaphites* zone (Juana Lopez equivalent), 1.5 miles west of Durango, NW1/4 SE1/4 sec. 18, T. 35 N., R. 9 W., Ignacio Quad., Colo. Collected by J. B. Reeside, Jr., 1920.
21. U.S.G.S. 12883—Reworked Eagle Ford Shale zone in the base of the Austin Chalk, exposures in bank of creek east of railroad, south of Colorado River, south of Austin, Travis County, Tex. Collected by L. W. Stephenson, 1924.
22. U.S.G.S. 13663—(Juana Lopez equivalent), 2 miles north of Whitewater, Grand Junction region, Colo. Collected by J. B. Reeside, Jr., 1926.
23. U.S.G.S. 14691—"Blue Hills Shale" (Carlile Shale, questionably from pockets of Juana Lopez Limestone at top of so-called Blue Hill Shale of older authors), *Lopha lugubris* zone, near Beloit, Kans. Collected by by J. B. Reeside, Jr., 1929.
24. U.S.G.S. 15923—Mancos Shale, 348 feet below Gallup Sandstone (Juana Lopez equivalent ?), triangulation point, Gallup, approximately center of sec. 12, T. 14 N., R. 2 W., southern San Juan Basin, N. Mex. Collected by C. B. Hunt and party, 1931.
25. U.S.G.S. 18876—"Codell ? Sandstone" (Juana Lopez Member at top of Codell), thin beds 30 feet below highly fossiliferous zone (of Mancos Shale), on Biltabito Road, 15 miles west of junction with highway to Gallup, 15 miles west of Shiprock bridge, San Juan County, N. Mex. Collected by N. W. Bass, 1943.

26. U.S.G.S. 20562—Upper Cretaceous (Juana Lopez equivalent ?), approximately 2 miles west-southwest of Hagan, sec. 6, T. 12 N., R. 6 E., Tejon Grant, N. Mex. Collected by C. E. Stearns, 1946.
27. U.S.G.S. 24443—Frontier Sandstone (Juana Lopez equivalent ?), 1.75 miles northwest of Newcastle, SE1/4 sec. 23, T. 5 S., R. 91 W., Glenwood Springs Quad., Colo. Collected by N. W. Bass, 1952.
28. U.S.G.S. 25592—Mancos Shale (Juana Lopez equivalent), 525 feet above base, section No. 2, southeast Gypsum Valley–Disappointment Valley area, aerial photo D.R.N. 2-10, San Miguel County, Colo. Collected by O. T. Marsh, 1955.
29. U.S.N.M. Cat. No. 8354—Colorado (Group: Juana Lopez equivalent), Colorado. Type specimen with no other locality data.
30. U.S.N.M. Cat. No. 9822—Upper Cretaceous (Juana Lopez equivalent), zone of *Prionocyclus macombi* ?, rocks east of Red River (Canadian), Santa Fe road, N. Mex. T. A. Conrad.
31. U.S.N.M. Cat. No. 20255—Middle Cretaceous, Colorado (Group: Juana Lopez equivalent), Vada del Chama, N. Mex.
32. Juana Lopez Member (top), Carlile Shale, Colorado Group, low cliff along the northwest side of Oak Creek, NE1/4 SW1/4 sec. 5, T. 27 S., R. 68 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1958.
33. Juana Lopez Member, Carlile Shale, Colorado Group, in a stream gully 1.3 to 1.5 miles north-northwest of Red Wing, on the Jones' Cattle Company Ranch, SW1/4 SE1/4 sec. 26, T. 26 S., R. 71 W. Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959.
34. Juana Lopez Member, Carlile Shale, Colorado Group, ½ mile east of Maes' School, north of an unimproved dirt road, along the Fort Hays limestone hogback, SE1/4 sec. 11, T. 26 S., R. 69 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1958.
35. Juana Lopez Member, Carlile Shale, Colorado Group, along the Fort Hays Limestone hogback south of unimproved dirt road, 0.8 mile southeast of Maes' School, NW1/4 NE1/4 sec. 14, T. 26 S., R. 69 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1958.
36. Juana Lopez Member, Carlile Shale, Colorado Group, on the southeast side of Oak Creek, 0.2 mile southwest of Badito, NW1/4 NE1/4 sec. 8, T. 27 S., R. 68 W., Huerfano County, Colo. Collected by E. G. Kauffman, 1958.
37. Juana Lopez Member, Carlile Shale, Colorado Group, in a subsidiary stream valley of Pantleon Creek, north of an unimproved road crossing sec. 28, on the Jones' Cattle Company Ranch, S1/2 NW1/4 sec. 28, T. 26 S., R. 71 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959.
38. Juana Lopez Member, Carlile Shale, Colorado Group, 2-3 miles north of Thatcher, Colo., in Juana Lopez–Fort Hays limestone hogback, on east side of dirt road leading north from general store and Thatcher School, 50 to 100 yards east of road. Collected by E. G. Kauffman, 1961.
39. Juana Lopez Member, Carlile Shale, Colorado Group, 2-3 miles north of Thatcher, Colo., on west side of dirt road leading north from Thatcher

School, in two fault or slump blocks, 0.5 and 0.7 mile west of road. Collected by E. G. Kauffman, 1961.

Lopha bellaplicata bellaplicata (Shumard)

15. U.S.G.S. 7539 (same as listed for *Lopha lugubris*)—Eagle Ford Shale, layer No. 1, quarry of Texas Portland Cement Company, 2.5 miles due east of Eagle Ford, Dallas County, and 3 miles west of Trinity River at Dallas, Tex. Collected by L. W. Stephenson, 1911.
40. U.S.G.S. 741—Colorado Group (Codell Sandstone Member, Carlile Shale), near Charles Smith's Ranch, on Muddy Creek, 10 miles above Gardner Post Office, Huerfano Park, Huerfano County, Colo. Collected by T. W. Stanton, 1890.
41. U.S.G.S. 743—Colorado Group (Codell Sandstone Member, Carlile Shale), 1 mile east of Quillian's Ranch on Williams Creek, Huerfano Park, Huerfano County, Colo. Collected by T. W. Stanton, 1890.
42. U.S.G.S. 1310—Benton (Subgroup: Codell Sandstone Member, Carlile Shale), near 3-R Ranch, lat. 38°2′, long. 104°57′, Colo. Collected by G. K. Gilbert, 1893.
43. U.S.G.S. 1318—Benton (Subgroup: Codell Sandstone Member, Carlile Shale), near Turkey Creek, lat. 38°30′, long. 104°49′, Colo. Collected by G. K. Gilbert, 1893.
44. U.S.G.S. 439b—(Eagle Ford Shale), 2 miles east and 3 miles south of Denison, Tex. Collected by R. T. Hill, 1886.
45. U.S.G.S. 8081—Benton ? (Subgroup: Mancos Shale), on surface of steep slope at B-34, sec. 18, T. 10 N., R. 17 W., Zuni Indian Reservation, N. Mex. Collected by D. E. Winchester, 1912.
46. U.S.G.S. 10046—Eagle Ford Shale, 7 miles west of Palestine at the salt works, on ridge $\frac{1}{8}$ mile northeast of plant, Texas. Collected by O. B. Hopkins, 1915.
47. U.S.G.S. 11096—Eagle Ford Sandstone, in pebble bed 15 to 25 feet below Ector Chalk, in big gully 1 mile southeast of Bells, Tex. Collected by O. B. Hopkins, 1918.
48. U.S.G.S. 11732—Upper 3 feet of the Eagle Ford Shale, in quarry of the Texas Portland Cement Company plant west of Dallas, Tex. Collected by T. W. Stanton, 1923.
49. U.S.G.S. 12942—Eagle Ford Formation, Palestine salt dome, east of salt works, at an old cabin, Anderson County, Tex. Collected by L. W. Stephenson, 1924.
50. U.S.G.S. 14553—Sand of upper Eagle Ford age, Whitesboro road, 1.75 miles west of Sherman, Grayson County, Tex. Collected by L. W. Stephenson, T. W. Stanton, and J. B. Reeside, Jr., 1929.
51. U.S.G.S. 19017—Upper part of the Eagle Ford Shale, North-South Road, 1.7 miles W. by S. of Ellsworth, 5.4 miles southwest of Denison, Grayson County, Tex. Collected by R. T. Hazzard, 1941 (?).
52. U.S.G.S. 22608—Eagle Ford Shale, 3 miles southeast of Mountain Creek Power Plant, Dallas County, Tex. Collected by Mrs. Renfro.
53. U.S.N.M. Cat. No. 8024—Eagle Ford Shale, Collin County, Tex.
54. U.S.N.M. Cat. No. 11882—Eagle Ford Shale, near Sherman, Tex.

55. U.S.N.M. Cat. No. 22861—Colorado Group (Codell Sandstone Member), at Carlile Springs, 18 miles west of Pueblo, Colo.
56. U.S.N.M. Cat. No. 12383—Eagle Ford Shale, Denison, Tex.
57. B. F. Perkins collection No. 55-206—Upper Eagle Ford Shale, Turonian, Jefferson Blvd., roadcut, Dallas County, Tex. Collected by B. F. Perkins, 1955. U.S.N.M. accession 241760.
58. Codell Sandstone Member ("Pugnellus Sandstone" of Stanton, 1894), Carlile Shale, Colorado Group, 50 to 100 yards southwest of Lower Pass Creek School, along Colorado State Highway 305, SE1/4 sec. 7, T. 27 S., R. 70 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959, 1961.
59. Codell Sandstone Member ("Pugnellus Sandstone" of Stanton, 1894), Carlile Shale, Colorado Group, in a stream gully 1.3 to 1.5 miles north-northwest of Red Wing, on the Jones' Cattle Company Ranch, SW1/4 SE1/4 sec. 26, T. 26 S., R. 71 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959.
60. Codell Sandstone Member ("Pugnellus Sandstone" of Stanton, 1894), Carlile Shale, Colorado Group, in a subsidiary stream valley of Pantleon Creek, north of an unimproved dirt road crossing sec. 28 on the Jones' Cattle Company Ranch, S1/2 NW1/4 sec. 28, T. 26 S., R. 71 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959.
61. Codell Sandstone Member ("Pugnellus Sandstone" of Stanton, 1894), Carlile Shale, Colorado Group, in a wooded area 0.4 mile east of Turkey Creek, NE1/4 NW1/4 sec. 22, T. 25 S., R. 69 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959.

