Giant Upper Cretaceous Oysters from the Gulf Coast and Caribbean

GEOLOGICAL SURVEY PROFESSIONAL PAPER 483-H

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By NORMAN F. SOHL *and* ERLE G. KAUFFMAN

CONTRIBUTIONS TO PALEONTOLOGY

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These exceptionally massive species are among the most unusual Cretaceous ostreids, are stratigraphically restricted, and provide a basis for refined correlation

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CONTRIBUTIONS TO PALEONTOLOGY

GIANT UPPER CRETACEOUS OYSTERS FROM THE GULF COAST AND CARIBBEAN

By Norman F. Sohl and Erle G. Kauffman

ABSTRACT

Two unusually massive ostreid species, representing the largest and youngest Mesozoic members of their respective lineages, occur in Upper Cretaceous sediment of the gulf coast and Caribbean areas. Their characteristics and significance, as well as the morphologic terminology of ostreids in general, are discussed.

Crassostrea cusseta Sohl and Kauffman n. sp. is the largest known ostreid from Mesozoic rocks of North America; it occurs sporadically in the Cusseta Sand and rarely in the Blufftown Formation of the Chattahoochee River region in Georgia and Alabama. It is especially notable in that it lacks a detectable posterior adductor muscle scar on large adult shells. *C. cusseta* is the terminal Cretaceous member of the *C. soleniscus* lineage in gulf coast sediments; the lineage continues, however, with little basic modification, throughout the Cenozoic, being represented in the Eocene by *C. gigantissima* (Finch) and probably, in modern times, by *C. virginica* (Gmelin). The *C. soleniscus* lineage is the first typically modern crassostreid group recognized in the Mesozoic.

Arctostrea aguilerae (Böse) occurs in Late Campanian and Early Maestrichtian sediments of Alabama, Mississippi, Texas(?), Mexico, and Cuba. The mature shell of this species is larger and more massive than that of any other known arctostreid. *Arctostrea* is well represented throughout the Upper Jurassic and Cretaceous of Europe, but in North America, despite the great numbers and diversity of Cretaceous oysters, only *A. aguilerae* and the Albian form *A. carinata* are known. The presence of *A. aguilerae* in both the Caribbean and gulf coast faunas is exceptional, as the Late Cretaceous faunas of these provinces are generally distinct and originated in different faunal realms.

INTRODUCTION

An unusually diverse assemblage of ostreid species and a great abundance of individuals have always been hallmarks of Upper Cretaceous deposits in the Gulf Coastal Plain province. Even at present, careful collecting by paleontologists continues to turn up new and frequently bizarre species, adding to an already impressive list of oysters available for biostratigraphic, taxonomic, and evolutionary studies. The giant species described here are among the most unusual ostreids to be discovered in modern times. Both are exceptionally massive, representing the largest and final development of their respective species groups in the gulf coast Upper Cretaceous. Despite their rare and scattered occurrence, both species are stratigraphically restricted and provide a good basis for refined correlation (fig. 1).

Crassostrea cusseta is unique in many ways. Its great size and massive shell are unequaled among American Mesozoic oysters. It is the youngest as well as the largest known member of the *C. soleniscus* lineage in Cretaceous rocks; this lineage, the first typically modern crassostreid group known from the Mesozoic, appears to transgress the Mesozoic-Cenozoic boundary with little modification other than loss of marginal denticles and gives rise to large modern crassostreid types typified by the Eocene *C. gigantissima* (Finch) (=*C. georgiana* Conrad) and the Recent *C. virginica* (Gmelin). A gradual increase in size and massiveness characterizes the lineage from its Cretaceous origin to the development of *C. gigantissima.* Subsequent *Crassostrea* are smaller and more varied. A second significant evolutionary trend seems to involve a gradual reduction of the marginal denticles, which are well developed over the commissure in *C. soleniscus* and gradually disappear in younger species of the lineage. On large adult valves of *C. cusseta,* a posterior adductor muscle scar is not visible, a rare phenomenon among oysters, possibly indicating atrophy of the muscle in old age.

Arctostrea aguilerae (Böse), equally impressive because of its great size and massive shell, is the largest known member of the genus. Its distribution is equally significant. Few species of invertebrates are found in both the Upper Cretaceous deposits of the Caribbean and those of the Gulf Coastal Plain province. *Arctostrea aguilerae* is one of these, exhibiting an extensive gulf coast–Caribbean dispersal that transcends the faunal provinciality of the two areas. This species exhibits a nearly continuous distribution on the Gulf Coastal Plain and is known from Alabama, Mississippi, Texas(?), and Mexico (fig. 2). In addition, it is represented at six localities in Cuba.

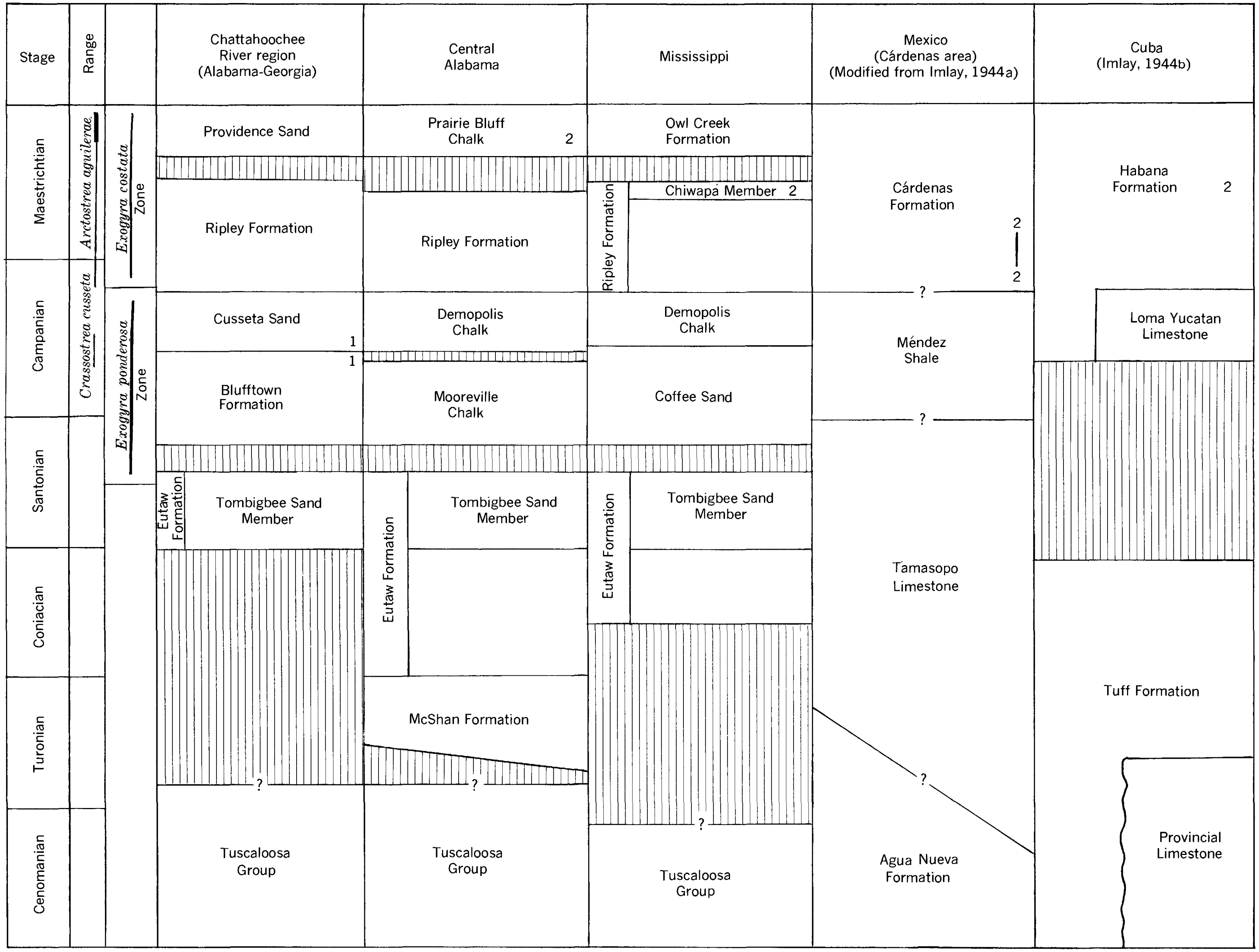

FIGURE 1.—Correlation chart of Upper Cretaceous rocks bearing *Crassostrea cusseta* Sohl and Kauffman n. sp. and *Arctostrea aguilerae* (Böse). 1, Stratigraphic range of *C. cusseta;* 2, stratigraphic range of *A. aguilerae.*