Lopha bellaplicata novamexicana new subspecies

62. U.S.G.S. 738—Colorado Group (septarian limestone concretion zone, upper Blue Hill Shale Member, Carlile Shale), near Badito, Huerfano County, Colo. Colected by T. W. Stanton, 1890.
63. U.S.G.S. 3295—Colorado Group (Mancos Shale ?), Carthage, N. Mex. Collected by W. T. Lee, 1905.
64. U.S.G.S. 3297—Colorado Group (Mancos Shale ?), ½ mile south of 3295, Carthage, N. Mex. Collected by W. T. Lee, 1905.
65. U.S.G.S. 5303—Colorado Group, Benton (Subgroup: Mancos Shale), 710 feet above the Dakota Sandstone, SW1/4 NE1/4 sec. 9, T. 5 S., R. 2 E., New Mexico, P. M., 0.5 mile N. 30° from Manilla Mine, Carthage, N. Mex. Collected by J. H. Gardner, 1908.
66. U.S.G.S. D2042—Massive sandstone in the Mancos Shale, zone of *Collignoniceras hyatti*, just north of U. S. Highway 380, 7.75 miles east of San Antonio, Socorro County, N. Mex. Collected by W. A. Cobban.
67. Blue Hill Shale Member, Carlile Shale, Colorado Group, in septarian limestone concretions 10 to 15 feet below the top of the member, and in lenticular limestone beds at the Blue Hill-Codell Sandstone contact, lower part of the zone of *Collignoniceras hyatti*, 100 yards southwest of Lower Pass Creek School, just west of Colorado State Highway 305, SE1/4 sec. 7, T. 27 S., R. 70 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959, 1961.

68. Upper Blue Hill Shale Member, Carlile Shale, Colorado Group, in a 2-inch limestone overlying cone-in-cone beds, septarian limestone concretion zone, zone of *Collignoniceras hyatti,* stream gully 1.3 to 1.5 miles north-northwest of Red Wing, on the Jones' Cattle Company Ranch, SW1/4 SE1/4 sec. 26, T. 26 S., R. 71 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959.
69. Blue Hill Shale Member, Carlile Shale, Colorado Group, zone of septarian limestone concretions in upper 10 feet of member, 1 mile east of Williams Creek, ½ mile south of unimproved dirt road, W1/2 NE1/4. sec. 12, T. 25 S., R. 70 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959, 1961.
70. Blue Hill Shale Member, Carlile Shale, Colorado Group, zone of septarian limestone concretions in upper 20 feet of member, along the Fort Hays Limestone hogback south of an unimproved dirt road, 0.8 mile southeast of Maes' School, NW1/4 NE1/4 sec. 14, T. 26 S., R. 69 W., Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1958.
71. Blue Hill Shale Member, Carlile Shale, Colorado Group, zone of septarian limestone concretions in upper 25 feet of member, below Codell Sandstone–Juana Lopez limestone hogback 0.5 mile north of Colorado State Highway 69, near center of sec. 31, T. 26 S., R. 68 W., 1.4 miles east of Farisita, Huerfano Park, Huerfano County, Colo. Collected by E. G. Kauffman, 1959.
72. Blue Hill Shale Member, Carlile Shale, Colorado Group, septarian limestone concretion zone in upper 15 feet of member, just below Juana Lopez-Fort Hays Limestone hogback, 2-3 miles north of Thatcher, Colo., 50 to 100 yards east of an improved dirt road leading north from general store and Thatcher School. Collected by E. G. Kauffman, 1961.
73. Blue Hill Shale Member, Carlile Shale, Colorado Group, septarian limestone concretions in upper part of member, 1 mile north of the Arkansas River, on slopes surrounding a dry tributary, SE1/4 NE1/4 sec. 25, T. 20 S., R. 66 W., Pueblo County, Colo. Collected by E. G. Kauffman and F. Collier, 1962.

Lopha bellaplicata bellaplicata var. A.

Collected in the Codell Sandstone Member, Carlile Shale, Colorado Group, at localities 41, 58, 59, 60, and 61, previously cited under *Lopha bellaplicata.*

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EXPLANATION OF PLATES

U.S.N.M. = United States National Museum
U.M.M.P. = University of Michigan Museum of Paleontology
U.S.G.S. = United States Geological Survey

PLATE 1

Lopha lugubris (Conrad)

Fig. 1. Lateral view (×I) of a left valve with reverse curvature; a hypotype from a calcarenite bed between typical Austin Chalk and Eagle Ford Shale (locality 16, U.S.G.S. loc. 7579); U.S.N.M. 132154.

Fig. 2. Lateral view of a typical left valve (×I); Stanton's hypotype from Mancos, Colo. (locality 4, U.S.G.S. 833), the original of his plate 4, figure 3 (1893); U.S.N.M. 22859b.

Fig. 3. Lateral view (×2) of a left valve with abnormally small attachment area; a hypotype (locality 38); U.S.N.M. 132155.

Fig. 4. Lateral view (×1) of a typical left valve, the lectotype; the original of Conrad's (1857) plate 10, figure 5b, (locality 30, east of Red River, Santa Fe Road, N. Mex.); U.S.N.M. 9822.

Fig. 5. Lateral view (×2) of a typical left valve; a hypotype from the upper Eagle Ford Shale of Texas (locality 15, U.S.G.S. 7539); U.S.N.M. 132156.

Fig. 6. Lateral view (×2) of a left valve with well-developed reverse curvature of the exogyroid beaks and umbo; a hypotype from Huerfano Park, Colo. (locality 34) in the Juana Lopez Member (Carlile Shale); U.M.M.P. 43472.

Fig. 7. Lateral view (×2) of a typical left valve; a hypotype from the zone of *Prionocyclus wyomingensis wyomingensis,* near Casa Salazar, N. Mex. (locality 17, U.S.G.S. 7993); U.S.N.M. 132157.

Fig. 8. Lateral view (×2) of an unusually erect left valve; a hypotype from the upper 3 feet of the Eagle Ford Shale, Texas (locality 48, U.S.G.S. 11732); U.S.N.M. 132158.

Fig. 9. Lateral view (×2) of a left valve with a large, flat attachment scar and somewhat restricted plicae; a hypotype from the Juana Lopez Member, Huerfano Park, Colo. (locality 34); U.M.M.P. 43464.

Fig. 10. Lateral view of a left valve (×2); a hypotype from the Juana Lopez Member, Huerfano Park, Colo. (locality 34); U.M.M.P. 43472.

Fig. 11. Lateral view (×2) of a distorted left valve with plicae limited to the margins; a hypotype from Mancos, Colo. (locality 4, U.S.G.S. 833); U.S.N.M. 22210a.

Fig. 12. Lateral view (×2) of a nearly smooth left valve with only faint marginal plicae; a hypotype from the Juana Lopez Member, Huerfano Park, Colo. (locality 34); U.M.M.P. 43465.

Fig. 13. Lateral view (×2) of an erect left valve with a large scar and relatively few, restricted, marginal plicae; a hypotype from the Juana Lopez Member, Huerfano Park, Colo. (locality 36); U.M.M.P. 43476.

Fig. 14. Lateral view (×2) of a left valve with radiating ornament restricted to marginal crenulations; a hypotype from the upper Eagle Ford Shale of Texas (locality 15, U.S.G.S. 7539); U.S.N.M. 132159.

Fig. 15. Interior view (×2) of a large left valve showing internal reflection of ornamentation, marks of the attachment area, and the normal position of the muscle scar; a hypotype, the original of Stanton's plate 4, figure 5 (1893) (locality 4, U.S.G.S. 833); U.S.N.M. 22859a.

Fig. 16. Interior view (×2) of a left valve showing nature of cardinal area, denticles, muscle scar, and internal reflection of the ornamentation; a hypotype from Colorado (locality 29); U.S.N.M. 8354.

Fig. 17. Interior view (×2) of a left valve showing fine interior lines on inner surface, denticles, cardinal area, and muscle scar; a hypotype from the zone of *Prionocyclus wyomingensis wyomingensis* (Juana Lopez equivalent), near Casa Salazar, N. Mex. (locality 17; U.S.G.S. 7993); U.S.N.M. 132160.

Fig. 18. Interior view (×2) of a left valve; hypotype illustrated by Meek on plate 1, figure 1a (1876), from Vada del Chama, N. Mex. (locality 31); U.S.N.M. 20255.

Plate 2

Lopha lugubris (Conrad)

Fig. 1. Lateral view (×2) of an unusually elongate right valve showing strong lamellae developed at beginning of plicate stage of valve, and weak plicae; a hypotype from the upper Eagle Ford Shale of Texas (locality 15, U.S.G.S. 7539); U.S.N.M. 132161.

Fig. 2. Lateral view (×2) of a typical plicate right valve, showing abrupt formation of plicae at margin of smooth stage; hypotype illustrated by Stanton (1893, pl. 4, fig. 2), from Huerfano Park, Colo. (locality 3, U.S.G.S. 827); U.S.N.M. 22860a.

Fig. 3. Lateral view of a right valve (×2); a hypotype from Rattlesnake Buttes, Colo. (locality 2, U.S.G.S. 747); U.S.N.M. 22008a.

Fig. 4. Lateral view (×2) of an unusually elongate, curved, plicate right valve; a hypotype from the zone of *Prionocyclus wyomingensis wyomingensis* (Juana Lopez equivalent) near Casa Salazar, N. Mex. (locality 17, U.S.G.S. 7993); U.S.N.M. 132162.

Fig. 5. Lateral view (×2) of a coarsely plicate right valve showing sharp demarcation between smooth stage and plicate portion of valve; a hypotype from near Mancos, Colo., in the Juana Lopez equivalent (locality 10, U.S.G.S. 2019); U.S.N.M. 132163.

Fig. 6. Lateral view (×2) of a plicate right valve characteristic of the species, showing abrupt origin of plicae, and reflection of attachment surface on smooth stage of valve; a hypotype from the upper Eagle Ford Shale of Texas (locality 15, U.S.G.S. 7539); U.S.N.M. 132164.

Fig. 7. Lateral view (×2) of a right valve showing reflection of attachment surface on smooth stage, and restriction of plicae to marginal area. This form is intermediate between plicate and nonplicate types. A hypotype from near Mancos, Colo. (locality 4, U.S.G.S. 833); U.S.N.M. 22210b.

Fig. 8. Lateral view (×2) of a right valve with radiating ornament limited to crenulations in marginal lamellae; a hypotype from Huerfano Park, Colo. (locality 34); U.M.M.P. 43470.

Fig. 9. Lateral view (×2) of an elongate, nonplicate right valve; a hypotype from Huerfano Park, Colo. (locality 32); U.M.M.P. 43487.

Fig. 10. Lateral view (×2) of a smooth right valve showing reflection of attachment surface (probably an *Inoceramus* shell) on exterior of upper valve; a hypotype from near Mancos, Colo. (locality 4, U.S.G.S. 833); U.S.N.M. 22211.

Fig. 11. Lateral view (×2) of a smooth right valve showing nature of growth lines and fine lamellae; a hypotype from Huerfano Park, Colo. (locality 58) in the Juana Lopez Member; U.M.M.P. 43484.

Fig. 12. Lateral view (×2) of a small right valve with well-developed marginal lamellae, and faint crenulations on the anterior and ventral borders; a hypotype from Huerfano Park, Colo. (locality 33) in the Juana Lopez Member; U.M.M.P. 43471.

Fig. 13. Interior view (×2) of a thick right valve showing unusually deep but typically shaped posterior adductor muscle scar, traces of fine radiating incised lines on inner surface of valve; a hypotype from Rattlesnake Buttes, Colo. (locality 2, U.S.G.S. 747) in the Juana Lopez Member; U.S.N.M. 22008b.

Fig. 14. Interior view (×2) of a small right valve with unusually large cardinal area, typical muscle scar, and well-developed denticles (represented by notches); a hypotype from Rattlesnake Buttes, Colo. (locality 2, U.S.G.S. 747), in the Juana Lopez Member; U.S.N.M. 22008b.

Fig. 15. Lateral view (×2) of a typical right valve, nonplicate, and with reverse curvature; a hypotype from Huerfano Park, Colo. (locality 34), in the Juana Lopez Member; U.M.M.P. 43486.

Fig. 16. Interior view (×2) of a typical right valve showing nature of cardinal area, well-developed denticles, a typical muscle scar, and fine, sinuous, incised lines on the inner valve surface; a hypotype from the Mancos Shale, San Miguel County, Colo. (locality 28, U.S.G.S. 22592); U.S.N.M. 132258.

Fig. 17. Interior view (×2) of a right valve with unusually large resilifer and muscle scar, well-developed denticles; a hypotype from near Whitewater, Colo., from the Juana Lopez Member equivalent in the Mancos Shale (locality 22, U.S.G.S. 13663); U.S.N.M. 132165.

Plate 3

(All figures ×1)

Lopha bellaplicata bellaplicata (Shumard)

Figs. 1, 3, 9, 11, 15, 18. Lateral views of typical left valves of the species, placed in a growth series; note characteristic outline, nature and extent of auricles and auricular sulci, small attachment scars, nature of plicae and height of smooth stage; all specimens hypotypes from the upper Eagle Ford Shale, 2.5 miles east of Eagle Ford, Dallas County, Tex. (locality 15, U.S.G.S. 7539). Catalog Nos.: 1 (U.S.N.M. 132213), 3 (U.S.N.M. 132215), 9 (U.S.N.M. 132220), 11 (U.S.N.M. 132222, the neotype), 15 (U.S.N.M. 132225), and 18 (U.S.N.M. 132228).

Fig. 2. Lateral view of a left valve, abnormally short owing to reduced posterior auricle; a hypotype from the upper Eagle Ford Shale, 2.5 miles east of Eagle Ford, Dallas County, Tex. (locality 15, U.S.G.S. 7539); U.S.N.M. 132214.

Fig. 4. Lateral view of a left valve with reduced posterior auricle, unusually large attachment scar and prominent umbo; a hypotype from the upper Eagle Ford Shale of Texas (locality 15, U.S.G.S. 7539, cited above); U.S.N.M. 132216.

Fig. 5. Lateral view of a worn left valve with unusually large smooth stage; a hypotype from the Eagle Ford Shale at Sherman, Tex. (locality 54), the original of Stanton's plate 4, figure 8 (1893); U.S.N.M. 11882a.

Fig. 6. Lateral view of a left valve with unusually large attachment scar; posterior auricle broken; a hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 15, U.S.G.S. 7539, cited above); U.S.N.M. 132217.

Fig. 7. Lateral view of an abnormal left valve; note unusual height, reduction of auricles, broad plicae, a hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 57); U.S.N.M. 132218.

Fig. 8. Lateral view of an unusual left valve with broad plicae, fluted at their intersection with coarse concentric lamellae, and abnormally large smooth umbonal area. This form is possibly transitional to *Lopha panda* (Morton). A hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 15, U.S.G.S. 7539, cited above); U.S.N.M. 132219.

Fig. 10. Lateral view of a typical left valve with abnormally projecting beak and early umbo; a hypotype from the upper Eagle Ford sands, 1.75 miles west of Sherman, Tex. (locality 50, U.S.G.S. 14553); U.S.N.M. 132221.

Fig. 12. Lateral view of a left valve, unusual in having a nearly centrally situated beak and broad plicae; a hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 15, U.S.G.S. 7539, cited above); U.S.N.M. 132223.

Fig. 13. Lateral view of White's hypotype (1879, pl. 4, figs. 3a, b) from the Eagle Ford Shale at Denison, Tex. (locality 56); U.S.N.M. 12383.

Fig. 14. Lateral view of a typical adult left valve; a hypotype from upper Eagle Ford sands, 1.75 miles west of Sherman, Tex. (locality 50, U.S.G.S. 14553); U.S.N.M. 132224.

Fig. 16. Lateral view of an unusually elongate, high left valve, more inclined than normal, and with a large attachment scar; a hypotype from Dallas County, Tex. (locality 57); U.S.N.M. 132226.

Fig. 17. Lateral view of a typical left valve with an unusually large attachment scar, a hypotype from the upper Eagle Ford Shale, 2.5 miles east of Eagle Ford, Dallas County, Tex. (locality 15, U.S.G.S. 7539, cited above); U.S.N.M. 132227.

Plate 4

(All figures $\times 1$)

Lopha bellaplicata bellaplicata (Shumard)

Fig. 1. Lateral view of a left valve from White's syntype lot of *Lopha blacki.* Note that other than the projecting beak and umbo, deformed by the

attachment scar, and the rounded nature of the plicae (worn), the nature of the valve is identical with those of *L. bellaplicata bellaplicata* illustrated on plates 3 and 4; hypotype (of *L. bellaplicata bellaplicata*) from the upper Eagle Ford Shale, Collin County, Tex. (locality 53); U.S.N.M. 8024a.

Fig. 2. Lateral view of a large left valve with unusually well developed posterior auricle and faint, worn plicae; hypotype from upper Eagle Ford sands, 1.75 miles west of Sherman, Tex. (locality 50, U.S.G.S. 14553); U.S.N.M. 132229.

Fig. 3. Lateral view of a typical left valve. Note change in prominence of plicae at midshell, giving rise to faint plicae similar to those on *L. blacki* (White). A hypotype from the upper Eagle Ford Shale, 2.5 miles east of Eagle Ford, Dallas County, Tex. (locality 15, U.S.G.S. 7539); U.S.N.M. 132230.

Fig. 4. Lateral view of an unusually flat left valve with abnormal prosocline inclination, a hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 57); U.S.N.M. 132231.

Fig. 5. Lateral view of an adult left valve showing extensive bifurcation of plicae, and unusually reduced posterior auricle; a hypotype from the upper Eagle Ford Shale, 2.5 miles east of Eagle Ford, Dallas County, Tex. (locality 15, U.S.G.S. 7539); U.S.N.M. 132232.

Fig. 6. Lateral view of the smoothest specimen from White's syntype lot of *L. blacki,* considered here a smooth variant of *L. bellaplicata bellaplicata* (Shumard). The original of White's plate 46, figure 2 (1884). Hypotype from the upper Eagle Ford Shale, Collin County, Tex. (locality 53); U.S.N.M. 8024b.

Fig. 7. Lateral view of a large left valve showing large attachment scar but otherwise typical of the species; hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 15, U.S.G.S. 7539, cited above); U.S.N.M. 132233.

Fig. 8. Interior view of a left valve showing nature and position of muscle scar, flattened lateral lamellae forming part of commissure, and unusually massive cardinal area with characteristic structures; a hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 57); U.S.N.M. 132234.