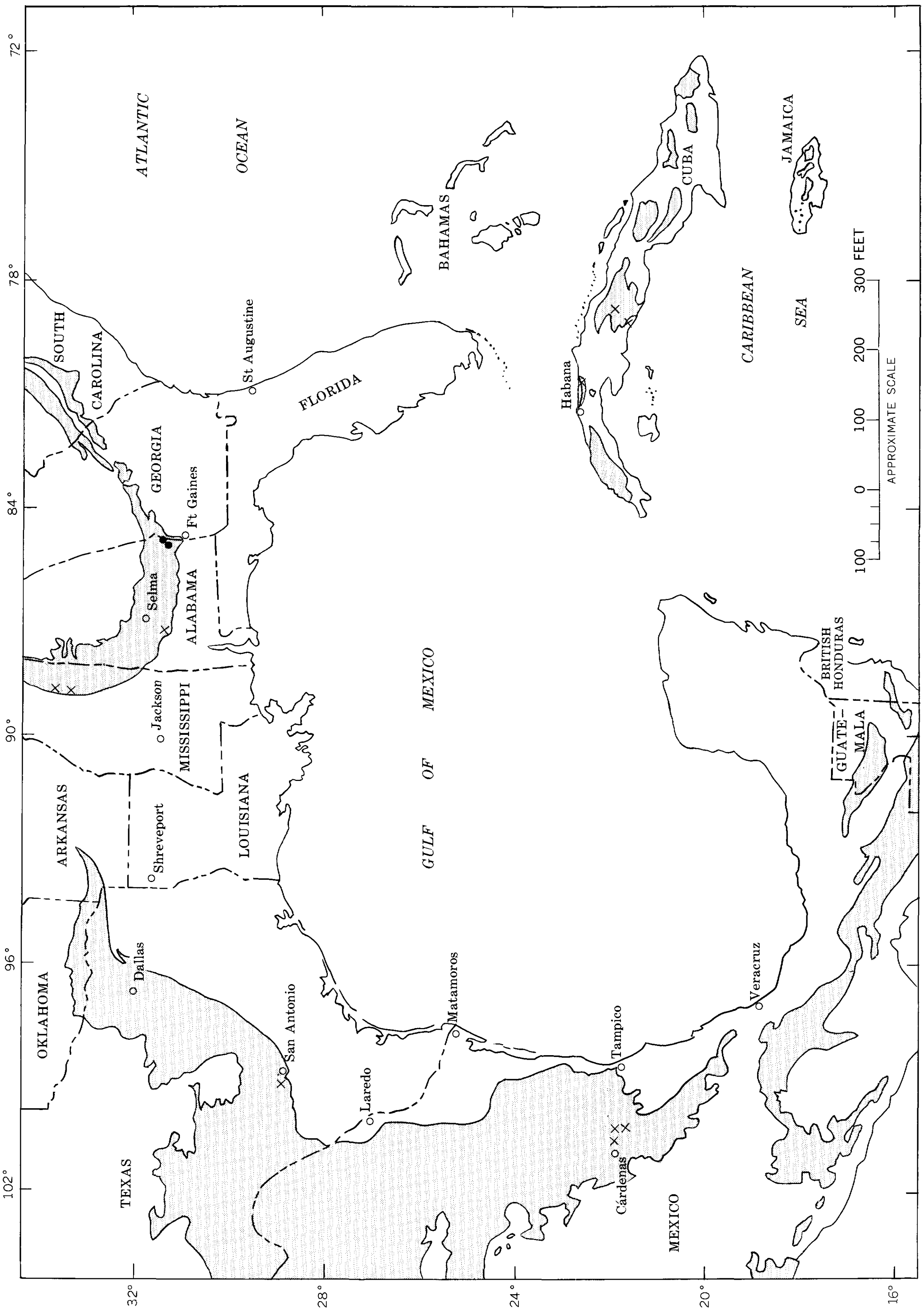

FIGURE 2.—Map showing distribution of *Crassostrea cusseta* Sohl and Kauffman n. sp. (●) and *Arctostrea aguilerae* (Böse) (×). Stippled area indicates extent of outcropping Cretaceous rocks.

EXPLANATION OF LETTER SYMBOLS

Di. Inclination angle of the dorsal part of the valve (above the point of posterior curvature) to the hinge line; measured between the plane of the hinge line and the average inclination of the dorsal part of the midline.

H. Height of the shell or valve, measured perpendicular to the plane of the hinge line.

HA. Height of the auricle, measured perpendicular to the plane of the hinge line.

HCA. Height of the cardinal area, measured perpendicular to the plane of the hinge line, between the dorsal margin and the ventral edge of the cardinal area.

HD. Height of that part of the shell possessing denticulate margins, measured perpendicular to the plane of the hinge line.

HL. Hinge line: a straight line connecting the ventrolateral margins of the cardinal area and delineating a plane of horizontal reference for all measurements. The hypothetical plane of the hinge line is perpendicular to the plane of the commissure.

HMS. Height of the muscle scar, or insertion area, measured perpendicular to the plane of the hinge line. This is not the longest diameter of the scar.

HPC. Height of that part of the shell dorsal to the point of abrupt posterior curvature, measured perpendicular to the plane of the hinge line.

L. Length of the valve, measured parallel to the plane of the hinge line, between the anteriormost and posteriormost projections of the valve when it is oriented with the hinge line horizontal.

LA. Length of the auricle, measured between the commissure and the lateral edge of the valve, parallel to the plane of the hinge line.

LCF. Lateral cardinal folds (new term): arched folds of the cardinal area on either side of the resilifer, bounded laterally in many species by shallow marginal cardinal troughs and (or) by raised lateral valve margins. The lateral part of the ligament attaches to part or all of each fold.

LCT. Lateral cardinal troughs (new term): concave troughs lying on either side of the midcardianl fold in the right valve, between the arched midcardinal fold and upturned lateral edges of the valve. The lateral part of the ligament attaches to these surfaces.

LHL. Length of the hinge line, measured along a line between the junctions of the ventral edge of the cardinal area and the lateral margins of the valve (commissure).

LM. Length of the midline of the valve, measured between the middorsal and midventral margins.

LMS. Length of the muscle scar, or area of muscle insertion, exposed on the interior surface of the valve; measured parallel to the plane of the hinge line.

MCT. Marginal cardinal troughs (new term): shallow, narrow troughs or grooves just inside the lateral margins of the valve on either side of the cardinal area. The troughs are bounded medially by the lateral cardinal folds and laterally by the raised outer margin of the cardinal area and (or) by overlapping calcite lamellae from the lateral edge of the shell. This structure is present in many ostreid species, being characteristic of some, merely a rare variant of others.

MDMS. Maximum diameter of the muscle scar, or insertion area.

MF. Midcardinal fold (new term): a shallow to highly arched, axially elongate fold situated centrally on the cardinal area of the right valve in some ostreid groups (in place of a resilifer). The midcardinal fold extends from the dorsal margin to the midventral edge of the cardinal area and fits into the resilifer of the left valve when the valves are articulated. The resilium attaches to part or all of this fold.

MLMF. Maximum length of midcardinal fold along its axis.

R. Resilifer: a triangular to rectangular, concave fossette situated centrally to subcentrally in the cardinal area. It extends from near the middorsal margin of the valve to the midventral edge of the cardinal area and is bounded laterally by flat to convex areas (lateral cardinal folds or plates) for attachment of the lateral ligament. The resilifer contains the resilium in living oysters. A resilifer is typically present on the left valve in the Ostreidae and also occurs on the right valve of many species groups. Where present on the right valve, it is commonly shallower than the corresponding structure on the left valve and is bounded ventrally by a raised lip. In species which have a resilifer only on the left valve, the right valve possesses a flat plate (midcardinal plate) or arched fold (midcardinal fold) in the central part of the cardinal area.

SC. Subcardinal cavities (new term): shallow to moderately deep reentrants of the floor of the valve beneath various structures of the cardinal area. Subcardinal cavities most commonly underlie the midcardinal and lateral cardinal folds and rarely occur below the resilifer or lateral cardinal troughs. These cavities are formed predominantly in species having a massive cardinal area. The terms "middle" and "lateral subcardinal cavity" may be applied to indicate the relative position of the cavities below the cardinal area.

TI. Total angle of inclination of the valve, measured between the plane of the hinge line (horizontal) and a straight line joining the beak with the midventral margin of the valve.

WR. Maximum width of the resilifer, measured perpendicular to the axis of this structure. The width of the midcardinal fold or plate is similarly measured.