Plate 5

(All figures $\times 1$)

Lopha bellaplicata bellaplicata (Shumard)

Figs. 1-4. Anterior (side) views of representative left valves, illustrating the range of variation in convexity. No. 1 is typical of the species. 1-3, Neotype and hypotypes from the upper Eagle Ford Shale, Dallas County, Tex. (locality 15, U.S.G.S. 7539); U.S.N.M. 132222 (fig. 1); U.S.N.M. 132228 (fig. 2); U.S.N.M. 132235 (fig. 3). 4, Hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 57); U.S.N.M. 132231.

Figs. 5-8. Lateral views of typical right valves, arranged in growth series. Note development of auricles (fig. 7 is atypical in this respect, having rounded auricles), anterior position of beaks, posterior curvature of beaks, nearly straight dorsal margin, height of smooth stage (greater than on average left valves), the abrupt appearance, prominence, and bifurcation of the plicae, and the well-developed concentric lamellae. Hypotypes from the upper Eagle Ford Shale, 1.5 miles east of Eagle Ford, Dallas County, Tex. (locality 15, U.S.G.S. 7539); U.S.N.M. 132236 (fig. 5); U.S.N.M. 132237 (fig. 6); U.S.N.M. 132238 (fig. 7); U.S.N.M. 132239 (fig. 8).

Fig. 9. Lateral view of a right valve from the syntype lot of "*Ostrea*" *blacki* White. Note the only difference between this specimen and typical right valves of *L. bellaplicata bellaplicata* is the height of the smooth stage. A hypotype of *L. bellaplicata bellaplicata* from the upper Eagle Ford Shale in Collin County, Tex. (locality 53); U.S.N.M. 8024c.

Figs. 10, 13. Lateral and interior views of an abnormal right valve lacking auricles and prominent plicae. Note nature of cardinal area and muscle scar, both characteristic for the species. A hypotype from the upper Eagle Ford Shale of Texas (locality 57, previously cited); U.S.N.M. 132240.

Fig. 11. Lateral view of a nearly smooth right valve of a mature shell, a marginal variant occurring with specimens illustrated in figures 5-8. Compare with figure 12, a syntype of *L. blacki* (White). Hypotype from the upper Eagle Ford Shale of Texas (locality 15, U.S.G.S. 7539, previously cited); U.S.N.M. 132241.

Figs. 12, 15. Lateral and interior views of a smooth right valve with faint plicae and well-developed interior features. Hypotype of *Lopha bellaplicata bellaplicata* from the upper Eagle Ford Shale of Collin County, Tex. (locality 53); U.S.N.M. 11882b.

Fig. 14. Lateral view of an unusually elongate right valve with characteristic ornamentation, somewhat worn; hypotype from the upper Eagle Ford Shale of Dallas County, Tex. (locality 15, U.S.G.S. 7539, previously cited); U.S.N.M. 132242.

Plate 6

Lopha bellaplicata bellaplicata (Shumard), variety A

Fig. 1. Lateral view (×1) of a typical left valve, showing shape, plicae, narrow beak and umbo, and small attachment scar. A hypotype from the Codell Sandstone Member, Carlile Shale, Huerfano Park, Colo. (locality 41, U.S.G.S. 743); U.S.N.M. 22011a.

Fig. 2. Lateral view (×2) of a left valve with an unusually large attachment scar; a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 59; U.M.M.P. 38052.

Fig. 3. Lateral view (×1) of a small plicate upper valve associated with *L. bellaplicata bellaplicata* var. A; a hypotype from the Codell Sandstone Member of Huerfano Park, Colo. (locality 58); U.S.N.M. 132259.

Fig. 4. Lateral view (×1) of a smooth, elongate right valve associated with specimens of *L. bellaplicata bellaplicata* var. A; a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 61); U.M.M.P. 43413.

Fig. 5. Lateral view (×2) of a left valve with unusually broad plicae; a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 59); U.M.M.P. 38051.

Fig. 6. Lateral view of a left valve (×1) with a prominent attachment scar; hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 41, U.S.G.S. 743); U.S.N.M. 22011d.

Fig. 19. Lateral view (×1) of a small left valve showing ventral flaring of the lateral margins; a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 61); U.S.N.M. 132249.

Lopha bellaplicata bellaplicata (Shumard): forma typica

Fig. 7. Lateral view (×1) of a small left valve typical of the species, a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 40, U.S.G.S. 741); U.S.N.M. 22009a.

Fig. 8. Lateral view (×1) of a left valve with moderately large attachment scar: a hypotype figured by Stanton (1893, pl. 4, fig. 4) from the Codell Sandstone Member, Huerfano Park, Colo. (locality 41, U.S.G.S. 743); U.S.N.M. 22860d.

Fig. 9. Lateral view (×1) of a left valve, characteristic of the species; hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 61); U.M.M.P. 38038.

Fig. 10. Lateral view of an unusual left valve (×1) with abnormally elongate posterior auricle, broad, faint plicae; a hypotype from the Codell Sandstone Member, Carlile Shale, Huerfano Park, Colo. (locality 61); U.M.M.P. 43482.

Fig. 11. Lateral view (×1) of a mature left valve, slightly longer than average, similar to Texas specimen illustrated on plate 3, figure 12; hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 40, U.S.G.S. 741); U.S.N.M. 22009b.

Fig. 12. Lateral view (×1) of a typical left valve, a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 59); U.M.M.P. 38039.

Fig. 13. Lateral view (×1) of a nearly symmetrical left valve with a large attachment scar and unusually inflated umbone, a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 41, U.S.G.S. 743); U.S.N.M. 22011b.

Fig. 14. Lateral view (×1) of a mature left valve with unusually deep attachment scar, abnormally situated dorsoposteriorly; a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 59); U.M.M.P. 38041.

Fig. 15. Lateral view (×1) of a large left valve with extended auricles, abnormally broad plicae, and subcentral beak; a Colorado variant of the species not yet found elsewhere; a hypotype from the Codell Sandstone Member, Carlile Springs, Colo. (locality 55); the original of Stanton's plate 4, figure 7 (1893); U.S.N.M. 22861.

Fig. 16. Interior view of a left valve (×1) showing normal cardinal area, denticles, internal reflection of ornamentation, and posterior adductor muscle scar, the hypotype figured by Stanton (1893, pl. 4, fig. 9), from the

Codell Sandstone Member, Huerfano Park, Colo (locality 41, U.S.G.S. 743); U.S.N.M. 22860b.

Fig. 17. Lateral view of a typical right valve from Colorado (×2) showing limited extent of plicae, concentric ornamentation, shape; a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 61); U.M.M.P. 43466.

Fig. 18. Lateral view (×2) of a totally nonplicate right valve, otherwise typical of the species; a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 59); U.M.M.P. 43483.

Fig. 20. Lateral view (×1) of a large, unusually high right valve, showing typical development of the concentric lamellae; a hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 15, U.S.G.S. 7539); U.S.N.M. 132250.

Fig. 21. Lateral view (×1) of a nearly smooth right valve showing a few, sinuous, irregular plicae near margin; a hypotype from the Codell Sandstone Member, Huerfano Park, Colo. (locality 59); U.M.M.P. 43478.

Figs. 22, 23. Dorsal and posterior views (×1) of a small left valve with plicae less extensive than average, and an unusually large attachment scar; the hypotype illustrated by Stanton (1893, pl. 4, fig. 6), from the Codell Sandstone Member, Huerfano Park, Colo. (locality 41, U.S.G.S. 743); U.S.N.M. 22860c.

Fig. 24. Lateral view of a large, old right valve showing degeneration of radial ornamentation near margin, and increase in number and prominence of the concentric lamellae with age; a hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 15, U.S.G.S. 7539); U.S.N.M. 132251.

Plate 7

(All figures ×1)

Lopha bellaplicata novamexicana Kauffman, new subspecies

Figs. 1, 2. Lateral views of immature left valves, typical of the subspecies. Note general similarity to immature left valves of *L. bellaplicata bellaplicata* (pl. 3) but the smaller auricles and more inclined posterodorsal margin in the subspecies *novamexicana* at this and later growth stages. Paratypes from the zone of *Collignoniceras hyatti* (Stanton), Mancos Shale, Socorro County, N. Mex. (locality 66, U.S.G.S. D2042); U.S.N.M. 132260 (fig. 1), and 132261 (fig. 2).

Fig. 3. Lateral view of a young adult left valve, typical of the subspecies except for narrow auricular sulci. Note broad plicae. A paratype from the Colorado Group (Mancos?), Carthage, N. Mex. (locality 64, U.S.G.S. 3297); U.S.N.M. 132262.

Figs. 4, 5. Lateral and interior views of a typical adult valve showing broad, widely spaced plicae, few in number, inclined posterodorsal margin, broad posterior auricular sulcus, and the nature of the cardinal area and muscle scar. A paratype from the Mancos Shale, Socorro County, N. Mex. (locality 66, U.S.G.S. D2042); U.S.N.M. 132263.

Fig. 6. Lateral view of a small, incomplete, right valve showing broad plicae and short smooth stage. A paratype from the Mancos Shale, Socorro County, N. Mex. (locality 66, U.S.G.S. D2042) ; U.S.N.M. 132264.

Fig. 7. Lateral view of a small, unusually curved right valve with recurved beak and umbo, short smooth stage limited to umbo, and typical plicae. A paratype from the Colorado Group (Mancos Shale?), Carthage, N. Mex. (locality 64, U.S.G.S. 3297) ; U.S.N.M. 132262.

Fig. 8. Lateral view of an adult right valve similar in shape to those of *L. bellaplicata bellaplicata,* but with a much shorter smooth umbonal area. Note coarse lamellae, characteristic plicae. A paratype from the Colorado Group (Mancos) at Carthage, N. Mex. (locality 63, U.S.G.S. 3295) ; U.S.N.M. 132265.

Fig. 9. Lateral view of a right valve with reverse inclination (opisthocline) and enlarged anterior auricle. Note broad plicae, short smooth stage limited to umbo. A paratype from the Mancos Shale, zone of *Collignoniceras hyatti,* Socorro County, N. Mex. (locality 66, U.S.G.S. D2042) ; U.S.N.M. 132266.

Fig. 10. Lateral view of a left valve, characteristic of the subspecies. Note broad plicae, few in number, broad posterior auricular sulcus, inclination of posterodorsal margin. The holotype, from a massive sandstone in the Mancos Shale, zone of *Collignoniceras hyatti,* Socorro County, N. Mex. (locality 66, U.S.G.S. D2042) ; U.S.N.M. 132267.

Fig. 11. Lateral view of a left valve with narrow plicae, otherwise typical of the subspecies; a paratype from the septarian limestone concretion zone, upper Blue Hill Shale Member, Huerfano Park, Colo. (locality 62, U.S.G.S. 738) ; U.S.N.M. 22012.

Fig. 12. Lateral view of a left valve with narrow ribs, or plicae, occurring along with normal individuals of the subspecies in the Mancos Shale near Carthage, N. Mex. (locality 63, U.S.G.S. 3295). Compare this with figure 11, from the Blue Hill Shale Member, Huerfano Park, Colo. A paratype, U.S.N.M. 132268.

Fig. 13. Lateral view of an unusually broad variant of the subspecies from the Blue Hill Shale Member, Huerfano Park, Colo. (locality 69), closely comparable to marginal variants of *L. bellaplicata bellaplicata* from the Codell Sandstone in the same area (see pl. 6, fig. 15). A paratype; U.S.N.M. 132269.

Fig. 14. Lateral view of a high left valve with reduced posterior auricle; paratype from the Mancos Shale at Carthage, N. Mex. (locality 65, U.S.G.S. 5303) ; U.S.N.M. 132270.

Fig. 15. Lateral view of an exfoliated left valve, showing characteristic outline and radial ornamentation; a paratype from the Mancos Shale at Carthage, N. Mex. (locality 64, U.S.G.S. 3297) ; U.S.N.M. 132271.

Fig. 16. Lateral view of a robust left valve, characteristic of the subspecies; a paratype from the Mancos Shale, zone of *Collignoniceras hyatti,* Socorro County, N. Mex. (locality 66, U.S.G.S. D2042) ; U.S.N.M. 132272.

Fig. 17. Lateral view of a left valve with posterior auricle larger than normal and density of plicae approaching that of *L. bellaplicata bellaplicata;* a paratype from the Mancos Shale, Carthage, N. Mex. (locality 65, U.S.G.S. 5303) ; U.S.N.M. 132273.

Fig. 18. Lateral view of a large left valve, characteristic of the subspecies; a paratype from the Mancos Shale at Carthage, N. Mex. (locality 64, U.S.G.S. 3297); U.S.N.M. 132274.

Fig. 19. Lateral view of an unusually high left valve, otherwise characteristic of the subspecies; a paratype from the Mancos Shale at Carthage, N. Mex. (locality 65, U.S.G.S. 5303); U.S.N.M. 132275.

Plate 8

Lopha bellaplicata novamexicana Kauffman, new subspecies

Fig. 1-3. Anterior views of left valves illustrating the range in convexity, the great convexity of the umbonal region, and the dorsal position of the high point of the valve. All specimens from the Mancos Shale of New Mexico, zone of *Collignoniceras hyatti.* 1, U.S.N.M. 132282, from locality 66. 2, U.S.N.M. 132271, from locality 64. 3, U.S.N.M. 132276, from locality 66. All figures ×1.

Fig. 4. Lateral view (×1) of a left valve, characteristic of the subspecies except for fainter plicae; paratype from locality 66, U.S.G.S. D2042, Mancos Shale, zone of *Collignoniceras hyatti,* Socorro County, N. Mex. U.S.N.M. 132277.

Fig. 5. Lateral view (×1) of a left valve with large vertical attachment scar and unusually fine plicae; paratype from the Mancos Shale, zone of *Collignoniceras hyatti,* Socorro County, N. Mex. (locality 66, U.S.G.S. D2042); U.S.N.M. 132278.

Fig. 6. Lateral view (×1) of a large left valve transitional with *L. bellaplicata bellaplicata* in development of plicae and auricular sulci, but retaining characteristic shell form of the subspecies; a paratype from the Mancos Shale, zone of *C. hyatti,* Socorro County, N. Mex. (locality 66, U.S.G.S. D2042); U.S.N.M. 132279.

Fig. 7. Lateral view of a large left valve (×1) characteristic of the subspecies; a paratype from the zone of *C. hyatti,* Mancos Shale, Socorro County, N. Mex. (locality 66, U.S.G.S. D2042); U.S.N.M. 132280.

Fig. 8. Lateral view (×1) of a typical left valve with worn plicae; a paratype from the zone of *C. hyatti,* Mancos Shale, Socorro County, N. Mex. (locality 66, U.S.G.S. D2042); U.S.N.M. 132281.

Fig. 9. Lateral view (×1) of a typical large, adult left valve; a paratype from the zone of *C. hyatti,* Mancos Shale, Socorro County, N. Mex. (locality 66, U.S.G.S. D2042); U.S.N.M. 132282.

Lopha bellaplicata bellaplicata (Shumard)

Fig. 10. Thin section (×4) through the umbo and cardinal area of a large left valve; section parallel to the hinge line. Note major layers in subnacreous layer, and fine crystalline calcite sheets within them. Fine layers inclined to plane of major layers over umbo, parallel to this plane laterally; a hypotype from the upper Eagle Ford Shale, Dallas County, Tex. (locality 15, U.S.G.S. 7539); U.S.N.M. 132283.

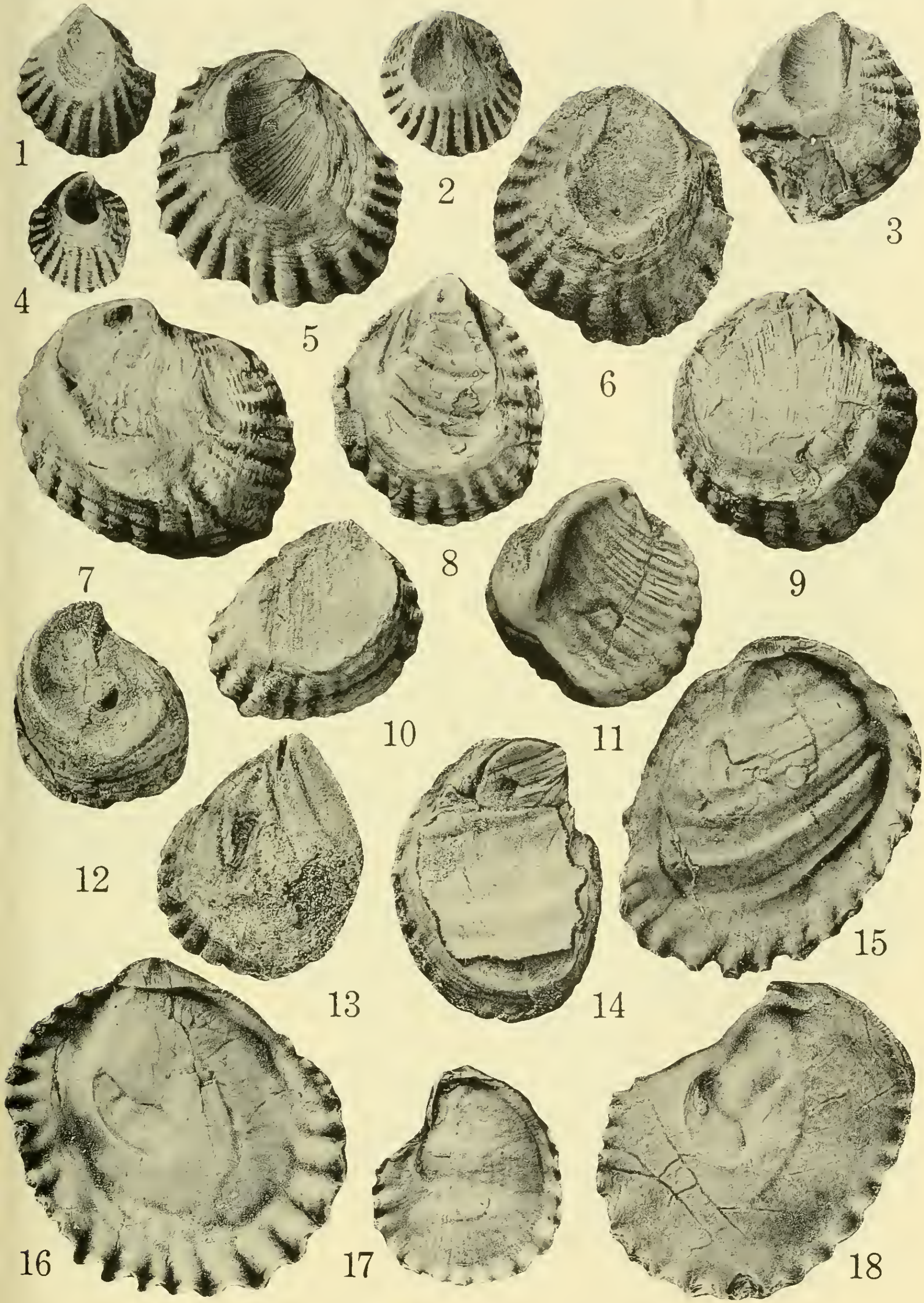
Fig. 11. Thin section (×4) taken along the median plica, showing the structure of the subnacreous shell layer, the "hingement" of the valves, position

of the ligament, and the position of the cardinal axis on the cardinal plate. Note that subnacreous layer is composed of distinct major calcite layers (lamellae) parallel to the surface of the shell; each layer is composed of fine fibrous-appearing calcite crystals or plates inclined to the plane of the major layers, and in many cases, with opposed inclination within or between major layers. A hypotype from sands of upper Eagle Ford age, Grayson County, Tex. (locality 50, U.S.G.S. 14553); U.S.N.M. 132284.