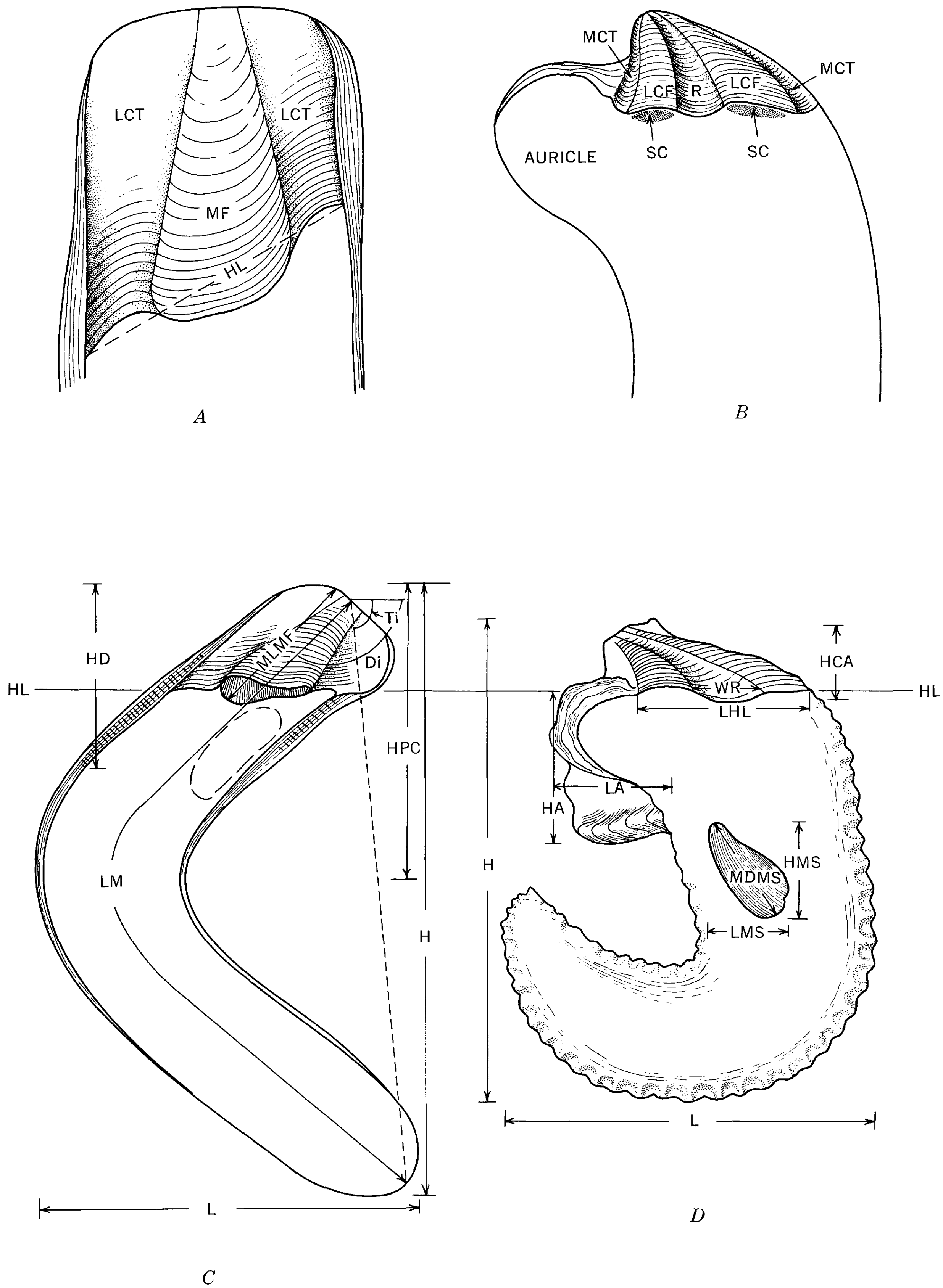

FIGURE 3.—Morphology of the Ostreidae: terminology and measurements. Explanation of symbols in text. *A*, Cardinal area, right valve of *Crassostrea cusseta;* *B*, dorsal half of interior, left valve of *Arctostrea aguilerae;* *C*, interior view, right valve, of *Crassostrea cusseta;* *D*, interior view, left valve of *Arctostrea aguilerae.*

The shell form *Arctostrea* is not known among Cenozoic and Recent oysters, and this unique group is here recognized as a distinct genus. *Arctostrea* is characterized by its massive narrow curved shell, cross-laminated shell structure, quadrate to triangular valve cross section, surface sculpture, and its deep muscle scar.

The genus *Arctostrea* is well represented in Europe throughout the Cretaceous by a relatively continuous sequence of forms. Its stratigraphic distribution, however, is very discontinuous in North America, where it is represented by only two species: *A. carinata* (Lamarck) from the Albian (Fredericksburg and Washita Groups) and *A. aguilerae* (Böse) from the Upper Campanian and Lower Maestrichtian. No explanation can be offered for the absence of *Arctostrea* throughout the lower part of the Upper Cretaceous in an area so rich in ostreid elements. Cenomanian, Turonian, and Santonian faunas of North America and western Europe are very similar, yet arctostreids, which characterize the lower part of the European Upper Cretaceous sequence [*A. pectinata* or *columbrina* from the Santonian; *A. carinata, ricordeana,* and *diluviana* (in part) from the Turonian], are not known from corresponding North American sedimentary rocks. This is unusual, because ostreids are among the most cosmopolitan of Cretaceous pelecypods.

The present study is one of the first in a continuing investigation of American Cretaceous oysters by the authors. In an effort to standardize morphologic terminology in the ostreids, a brief review of existing nomenclature and some pertinent new terms are presented. The amended descriptions of *Crassostrea* and *Arctostrea* used in this study include paleontological and malacological concepts in use at present and define more restricted and more natural boundaries for the taxa. They are considerably expanded over previous attempts and provide data for a much greater number of shell characters than were used in the past as a basis for supraspecific classification.

We express our appreciation to R. W. Imlay, of the U.S. Geological Survey, and to R. S. Boardman and P. M. Kier, of the U.S. National Museum, for their criticism of the manuscript. Discussions with Dr. H. B. Stenzel of the Shell Development Co. regarding generic taxonomy were very helpful. Photography was done by Jack Scott and his staff, and drawings were done by Larry B. Isham, all of the U.S. National Museum. To them we express our thanks. Members of the Mid-South Earth Science Club generously donated specimens of *Arctostrea aguilerae* for study.

MORPHOLOGIC TERMINOLOGY AND MEASUREMENTS

The proper interpretation of ostreid species and subspecies depends upon an intimate knowledge of morphologic features that are useful in the differentiation of taxa, the normal variation limits of populations, and the effect of environment on morphological variation. To achieve this, many modern workers have applied population systematics to this group and have found it necessary to reevaluate the importance of various shell structures in delineating taxa. This need has led to a search for features—to use as a basis for ostreid taxonomy—that are less affected by environment than are shape, ornamentation, and convexity. Structures of the cardinal area, muscle scar, denticles, and shell structure hold great promise in this respect. The value and of other features is yet untested.

Wherever possible, standard pelecypod terminology has been used in this study (after Newell, 1937, 1942; Shrock and Twenhofel, 1953), but there are structures, particularly those of the cardinal area, for which there is no standardized terminology. Inasmuch as these structures play a leading role in modern ostreid taxonomy, it is desirable that they be defined. New or revised terms used in this paper are defined on page H4 and are illustrated in figures 3*A* and 3*B*.

Similarly, measurements and ratios not commonly used in studies dealing with the Ostreidae are presented for the species described. These measurements and ratios, in addition to the standard measurements, are in part illustrated in figures 3*C* and 3*D* and are summarized in tables 1 and 2. The unusual structure of the ostreid species described herein necessitates many of these additional measurements. Other structures are investigated simply as possible criteria for the recognition and differentiation of taxa. Proper evaluation of their utility must await broader studies of the species groups to which *Crassostrea cusseta* and *A. aguilerae* belong. For all measurements the specimens were oriented so that the hinge line delineated a horizontal plane of reference perpendicular to the plane of the commissure.

The symbols used in figure 3 are given in alphabetical order on page H4.

SYSTEMATIC PALEONTOLOGY

Genus CRASSOSTREA Sacco: emended

1897. Sacco, Federico, I molluschi dei terreni terziarii del Piemonte e della Liguria: Clausen, Torino, v. 23, p. 15.

1941. McLean, R. A., The oysters of the western Atlantic: Acad. Nat. Sci. Philadelphia, Notulae naturae, no. 67, p. 8, pl. 1, figs. 1–4.

1950. Gunter, Gordon, The generic status of living oysters and the scientific name of the common American species: Am. Midland Naturalist, v. 43, no. 2, p. 438–449.

1954. Thomson, J. M., The genera of oysters and the Australian species: Australian Jour. Marine and Freshwater Research, v. 5, no. 1, p. 141, 142.

Type species.—Ostrea virginica Gmelin, by original designation.

DIAGNOSIS

Prodissoconch inequivalve, inequilateral; anterior ligament outside cardinal area; short hinge bears two toothlike denticles at each end. Adult shell variable in form, large in size, elongate along midline, straight to curved; left valve larger and more massive than right. Radial ornament unequally developed on left and right valves. Surface of left valve smooth to finely and irregularly plicate or costate. Right valve smooth to faintly plicate, flat. Left valve deeply cupped dorsally and centrally; valves normally show subcardinal cavities. Cardinal area of left valve composed of well-defined central triangular resilifer and subequal triangular lateral cardinal folds or plates. Cardinal area of right valve composed of midcardinal fold or central plate and subequal lateral cardinal troughs or plates. Adductor muscle scar ventroposterior, normally colored, large, shallow, semicircular to semielliptical; flat side dorsal and nearly perpendicular to midline. Mesozoic forms have simple ovoid to elongate denticles; Cenozoic forms have nondenticulate adult valves. Shell lamellate.

REMARKS

Numerous modern species of oysters have been extensively studied biologically, owing to their commercial importance. This work, though not done primarily for taxonomic purposes, has greatly aided neontologists in forming a natural classification of modern ostreids based primarily on the anatomy and reproductive habits of the animal. The majority of contemporary ostreid workers dealing with living species do not regard shell form or ornamentation as a good basis for classification because they are cognizant of the great variation of ostreid shell growth in response to different environments. The work of these men is of great interest to the paleontologist, who has relied upon shell morphology in classification and who now finds himself with little basis for the largely artificial divisions that he has recognized in the past.

It is significant that certain structures of the shell, many of them not previously used by paleontologists, are consistent with the natural divisions of the neontologists. The prodissoconch features are primary among these. The position of the posterior adductor muscle scar varies with the presence or absence of a promyal chamber. Subcardinal cavities also reflect the presence of this structure. The identification of modern crassostreid types in Cretaceous sediments is based on the neontological concept of the genus, as put forth by Ranson (1948, 1950: he used the term *Gryphaea,* later rejected), Gunter (1950), Thomson (1954), and others.