Lopha lugubris (Conrad)

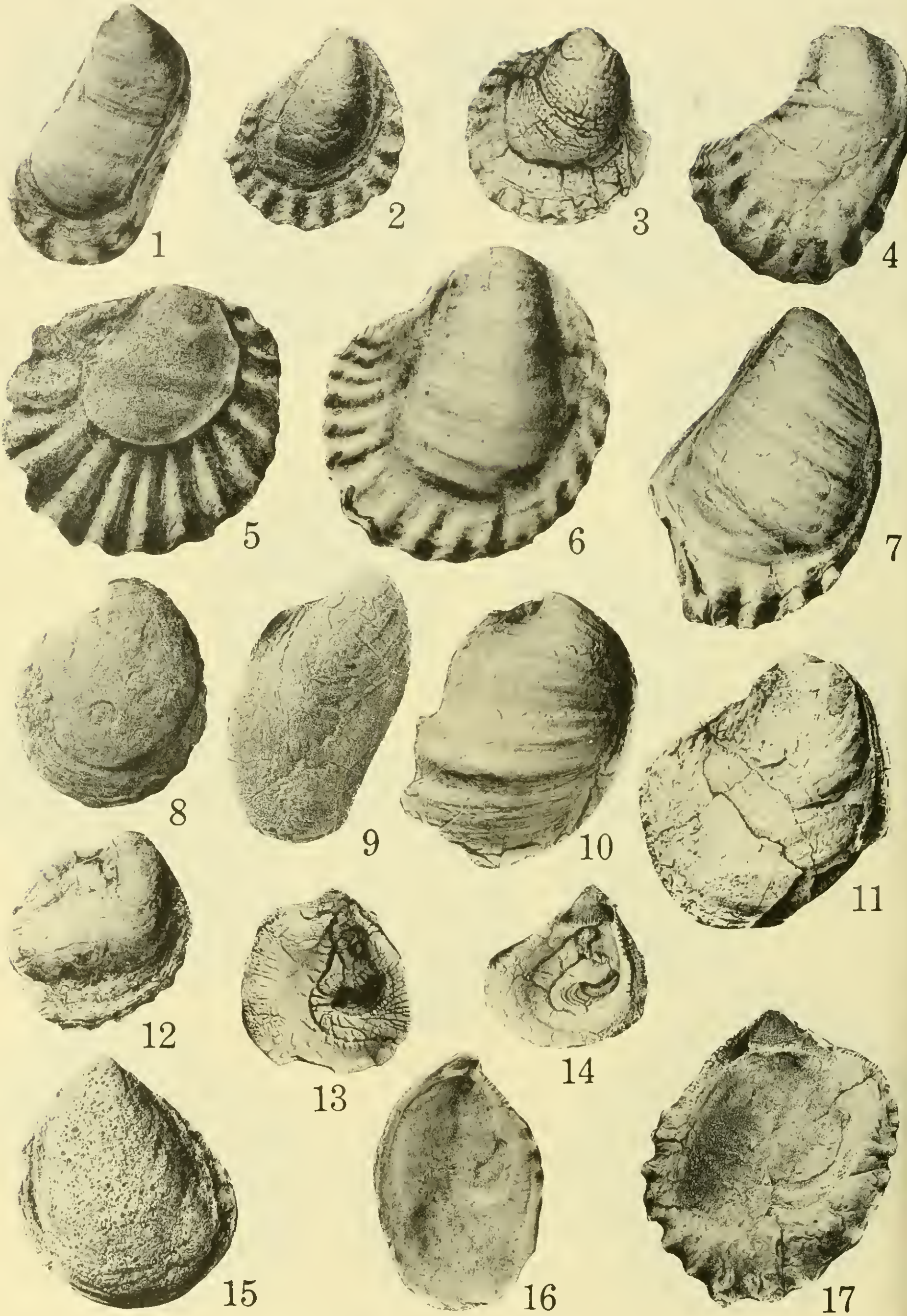
Fig. 12. Thin section (×8) through part of the left valve, showing major calcite lamellae in subnacreous layer and minor inclined fibrous calcite crystals or plates within them, as described for figure 11. A hypotype from New Mexico (locality 1, U.S.G.S. 513) in the zone of *Prionocyclus wyomingensis*. U.S.N.M. 132285.

PLATES



LOPHA LUGUBRIS (CONRAD): LEFT VALVE

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



LOPHA LUGUBRIS (CONRAD): RIGHT VALVE

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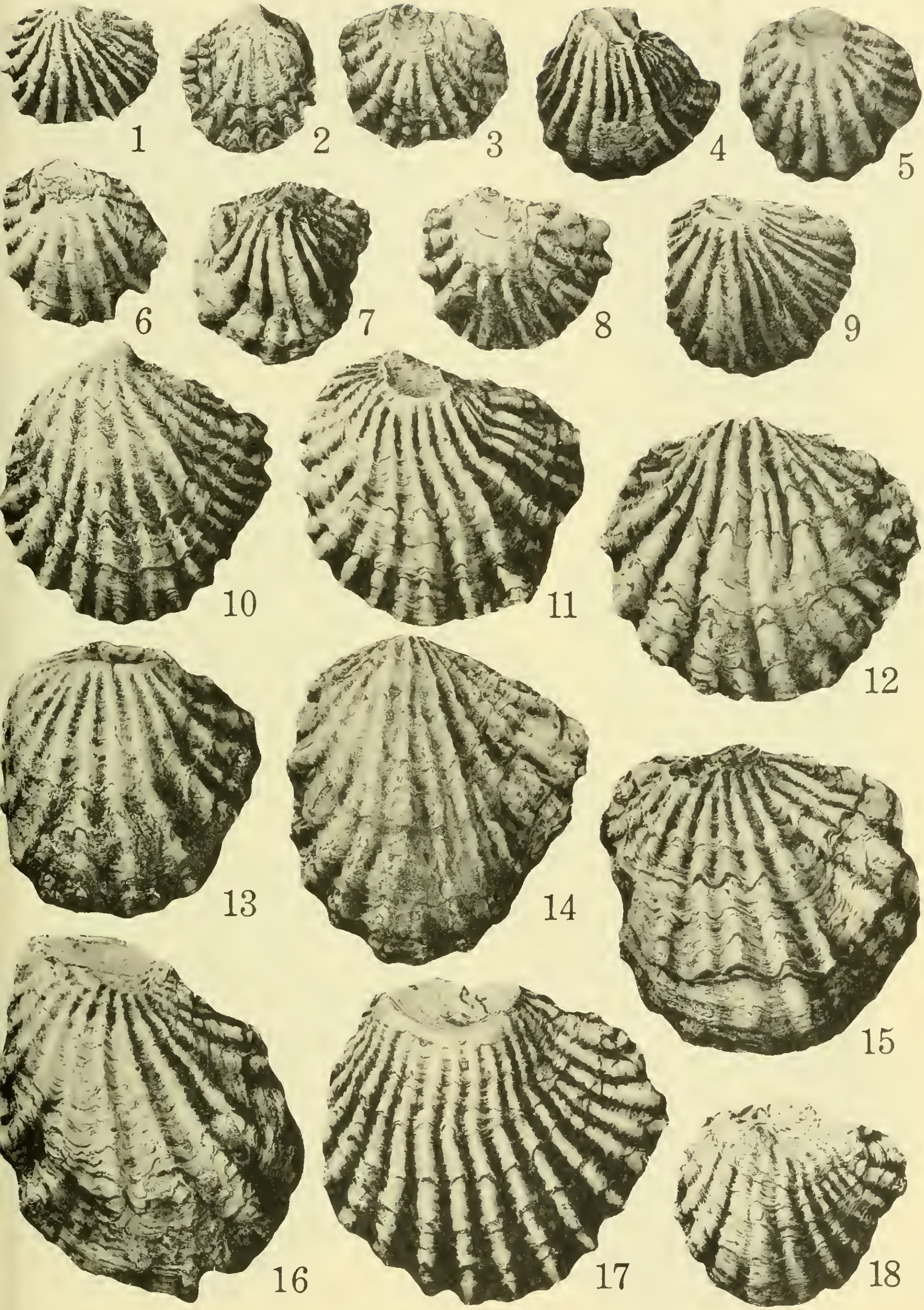