Modern *Crassostrea* are dioecious, and the eggs are deposited, fertilized, and developed in the water outside the shell. This is the main characteristic used to separate the genus from *Ostrea,* which contains wholly monoecious, larviparous species. Correspondingly, species of *Crassostrea* produce a much greater number of eggs than do species of *Ostrea*—about 50 million in studied species—and the eggs are smaller. Small gill ostia and the presence of a promyal chamber further differentiate *Crassostrea* from *Ostrea.* To accommodate the promyal chamber, the dorsal part of the left valve is deeply cupped, and the posterior adductor muscle scar is displaced ventrally and posteriorly, occurring well down toward the feeding margin of the shell. Both shell features characterize the *Crassostrea soleniscus* lineage of the Upper Cretaceous. Many *Crassostrea* have well developed subcardinal cavities, and these again reflect the presence of the promyal chamber and the displacement of the viscera. This feature is well defined in *C. cusseta* and in some specimens of *C. soleniscus.*

Denticles are present on the commissure and are reflected on the lateral margins of the valves in all members of the *Crassostrea soleniscus* lineage. All other Mesozoic *Crassostrea* that we have examined in detail seem to have them as well. On the other hand, the Cenozoic *Crassostrea,* even within this same lineage, lack denticles. Of the American Cenozoic *Crassostrea* examined, only the Early Tertiary representatives of *C. gigantissima* exhibit denticles, and in this species they are restricted to the juvenile shell and probably reflect an ancestry in the denticulate Mesozoic lineage of *C. soleniscus.*

Further examination of most Mesozoic and Cenozoic *Crassostrea* will be required to determine whether this difference is as consistent as it seems to be in the American species. If the distinction proves consistent, division of *Crassostrea* into two subgenera seems warranted. Such a study is unfortunately beyond the scope of the present paper.

Crassostrea cusseta Sohl and Kauffman n sp.

Plate 4, figures 5, 9, 10; plate 5, figures 1–4

MATERIAL

Fifteen well-preserved specimens from the base of the Cusseta Sand (Upper Cretaceous) at six localities in Georgia and Alabama. One specimen from the upper Blufftown Formation of Alabama. Six specimens nearly complete, lack only ventral extremity; remainder retain dorsal one-third of valve, including cardinal structures. Numerous additional fragments.

Description

General form.—Summary of measurements presented in table 1. Shell exceptionally large and massive, moderately inequivalve. Left (lower, attached) valve much more convex, slightly larger than right (upper, free) valve. Valves close fitting, of similar shape, highly inequilateral, and strongly curved posteriorly (pl. 4, fig. 10). Valve inclination typically opisthocline to nearly acline; average angle 95°. Height of shell greater than length: average ratio 1:0.577; average measurements of adult specimens: height, 377 mm; length, 211 mm; thickness of left valve, 65.6 mm; thickness of right valve, 59.4 mm.

Marginal outline relatively uniform for members of *Ostrea*. Some valves elongate, spatulate, and slightly curved toward posterior; valves more commonly subcrescentic and strongly curved posteriorly. Posterior curvature abrupt on most specimens (pl. 5, fig. 4), gradual on rare individuals. Point of initial posterior curvature is ⅓–½ the total height from the dorsal margin (pl. 5, fig. 4). Dorsal margin blunt, straight to slightly curved, not parallel to hinge line; dorsolateral margins narrowly and unevenly rounded, lateral margins straight to slightly curved and subparallel dorsally in absence of well-defined posterior auricle, slightly to moderately curved medially at point of posterior bend (anterior margin convex, posterior concave in outline), straight and subparallel ventrally; ventral margin unknown. On valves having posterior auricle, dorsoposterior margin moderately rounded (convex outward) at auricle, recessed (concave) below it (pl. 5, fig. 1).

Right valve uniformly slightly convex; left valve moderately to highly arched, convexity unevenly distributed. Umbonal area flattened on all right and on some left valves. Greatest convexity of left valve just anterior to midline along a narrow, sharp, irregular ridge bordering attachment scar (pl. 5, fig. 4) and ventral to this, along a moderately rounded subcentral fold Large gently rounded irregular folds, undulations, and constrictions superimposed on normal form of valves in many specimens. Point of greatest convexity of either valve dorsocentral. Anterior slope of left valve moderate to steep on most specimens, vertical or overhung on a few specimens; posterior slope moderately inclined; dorsal and ventral slopes gentle. Lateral edge of valves thick, steeply inclined (predominantly vertical) to plane of commissure.

TABLE 1.—*Summary of measurements for* Crassostrea cusseta *Sohl and Kauffman n. sp. from Georgia and Alabama*

Character	Number of specimens	Range	Average
Valve height (H), actual ______ millimeters	3	331–420	377
Length along midline (LM) ______ do	4	406.4–508	435
Valve length (L) ______ do	4	187–250	211
Ratio—length:height (L:H) ______	3	0.54:1–0.60:1	0.57:1
Thickness, left valve ______ millimeters	4	60–78.8	65.6
right valve ______ do	10	42–79	59.4
Curvature of beak:			
Left valve:			
Prosogyrate ______ percent	1	______	25
Opisthogyrate ______ do	3	______	75
Right valve:			
Prosogyrate ______ do	6	______	54.5
Opisthogyrate ______ do	5	______	45.5
Curvature of shell:			
Left valve:			
Anterior ______ do	0	______	00.0
Posterior ______ do	4	______	100.0
Right valve:			
Anterior ______ do	1	______	14.3
Posterior ______ do	6	______	85.7
Height (beak to point) of shell curvature (HPC) ______ millimeters	7	110–210	143
Number of concentric lamellae in 10 mm distance (along midline height):			
At 30 mm height ______	1	______	3
At 50 mm height ______	1	______	3
At 75 mm height ______	1	______	1
At 100 mm height ______	6	2–7	3.2
At 150 mm height ______	6	2–6	4.3
At 200 mm height ______	4	2–3	2.8
At 250 mm height ______	4	1–5	3.0
At 300 mm height ______	2	1–5	3.0
At 350 mm height ______	1	______	2.0
Posterior auricle:			
Height (HA) ______ millimeters	4	57.3–146	89.5
Length (LA) ______ do	4	36–69	48.1
Ratio—height of auricle to height of cardinal area (HA:HCA) ______ degrees	4	0.55:1–1.5:1	0.95:1
Angle of inclination (Ti):			
Total ______ do	3	68–114	95
Dorsal half of valve (Di) ______ do	3	29–73	51.7
Angle between hinge line and dorsal margin degrees	6	5–67	36
Length, hinge line (LHL) ______ millimeters	13	48–153	99
Height, cardinal area (HCA) ______ do	13	74–158	112.4
Ratio—length of hinge line to height of cardinal area (LHL:HCA) ______	13	0.30:1–1.35:1	0.91:1
Midcardinal fold (MF) (right valve):			
Maximum length along axis (MLMF) millimeters	14	74–158	118
Maximum width perpendicular to axis millimeters	10	30–65	47
Terminal elevation above floor of cardinal area ______ millimeters	9	11–32	21
Ratio—terminal elevation to maximum width ______	9	0.20:1–0.7:1	0.47:1
Resilifer (left valve):			
Maximum width (WR) ______ millimeters	3	38–58	45
Maximum depth ______ do	3	23–29	27
Ratio—depth to width ______	3	0.5:1–0.72:1	0.61:1
Denticles:			
Valves having denticles ______ percent	13	______	85
Height of denticulate lateral margins (HD) ______ millimeters	6	112–305	172.5
Total margin denticulate (in terms of total height) ______ percent	2	38.2–72.9	55
Number in 10 mm distance ______	9	6–12	9.3
Muscle scar:			
Maximum diameter (MDMS) millimeters	2	67.2–85	76
Height (HMS) ______ do	2	58–85	71
Length (LMS) (width) ______ do	2	31–57	44
Height, beak to dorsal margin of scar millimeters	2	98–186	142
Attachment scar:			
Height ______ do	3	70–170	126
Length (along surface of shell) ______ do	3	57–98	82

Beaks and umbos.—Beak blunt, indistinct, worn on most specimens. Umbo flat, poorly defined, obscured on left valve by attachment scar. Beak and umbo in left valves, suborthogyre and straight to opisthogyre and moderately curved, attaining one-quarter or rarely one-half of a volution. Prosogyre and opisthogyre beaks and umbos equally represented in right valves.

Posterior auricle.—Most specimens have slight dorsoposterior emargination. Well-developed posterior auricle present on 25 percent of specimens examined. Auricle semicircular in outline, moderately rounded, typically small; vertical diameter normally less, rarely more, than that of midcardinal fold or resilifer (pl. 5, fig. 1, typical of species). Auricle of right valve formed by dorsolateral emargination of posterior lateral cardinal trough (pl. 5, fig. 1); trough broader, shallower, and margin thicker at auricle than over rest of cardinal area. Auricle of left valve formed by expansion of posterior lateral cardinal fold and acute infolding of dorsoposterior margin (pl. 5, fig. 2); rarely, a shallow trough separates these two parts of auricle. Lateral margins of auricles on both valves typically notched or infolded, producing bend in plane of commissure (pl. 5, fig. 1). All gradations noted between faint emargination of dorsoposterior border and prominent auricles such as those illustrated. Average measurements of well-developed auricles on adult specimens: height, 89.5 mm; length, 48.1 mm; average ratio of auricle height to cardinal area height, 0.95:1.

Attachment area.—Attachment area or scar, medium to large (average dimensions: height, 125.7 mm; length, 81.7 mm), situated dorsoposteriorly on posterior flank of subcentral ridge (pl. 5, fig. 4), and subrounded to ovate in outline. Area slightly concave, obscuring normal ornamentation but not well defined or associated with secondary calcareous deposits. Animal apparently attached throughout life.

Ornamentation.—Ornamentation of both valves consists of coarse, crowded, irregular, overlapping concentric lamellae of several sizes (pl. 4, fig. 10; pl. 5, fig. 4). Lamellae flat, totally in contact with preceding surfaces, unevenly spaced, more crowded laterally than centrally. Beaks and umbos worn; early ornamentation unknown.

Cardinal area.—Cardinal area elongate, subtriangular in specimens that have short dorsal margin (pl. 5, fig. 2), grading to subrectangular (pl. 5, fig. 1); height greater than length. Hinge line moderately long, slightly curved (concave ventrally), not parallel to dorsal margin; angle between them acute (pl. 5, fig. 3), averaging 36°. Hinge line rarely perpendicular to axis of midcardinal fold or resilifer; angle between them acute (pl. 5, fig. 1). Apically, cardinal area curved posteriorly to varying degrees, depending on curvature of umbone and beak (pl. 5, fig. 2). Average measurements, cardinal area: height, 112.4 mm; length, 99 mm.

Cardinal area of right valve includes prominent midcardinal fold bounded by deep, narrow lateral cardinal troughs (pl. 4, fig. 9). Midcardinal fold elongate, narrow, subtriangular to rectangular; height two to three times width, sides typically straight and subparallel to gently diverging (pl. 4, fig. 9; pl. 5, fig. 1). Fold highly arched and has greatest convexity ventrally; top flattened to slightly convex; sides steeply inclined to vertical; ventral termination irregularly rounded; vertical to moderately inclined ventral flank. Lateral cardinal troughs narrow, deep, steep sided, elongate; bounded medially by flanks of midcardinal fold, laterally by raised, thickened marginal rim of valve. Anterior cardinal trough broader than posterior (pl. 4, fig. 9); individual trough width variable from place to place and from specimen to specimen. Anterior trough narrowest dorsally, broadest medially, becoming narrow again ventrally (pl. 4, fig. 9). Ventral one-half of posterior trough exceptionally narrow; dorsal one-half somewhat flared and shallower on individuals lacking well-defined auricle (pl. 4, fig. 9), abruptly flared and much shallower, with gently inclined lateral margin, on individuals having well-developed posterior auricle (pl. 5, fig. 1). Both troughs narrow abruptly and become shallow at dorsal extremity. Posterior trough somewhat deeper than anterior trough on majority of specimens, and continuous with slightly depressed area in dorsoposterior valve floor marking position of concealed muscle attachment area (pl. 4, fig. 9).

Cardinal area of left valve includes central resilifer and narrow lateral cardinal folds or platforms (pl. 5, fig. 2). Resilifer deep, elongate; height two to three times width; outline subtriangular, slightly flared ventrally (pl. 5, fig. 2). Depth of resilifer and convexity of lateral cardinal folds increase ventrally. Floor of resilifer broadly rounded; sides steep to vertical, overhanging at contact with lateral cardinal folds (pl. 5, fig. 2). Average measurements of resilifer: maximum width (ventral), 45 mm; terminal (ventral) depth, 27 mm; ratio of depth to width 0.61:1. Lateral cardinal folds narrow, equalling not more than one-half the width of the resilifer (pl. 5, figs. 2, 3); posterior fold broadest. Folds slightly to moderately and asymmetrically arched, rarely flattened; steepest flank of lateral cardinal folds adjacent to resilifer. Anterior fold bounded laterally by overlapping lamellar calcite plates which protrude from thick lateral edge of valve (pl. 5, fig. 3). Posterior lateral cardinal fold bounded ventrally at its outer edge by similar lamellae (pl. 5, fig. 3), but, in presence of well defined auricle, is expanded and merges dorsoposteriorly with infolded shell surface of auricle; rarely, posterior lateral cardinal fold is separated from infolded shell surface of auricle by a shallow sulcus (pl. 5, fig. 2). Both lateral cardinal folds terminating ventrally in a shelf overhanging floor of valve, forming shallow to moderately deep subcardinal cavities on either side of resilifer.

Surface markings on cardinal area of both valves consist of moderately prominent unequal widely and

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irregularly spaced incised horizontal lines and raised ridges, commonly associated with faint color banding. Horizontal structures transgressed at right angles by very fine crowded subequal raised vertical lines that are continuous across the fine horizontal ornament and discontinuous across major elements (pl. 5, fig. 3). Rest of shell interior smooth.

Denticles.—Denticles present on 85 percent of valves examined. On majority of specimens, denticles situated on dorsolateral margins of shell adjacent to, but outside of, commissure (pl. 4, fig. 5); rarely present on commissure or internally (pl. 5, fig. 3). Denticles faint to moderately prominent on lateral valve margins, medium sized, crowded (averaging 9.3 in 10 mm), narrow, elongate perpendicular to plane of commissure, more numerous on lateral edges of some calcite lamellae than on others, and commonly discontinuous across major sets of lamellae (pl. 4, fig. 5). Where present on internal surface of valve, denticles limited to a shallow trough just inside or on commissure (pl. 5, fig. 3), moderately prominent, subequally spaced, crowded, elongate perpendicular to margin of shell. Extent of denticulate lateral valve margin variable, typically about one-half total height of valve (averaging 55 percent of margin denticulate); denticles become fainter and more irregularly spaced ventrally.

Muscle scar.—Monomyarian. Terminal adult posterior adductor muscle scar not discernible on interior surface of any observed valve, probably posteroventral in position. Abandoned scar observed on two specimens in posterodorsal quadrant of valve, just below posterior one-half of resilifer and posterior lateral cardinal fold (pl. 5, fig. 2); scar originally obscured by covering of innermost calcite lamellae of subnacreous layer (pl. 5, fig. 2: peeled off for observation). Open lamellar structure underlies muscle scar in many shells, but somewhat caved on a few specimens (pl. 4, fig. 9). Scar, or insertion area, large, subovate, flat to very slightly concave; surface of area covered with fine to medium, thin, flat, overlapping calcite lamellae; lamellae irregularly spaced, crowded to sparse; their traces parallel those of exterior growth lines and lamellae. Attachment scars of Quenstedt's muscle just ventral from resilium or midcardinal fold, slightly posterior to midline. Attachment to small elevated knob in left valve, to small axially elongate trough in right valve.

Shell structure.—Nacreous layer and periostracum not preserved. Hypostracum confined to area of muscle attachment, not well preserved, and not studied in detail. Thick shell composed predominantly of subnacreous layer consisting of numerous subparallel horizontal sheets of calcite, tightly packed throughout most of shell; open lamellar structure common in area of muscle attachment. Subnacreous layer composed of two types of calcite layers, generally alternating; thick lamellae of coarsely crystalline calcite (average thickness 0.8 mm) separated by thin chalky layers, possibly remnants of former nacreous layers.

REMARKS

This remarkable species is the largest known ostreid from Mesozoic rocks of North America, as well as one of the earliest known modern types of *Crassostrea.* It is further unique in the massive development of the cardinal structures and, particularly, in the nature and position of the muscle scar.

It is difficult to interpret the absence of a muscle scar on large valves. The area of muscle insertion is visible on only 2 of 16 specimens. In both specimens, the area is large and shallow and is situated dorsally just below the posterior cardinal area, and was at one time covered by a few thin plates of lamellar calcite (pl. 5, fig. 2). On some specimens, the inner surface of the valve is caved over the covered scar (pl. 4, fig 9), and this caving indicates an open lamellar structure in the underlying shell layers. This structure in the area of muscle insertion is typical of many Ostreidae.

The observed muscle scars probably do not represent the last formed attachment area on the adult shell, but rather are remant scars on the muscle track. The normal position of the terminal adult attachment area in *Crassostrea,* including *soleniscus,* is in the posteroventral quadrant of the shell, near the posterior margin. On large, nearly complete specimens of *C. cusseta,* there is no discernible insertion area anywhere on the inner valve surface (pl. 4, fig. 9, pl. 5, fig. 3); the absence of a discernible insertion area denotes either that the terminal scar left no impression or that it is covered by the innermost calcite lamellae of the valve interior. On all specimens on which the position of the scar could be determined, either by peeling away shell layers or by noting a caved zone in the floor of the valve, the position of the scar was dorsoposterior; this is atypical of its final position in *Crassostrea.*

The lack of any discernible muscle scar on the interior surface of large *Crassostrea cusseta* valves can be explained in two ways. Either large old shells lacked a functional posterior adductor muscle, perhaps owing to atrophy, or the stress on the posterior adductor was so limited while it was performing its function that the muscle did not require a normal type of attachment area and inserted without leaving a trace on the smooth interior valve surface. An atrophied muscle seems a more practical explanation. Even the largest individuals of other giant oysters we have examined from Cretaceous, Tertiary, and Recent deposits have a well-defined insertion area, generally marked by prominent lines, grooves, or overlapping lamellae. Although the insertion area decreases in prominence with age on many species, we can find no examples of it becoming so faint as to be indistinguishable on the valve floor. On the largest and most complete valves of *C. cusseta*, only the ventral tip of the valve is missing, and the floor of the valve is completely exposed. Even the faintest trace of an insertion area should be evident, were it present. There is little possibility that the insertion area was limited to the most ventral part of the valve; no known oysters have an insertion area so situated.

We therefore assume that the absence of a muscle scar on the interior surface of large adult valves indicates atrophy of the adductor muscle and subsequent covering of the last formed scar by additional layers of calcite during late maturity and old age. Unfortunately, small adult specimens of this species are not yet known, and we cannot ascertain precisely at what point the scar disappeared. The thin covering over the insertion area on the two large valves in which the muscle scar was observed indicate that it was obscured late in the developmental history of the oyster. It is probable that this is a gerontic feature of the species. Unless the mantle margins became modified at this time, it is doubtful whether the oyster lived long after atrophy of the adductor muscle. Inactivation of the muscle would probably produce continual gaping of the shell, considerable inflow of clastic detritus, especially in turbid waters, and eventual clogging of the gills.