LOPHA BELLAPLICATA BELLAPLICATA (SHUMARD): LEFT VALVE. TEXAS

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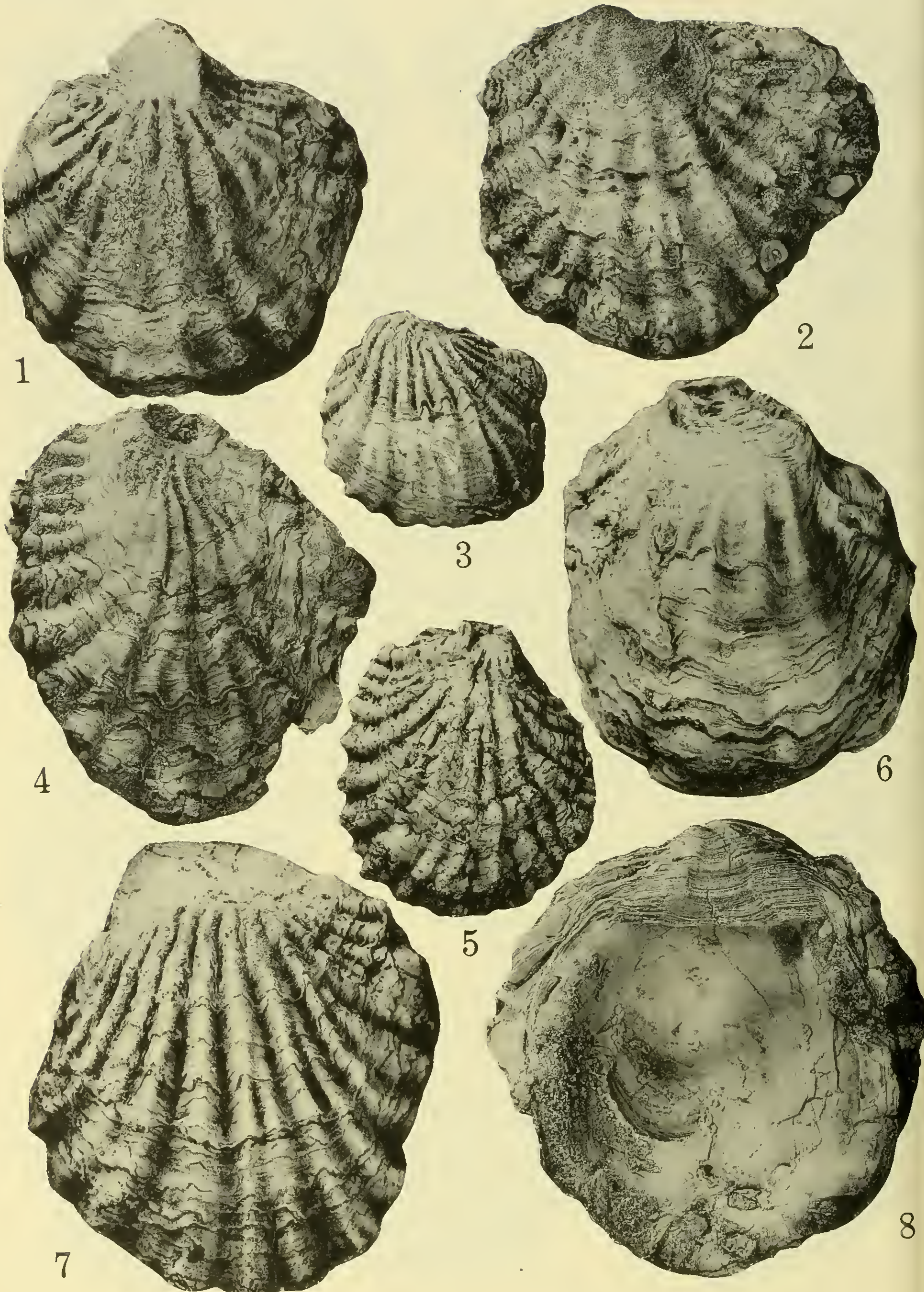

LOPHA BELLAPLICATA BELLAPLICATA (SHUMARD): LEFT VALVE, TEXAS

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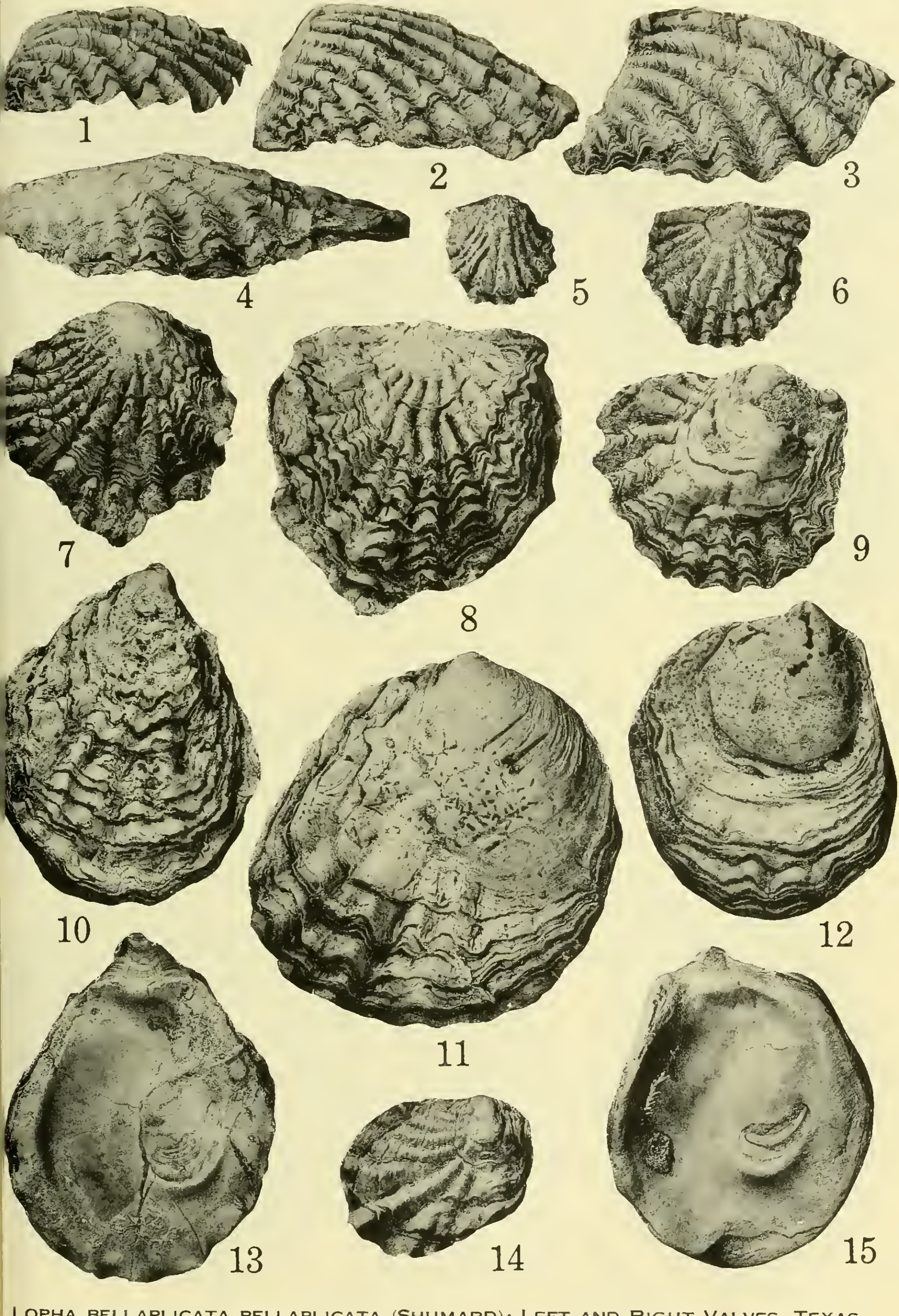