Crassostrea cusseta n. sp. belongs to a generalized and conservative lineage of oysters characterized by relatively smooth elongate massive shells, strong development of the cardinal structures, large shallow posteroventrally situated muscle scars, and deeply cupped left valve. The lineage had its beginnings in the early forms of *C. soleniscus* (Meek) and is probably represented today by *C. virginica* (Gmelin) on the Atlantic Coast. *C. cusseta* is the culmination of the lineage in Cretaceous rocks of North America. Another crassostreid stock, represented by *C. subtrigonalis* (Evans and Shumard) and *C. glabra* (Meek and Hayden), occurs in even younger Cretaceous rocks of the northern Western Interior (Upper Santonian and Maestrichtian). Both crassostreid lines transgress the Cretaceous-Tertiary boundary with little basic change and have modern counterparts.

The known representatives of the *C. soleniscus* lineage are characterized in their evolution by a gradual increase in size from their origin to the development of *C. gigantissima* of the Eocene. Younger crassostreids which apparently belong to the same lineage are smaller and more variable and have somewhat less massive shells. A gradual loss of denticles in adult shells of successively younger species is another notable trend. Denticles are well developed on young and adult valves of *C. soleniscus* and cover much of the dorsolateral and lateral margins. In *C. cusseta* the denticles are more restricted on the dorsolateral margins and migrate to the lateral edge of the valves on most large adults. The young of *C. gigantissima* are sparsely denticulate, whereas the adults lack denticles. Modern massive crassostreids, like *C. virginica*, rarely have denticles on the dorsolateral margins of the immature valve and completely lack them on the adult valve.

On the basis of shell characters which modern neontologists consider significant to ostreid classification, *C. cusseta* and other members of the lineage must be placed in *Crassostrea*. They possess the elongate large, massive shell typical of the genus; a deeply cupped left valve between the muscle scar and the cardinal area; a posteroventrally situated muscle scar (this is the assumed position of the terminal scar in *C. cusseta*); subcardinal cavities; a thick elongated cardinal area; and a shell composed predominantly of superimposed nonvesicular, nonchalky layers of lamellar calcite (subnacreous layer).

Comparison With Other Species

Crassostrea cusseta most closely resembles the youngest representatives of *C. soleniscus* Meek, an older species from which it was probably derived. The two are very similar in general shape, convexity, and development of the cardinal structures.

Crassostrea cusseta can be readily distinguished from *C. soleniscus*. It attains a larger size, has a relatively broader shell, and is much less variable in form than the older species. The average form and the range of variation of each species is distinct. *C. soleniscus* is characteristically very narrow, elongate, and straight, ranging to somewhat arcuate or broad and rounded, and has an exogyroid beak (Stephenson, 1952, pl. 16, figs. 1–4; pl. 17, figs. 7–10); *C. cusseta* is predominantly strongly curved posteriorly, or is subcrescentic, and does not attain the rounded form. Its beaks and umbos are blunt, broad, and flat and do not develop exogyroid coiling. *C. soleniscus* commonly has a narrow, attenuated, or sharply rounded dorsal margin. A small posterior auricle is rarely developed in *C. soleniscus* and, where present, is usually confined to rounded exogyroid variants. The auricle is formed in this species by outward and upward flaring of the posterior lateral cardinal margin. *C. cusseta* commonly develops a larger and more prominent posterior auricle. On the left valve, the auricle is formed by acute inbending of the lateral shell margin; on the right valve, by lateral expansion of the posterior lateral cardinal trough and infolding of the lateral rim of the trough. Concentric lamellae are more numerous and more crowded on *C. soleniscus* than on *C. cusseta* and are transgressed on the umbos of small to moderate size individuals by fine costae. Costae have not been observed on *C. cusseta*.

Comparison of shell interiors reveals other distinctions between the two species. The most conspicuous difference is in the nature and position of the posterior adductor muscle scar—central to posterocentral and not covered in *C. soleniscus*, dorsoposterior and covered with lamellae on large valves of *C. cusseta*. The right and left cardinal areas of *C. soleniscus* are shorter and more curved than those of *C. cusseta*, and the mid-cardinal fold is relatively larger, diverging at a greater angle, and is less convex. Lateral cardinal troughs are very shallow or are commonly not developed in *C. soleniscus*; there is no well-defined lateral brim bordering the troughs or the central cavity of the shell. The right valves of *C. soleniscus* are, consequently, much shallower than those of *C. cusseta*, and, in some specimens, have a flat or convex interior surface.

The left valve of *C. soleniscus* has a larger, broader, shallower, and more rapidly expanding resilifer than does the equivalent valve of *C. cusseta*. In addition, the resilifer of *C. soleniscus* is not well delineated from the lateral cardinal folds, and the folds themselves are narrower and flatter than those of *C. cusseta*. The folds slope into, rather than away from, the resilifer. The lateral edges of overlapping surface lamellae do not form a marginal brim for the cardinal area in *C. soleniscus*, and there is no sulcus or groove separating the posterior lateral cardinal fold from the outer part of the auricle. Subcardinal cavities are rarely developed in *C. soleniscus*.

Denticles occur in both species, but they are smaller, more crowded, more commonly situated on the valve interiors or commissure, and less extensive on the dorsolateral margins of *C. soleniscus*.

Large massive oysters apparently related to *C. cusseta* also occur in the European Cretaceous. One of the most closely comparable species is *Crassostrea*? *pantagruelis* (Coquand) (1869, pl. 68, figs. 1, 2), which has a similar massive elongate shell, a dorsally situated muscle scar, and even greater development of the cardinal structures than has *C. cusseta*. Numerous details of the cardinal area, the exposed muscle scar of large adult shells, and the more curved, attenuated beak and umbo of the European species easily distinguish the two forms.

Crassostrea gigantissima (Finch) can be distinguished from *C. cusseta* by its well-defined, more ventrally situated muscle scar, less massive cardinal area, lack of denticles in the adult valve, lack or poor development of auricles, and fine radial sculpture on the dorsal part of many shells. Lateral cardinal troughs are not well defined in *C. gigantissima*.

Occurrence

Localities for Crassostrea cusseta:

USGS Mesozoic loc. 25563: Upper Cretaceous, upper part of the Blufftown Formation, Chattahoochee River, bluff at Florence, Stewart County, Ga. First concretionary layer and below. Collected by L. W. Stephenson and N. F. Sohl, Mar. 17, 1955.

USGS Mesozoic loc. 5902: Upper Cretaceous, Cusseta Sand, Chattahoochee River, opposite Woolridge landing, about 15 miles above Eufaula, Ala., on the Georgia side of the river. Collected by L. W. Stephenson, 1909.

USGS Mesozoic loc. 26027: Upper Cretaceous, Cusseta Sand (S–351), Chattahoochee River, west bank, below old Woolridge landing, 13.6 miles above Eufaula, Ala., 1 mile below the mouth of Roods Creek, sec. 18, T. 12 N., R. 30 E., Barbour County, Ala. Collected by N. F. Sohl and H. I. Saunders, Nov. 7, 1955.

USGS Mesozoic loc. 28541: Upper Cretaceous, Cusseta Sand (S–958), near old Woolridge landing, bluffs on west side of Chattahoochee River about 13.6–13.7 miles above Eufaula landing in Barbour County, Ala. Collected by N. F. Sohl, R. L. Rieke, and H. R. Bergquist, Oct. 26, 1961.

USGS Mesozoic loc. 5396: Upper Cretaceous, Cusseta Sand, Chattahoochee River, Roanoke Bluff, just below Woolridge landing, west bank, about 15 miles above Eufaula, Ala. Collected by L. W. Stephenson, July 22, 1907.

USGS Mesozoic loc. 26029: Upper Cretaceous, Cusseta Sand (S–327), Old Seale–Eufaula Road bridge over the Middle Fork of Cowickee Creek, 8.05 miles north of intersection of U.S. 241 and first bend of the creek upstream from the bridge, sec. 18, T. 12 N., R. 29 E., Barbour County, Ala. Collected by N. F. Sohl and H. I. Saunders, Oct. 30, 1955.

Crassostrea cusseta is most commonly found in Upper Cretaceous rocks of the Chattahoochee River region in Georgia and Alabama. With the exception of one fragmentary specimen (USGS Mesozoic loc. 25563) from the upper part of the Blufftown Formation, the species is restricted to the basal beds of the Cusseta Sand (fig. 1). *C. cusseta* occurs throughout 60 feet of sand and silt in this sequence.

The Blufftown specimen (USGS Mesozoic loc. 25563) came from beds in the lowermost part of unit 2 of Veatch and Stephenson's Florence Bluff section (1911, p. 155–156). Stephenson considered these beds as the lowest part of an expanded Ripley Formation that included the Cusseta Sand Member at its base. Subsequently this unit was placed first at the base of the Cusseta Sand (Cooke, 1943, p. 25) and then, later, in the upper part of the Blufftown Formation (Eargle, 1955, p. 36, 47). Disagreement as to the placement of this unit was the result of miscorrelation by Stephenson and Veatch of unit 2 with the fossiliferous units near Woolridge landing, several miles downstream on the Chattahoochee River.

Crassostrea cusseta is most abundant near Woolridge landing in Barbour County, Ala. (USGS 5902, 26027, 28451). Here it is concentrated in a 1-foot-thick zone in the middle of a 4-foot poorly sorted gray clayey, silty sand unit containing abundant worn shells and bone fragments. This unit is the basal bed of the Cusseta Sand and here overlies a clean unfossiliferous buff-colored crossbedded medium-grained sand. The contact of the two beds is undulatory, the undulations having a vertical magnitude of about 1 foot in a lateral distance of 15 feet. Specimens collected by Stephenson at Roanoke Bluff (USGS 5396) are from the same zone.