LOPHA BELLAPLICATA BELLAPLICATA (SHUMARD): LEFT AND RIGHT VALVES, TEXAS

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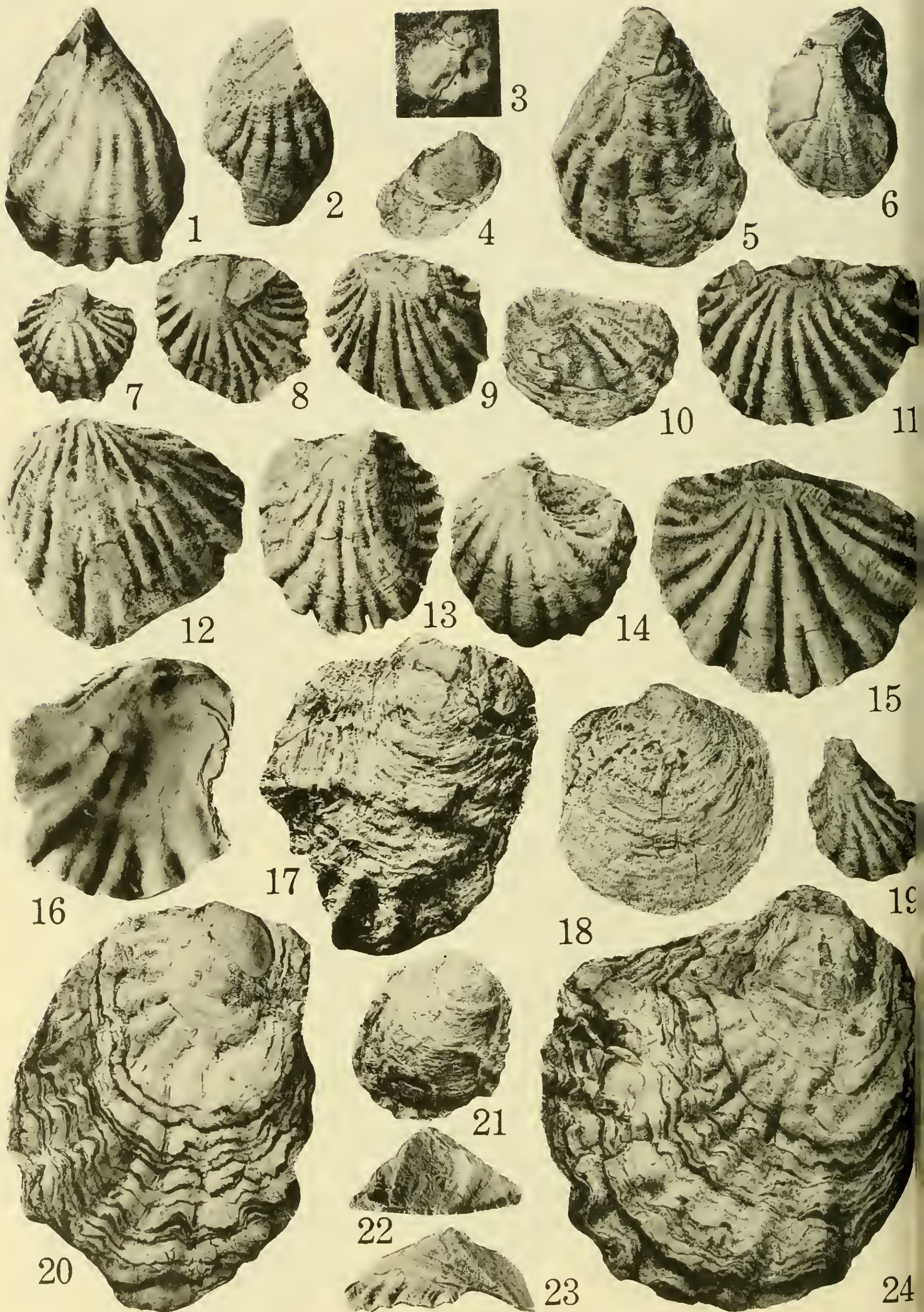
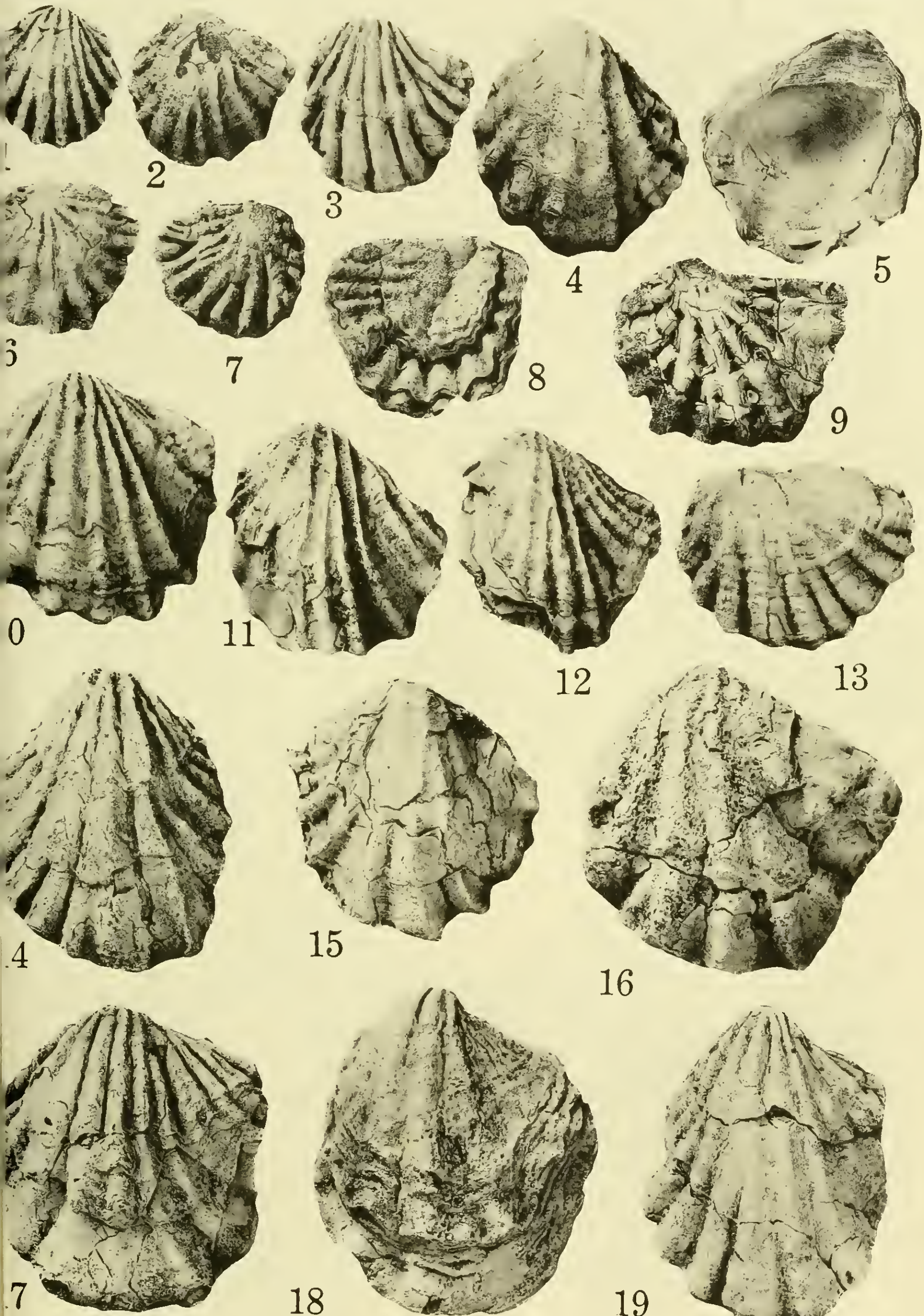


LOPHA BELLAPLICATA BELLAPLICATA (SHUMARD): VAR. A AND FORMA TYPICA: LEFT AND RIGHT VALVES. TEXAS AND COLORADO

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



LOPHA BELLAPLICATA NOVAMEXICANA KAUFFMAN, N. SUBSP.: LEFT AND RIGHT VALVES. COLORADO AND NEW MEXICO

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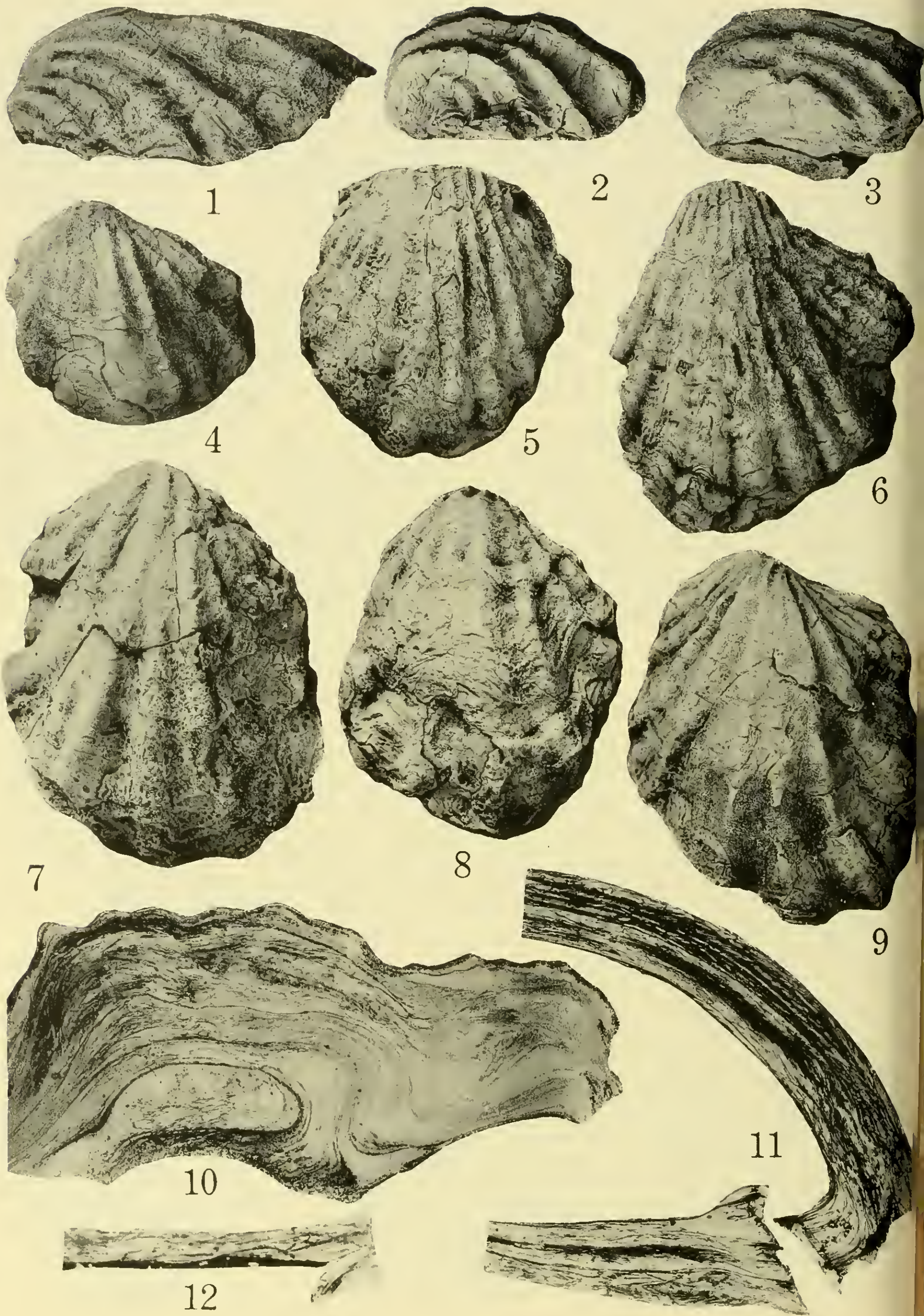

LOPHA BELLAPLICATA NOVAMEXICANA KAUFFMAN, N. SUBSP.: L. BELLAPLICATA BELLAPLICATA (SHUMARD): L. LUGUBRIS (CONRAD)

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