Crassostrea cusseta also occurs in the basal bed of the Cusseta Sand exposed on the Middle Fork of Cowickee Creek (USGS 26029), a tributary of the Chattahoochee River, Barbour County, Ala. As noted by Monroe (1941, p. 92), this bed contains worn shells, bones, and shark teeth.

The species is questionably represented in the Black Creek Formation of North Carolina by a large incomplete specimen figured by Stephenson (1923, pl. 37). Apparently Stephenson (1923, p. 141, pl. 36) regarded this and several other incomplete figured specimens as *C. cusseta:*

> A large species of oyster which I regard as identical with an undescribed species from the Ripley Formation (upper part of the *Exogyra ponderosa* zone) on [the] Chattahoochee River (Ga.-Ala.), at Woolridge landing (5396, 5902), and at Florence (5395), has been found at two localities in North Carolina.

The large specimen illustrated by Stephenson (1923, pl. 37) is comparable to *C. cusseta* in size, shell thickness, and inferred valve curvature but is too incomplete to allow definite identification. The smaller specimens illustrated by Stephenson (1923, pl. 36, figs. 1–4) from the Snow Hill Marl Member of the Black Creek Formation differ from *C. cusseta* by having strongly curved and more attenuated beaks and umbos and by having narrower cardinal areas; the two forms also differ in the development of various cardinal structures and in the position and exposed nature of the muscle attachment area. In these respects, the Snow Hill specimens are more nearly like *C. soleniscus* Meek, a species ancestral to *C. cusseta.*

Types

Holotype, a large, nearly complete left valve (pl. 5, figs. 3, 4) characteristic of the species, from the Cusseta Sand along the Chattahoochee River, below old Woolridge landing, Barbour County, Ala. (USGS Mesozoic loc. 26027); USNM 132057. Illustrated paratypes from the Cusseta Sand, USNM 132058–132061 inclusive. Measured, unillustrated paratypes from the Cusseta Sand, USNM 132062a, b; 132063 a–c; 132064 a–d. Unmeasured, unfigured paratypes used in description of species, from the Cusseta Sand, USNM 132065a, b; 132066 a–c: from the Blufftown Formation, USNM 132067.

Genus ARCTOSTREA Pervinquiere: emended

1910a. Pervinquière, Léon, Observations sur la nomenclature des Ostracés: Soc. géol. France Bull., ser. 4, v. 10, p. 645, 646.

1910b. Pervinquière, Léon, *Ostrea carinata:* Paleontologia Universalis, ser. 3, p. 197.

Type species.—Ostrea carinata Lamarck, by original designation.

Diagnosis

Shell normally small to moderate, elongate, narrow, falciform, highly inequilateral, strongly recurved medially or ventrally, subequivalved; left valve slightly larger and more convex than right valve; valves highly convex and have diamond to quadrate cross section. Small anterior and posterior auricles commonly developed dorsolaterally. Narrow crest (midline) of valves flat to narrowly rounded; lateral flanks steep, intersecting plane of commissure at 45°–90°. Adult ornament equally developed in both valves. Ornament along crest consists either of a sinuous central plication or of a complex of bifurcating sinuous plicae and costae arising from the midline, from which originate subequally developed, evenly spaced, moderate-size plicae that extend from the flanks to margin. Commissure trace zig-zag to sharply undulating; margin deeply incised at intersection with each plication. Beak small, opisthogyre, moderately curved. Cardinal area consists of well-defined triangular central resilifer and subequally to unequally developed lateral cardinal plates. Lateral margins have simple ovoid to elongate denticles. Muscle scar dorsoposterior, comma shaped, commonly incised, conspicuous, bordered by prominent lip. Shell lamellate, having individual lamellae composed of reticulate pattern of prominent vertical and very thin horizontal calcite plates.

Remarks

Arctostrea, which was proposed as a subgenus and which has since been used as a genus, subgenus, or section of *Ostrea* and *Lopha* (=*Alectryonia*), appears to deserve generic ranking on the basis of its shell form, cross section, and unique ornamentation pattern, and on the basis of the development and the dorsal position of its posterior adductor muscle scar. No other superspecific taxa approach this genus in all these respects, and the genus is not represented among modern oysters. *Rastellum* Schröter, in the sense of Faujas-Saint-Fond

(1799, pl. 28, fig. 7), is most closely related to *Arctostrea.* It differs by having a relatively flat posterior flank, a rounded crest, and a greatly expanded posterior auricle; it also differs in details of the ornamentation pattern. Further, the validity of *Rastellum* is in doubt. The problem is currently being investigated by Dr. H. B. Stenzel.

We are restricting the use of *Arctostrea* in this study to forms resembling the type species *Arctostrea carinata* (Lamarck). We do not include within the genus oysters like *Rastellum* of Faujas-Saint-Fond or palmate forms such as *Ostrea travisana* Stephenson and *Ostrea subovata* Shumard. These species have marginal variants which externally attain the general ornamentation pattern and narrow curved form of *Arctostrea*, but they lack the wide thick shells, with their diamond-shaped or subquadrate cross section, so typical of *Arctostrea;* further, the detail of the ornamentation and internal characteristics differ considerably. Rare varieties of *Arctostrea* attain a palmate form externally, owing to flaring of the posterior margin (pl. 4, fig. 3); but even these forms retain the narrow, closely spaced, typically curved internal shell margins of *Arctostrea* (pl. 4, fig. 4). Similarly shaped forms, such as *O. travisana*, are equally as broad internally as externally. The palmate form in *Arctostrea* is probably produced by crushing and overturning of the normally vertical posterior margin or in crowded growth situations that limit convex growth of the shell. *Arctostrea*, and forms closely related to it (*Rastellum*, the *O. travisana* lineage), appear to have had a common ancestry in the Jurassic. During the Cretaceous the two branches evolved concurrently and separately; rarely they produced somewhat similar forms that reflected their common ancestry; they never merged, however, through an intermediate morphologic series of forms.

Arctostrea aguilerae (Böse)

Plate 1, figures 1, 2; plate 2, figures 1–4; plate 3, figures 1–7; plate 4, figures 1–4, 6–8

1906. *Ostrea* (*Alectryonia*) *Aguilerae* Böse, Mexico Inst. Geol. Bol. 24, p. 47; pl. 2, fig. 2; pl. 4, fig. 5; pl. 6, figs. 1, 2.

1925. *Arctostrea atkinsi* Raymond, Boston Soc. Nat. History Occasional papers, v. 5, p. 183–185, pl. 7, figs. 1, 2.

Material

Thirty complete and fragmentary specimens from 11 localities in Mexico, Cuba, Alabama, Mississippi, and Texas (Upper Cretaceous: Upper Campanian, Lower Maestrichtian). Three specimens consist of articulated complete valves. The remainder are about equally divided between well-preserved to fragmentary right and left valves.

General Form

Summary of measurements presented in table 2. Shell exceptionally large and massive, somewhat inequivalved; left (lower, attached) valve commonly thicker and more massive than right (upper, free) valve; valves close fitting, interlocking along strongly plicate margin; valves inequilateral, moderately to very strongly curved posteriorly; dorsal inclination typically opisthocline, average angle 52°. Length somewhat greater than height: average ratio 1.08:1; average measurements of adult specimens: height, 161 mm; length, 151 mm; thickness of left valve, 51 mm; thickness of right valve, 47 mm.

Table 2.—*Summary of measurements for* Arctostrea aguilerae *(Böse)*

Character	Number of specimens	Range	Average
Valve length, actual, along midline (LM) millimeters	10	196–352	250
Valve height (H) do	10	116–186	161
Ratio—H:LM do	10	0.57–0.90:1	0.66:1
Length (L) do	10	119–200	151
Ratio—L:H	10	0.87–1.65:1	1.08:1
Maximum thickness:			
Left valve millimeters	6	30–71	51
Right valve do	6	33–76	47
Maximum width:			
Left valve do	5	71-115	87
Right valve do	5	66–87	77
Number of ribs, on anterior margin	10	23–49	30.2
On posterior margin	10	16–31	21.8
Number of millimeters per rib:			
Inner curve millimeters	8	4.4-8.3	6.5
Outer curve do	----------	5.9–9.7	8.0
Posterior auricle:			
Height (HA) do	8	26–46	33
Length (LA) do	5	12–34	22
Angle of inclination (Ti):			
Total degrees	9	25–92	52°
Dorsal half of shell (Di) do	12	94–142	118°
Length of hinge line (LHL) millimeters	12	34–63	52
Height of cardinal area (HCA) do	11	20–58	39
Ratio—length of hinge line to height of cardinal area (LHL:HCA)	10	0.93–2.0:1	1.43:1
Width of resilifer (WR):			
Right valve millimeters	6	12.8–28.3	21
Left valve do	6	13.2–29.6	19
Muscle scar:			
Height (HMS) do	7	25–46	36
Length (LMS) do	7	17–22	20
Maximum diameter (MDMS) do	11	28–47	33

Valves elongate, generally curved toward posterior, crescentic to fishhook shaped in outline. Point of maximum curvature usually ½–⅔ midline length from dorsal margin. Dorsal margin straight to subcentrally angulate, not parallel to hinge line; dorsolateral margins narrowly rounded; dorsoanterior margin straight to somewhat rounded; dorsoposterior margin roundly to irregularly convex at auricle, concavely recessed below auricle. Lateral margins moderately to strongly curved medially, subparallel to decidedly convergent toward point of greatest curvature (anterior convex; posterior straight to somewhat concave), usually well curved and subparallel ventrally; ventral margin narrowly rounded to subangulate.

Right and left valves highly convex; greatest convexity near point of maximum curvature, sloping to plane of commissure more gently dorsally than ventrally. Crest broadly arched; anterior slope usually vertical to steeply inclined outward; posterior slope overhanging to steeply inclined outward. Well-defined umbonal ridge bisects umbone, continues ventrally posterior to midline as axis of origin for primary plicae.

Description

Beaks and umbo.—Beak worn or obscured on all specimens. Umbo, if not obscured by attachment scar, bears median, curved, round-topped ridge; umbo opisthogyre, moderately curved for approximately one-half whorl.

Posterior auricle.—Posterior auricle well formed on majority of specimens. Auricle irregularly semicircular, small to proportionally large. Auricle of right valve formed by expansion of posterior cardinal trough margin, in some specimens in conjunction with moderate upfolding of dorsolateral shell margin; auricle bounded laterally by shell margin and medially by lateral cardinal trough. Auricle of left valve formed by lateral expansion of posterior marginal cardinal trough and corresponding moderate to strong infolding of dorsolateral shell margin. Variation in size of auricle great. Average measurements of auricles on adult specimens: height, 33 mm; length, 22 mm.

Attachment area.—Attachment area small to medium size (maximum size noted: height, 24 mm; length, 72.4 mm), situated dorsoposteriorly, in some specimens extending onto auricle. Outline irregularly oviform; area not normally well defined.

Ornamentation.—Ornamentation of both valves consists of numerous round-crested narrow chevron-shaped plicae that are irregularly accentuated to spinose projections or flutings at their intersection with lamellar growth rugae. Plicae arise by bifurcation and intercalation from a discontinuous subcentral plica that originates as an umbonal ridge, at midlength and toward the ventral margin, medial plica commonly forms high point of broadly arched upper valve surface and is close to steep posterior slope. Plicae finest dorsally, increasing in prominence ventrally over arched upper surface. Plicae of dorsolateral flank closely spaced and low, terminating at commissure in narrow, shallow alternating sulci and plicae. As shell thickens toward point of maximum valve curvature, plicae become more prominant, and valve flanks steepen, becoming vertical, continuation of plicae on vertical or highly inclined flanks forms low undulations, exposing chevron-shaped lamellar calcite plates; plicae gently arcuate ventrally, directed over flanks to commissure; Chevron-shaped terminations of imbricate plicae tightly interlock with corresponding V-shaped sulci of interplical area of opposite valve. Concentric sculpture consists of growth lines and overlapping lamellae. Average number of plicae: anterior margin, 30.2; posterior margin, 21.8. Average width of plicae at shell margin: anterior margin, 6.5; posterior margin, 8.0.

Internal impression of sculpture restricted to large crenulations on narrow raised valve margin. Plications narrowest, lowest, and most closely spaced on dorsolateral margin and at posterior margin at point of greatest valve curvature.

Cardinal area.—Cardinal area longer than high (average ratio 1.43 : 1), subtriangular to subrectangular. Length of hinge line variable, from about ⅓ to ⅙ midline valve length. Hinge line not parallel to dorsal margin; angle between them acute, from 20° to 45°; angle between hinge line and axis of resilifer acute, from 35° to 68°. Apically, resilifer curves posteriorly, curvature increasing dorsally. Average measurements, cardinal area: height, 39 mm; length, 52 mm.

Cardinal area of right valve comprises posteriorly curving triangular central resilifer, higher than wide, bordered by low, raised, flat-topped, equally to subequally broad, lateral cardinal platforms. Resilifer shallow; base very broadly rounded; sides steepest dorsally, more gently sloping ventrally. Average measurements of resilifer: maximum width, 21 mm; depth seldom exceeds 2 mm. Lateral cardinal folds quadrate in cross section and almost as wide to wider than resilifer; posterior fold usually broadest. Folds normally flat topped, less commonly gently arched; steepest margin borders resilifer. Anterior margin of lateral cardinal fold bounded by upturned lamellar plates of the lateral valve margin. Posterior lateral cardinal fold separated from auricle dorsoposteriorly by narrow, shallow to moderately deep incised sulcus. Ventral terminations of cardinal folds merge with valve floor or are raised moderately above it; subcardinal cavities poorly developed.

Cardinal area of left valve consists of posteriorly curved triangular resilifer, higher than wide, bordered by broad lateral cardinal folds or platforms. Resilifer shallow and broadly rounded to moderately deep and narrowly rounded. Sides of resilifer steepest dorsally, overhung slightly (pl. 1, fig. 2), gently sloping at ventral margin. Resilifer narrow dorsally, regularly expanding and becoming shallower ventrally. Average measurements of resilifer: width, 19 mm; depth, less than 5 mm. Lateral cardinal folds quadrate in cross section, flat topped to broadly arched, narrower than resilifer;

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taper dorsally. Medial flank of folds steepest anteriorly where sides may overhang resilifer. Lateral margin of anterior fold bounded by a narrow, deep to shallow, marginal cardinal trough (pl. 4, fig. 8); trough anteriorly bounded by upturned lamellae of shell margin. Posterior lateral cardinal fold broader than anterior fold on majority of specimens and bounded posteriorly by a narrow to moderately narrow steep sided marginal cardinal trough separating auricle from lateral cardinal fold (pl. 1, fig. 2; pl. 3, fig. 6; pl. 4, fig. 8). Lateral cardinal folds terminate ventrally in a shelf overhanging floor of valve in some specimens; form shallow to rather deep (pl. 3, fig. 6) subcardinal cavities.

Surface markings on cardinal area consist of unequal irregularly but closely spaced fine incised horizontal lines and coarser raised lamellar ridges; ridges coarsen on resilifer. Vertical cardinal sculpture consists of fine discontinuous microscopic lines. Remainder of shell interior smooth except for muscle attachment area.

Denticles.—Most mature thick-shelled individuals lack denticles. Denticles present on only one adult left valve (pl. 2, fig. 3). Denticles raised, subulate in outline, elongate normal to the valve margin; extend along posterior margin from dorsal part of auricle to a point about midheight of muscle scar; denticles longest and most prominent over auricular area, diminish in prominence ventrally; average number about 15 in 10 mm on auricular margin, 20 in 10 mm in latitude of muscle scar.

Muscle scar.—Monomyarian: posterior adductor scar situated dorsoposteriorly, almost entirely behind midline, near posterior margin. Scar large, lunulate; expands ventrally. Posterior, ventral, and anteroventral margins of scar raised above valve floor; form sharp-edged ridge that on some specimens overhangs valve floor toward posterior valve margin and develops a trough between valve margin and muscle scar. Dorsoanterior margin of muscle scar broken on most specimens, broadly arcuate, continuous with valve floor; overhangs deep oblique incised muscle insertion area. Scar floor longitudinally ridged by edges of lamellar shell layers; ridges crossed obliquely or at right angles by raised overriding threads and cords having variable strength and spacing; cords strongest ventrally (pl. 4, fig. 7). Average measurements, muscle scar: height, 36 mm; length, 20 mm; maximum diameter, 33 mm.

Shell structure.—Periostracum not preserved; hypostracum not observed. Main body of shell composed of thick calcite plates separated by nacreous(?) lamellae; plates rather uniform in thickness at medial part of shell but alternately taper to a thin edge marginally (pl. 4, fig. 6). On weathered surface (pl. 4, fig. 2), plates form a cross-hatched pattern suggestive of a vertical prismatic structure crosscut by secondary lamellae.

Remarks

Like most ostreids, *Arctostrea aguilerae* (Böse) exhibits a wide variation in shape and outline. Insofar as is known, this variability is not due to crowding. The studied available specimens evidently lived as discrete individuals. Variation is most noticeable in the amount of valve curvature. The narrowest and least curved variety is well typified by Raymond's (1925, pl. 7) holotype of the synonymous Cuban species *Arctostrea atkinsi* and by another specimen from Cuba here figured on plate 3, figure 5. Böse's (1906, pl. 6, figs. 1, 2) syntype of *Arctostrea aguilerae* displays moderate curvature. The greatest curvature is in gulf coast representatives of the species (pl. 2, fig. 6; pl. 1, figs. 1, 2), in which the ventral extremity is so strongly recurved that it almost extends to the plane of the hinge line.

Transverse cross sections through the center of the shell of *Arctostrea aguilerae* are quadrate (pl. 4, fig. 6) and have vertical sides and a broadly arched upper surface. This growth form normally produces a slender ventral valve outline. However, several specimens have a flared ventral flank caused by skewed growth along a posteriorly inclined midline plane (pl. 4, fig. 3; pl. 3, fig. 3), thus producing an overhung anterior slope and gentle posterior flank and giving a palmate appearance to the valve exterior. On such distorted shells, however, the interior margins of the commissure are subparallel and closely spaced, and they do not flare (pl. 4, fig. 4).

General surface sculpture is fairly constant, although some variation from the mean presented in our description was noted. Spines are present on all specimens but are erratically developed, ranging from low nodes on some specimens to elongate spinose projections extending 8 or 9 mm above the surface of the plicae on others. The surface of most specimens is partly worn, and the spines are not well preserved. The syntype figured by Böse (1906, pl. 6, fig. 2) has well developed spines, as do the specimens here figured on plate 1, figure 1; plate 2, figure 2. The plicae pattern varies primarily as a function of the shell shape. Rare shells that have a palmate posterior flank also have elongate continuous extensively bifurcating plicae. A similar pattern develops on thin-shelled specimens (Böse, 1906, pl. 2, fig. 2; pl. 2, fig. 2 herein).

Comparisons

Ostrea carinata Lamarck from the Cenomanian of France, the type species of *Arctostrea*, is smaller than *A. aguilerae* (Böse), rarely exceeding its holotype

(Pervinquière, 1910b, p. 197, figs. a, b) in size (height about 73 mm). Like *Arctostrea aguilerae*, some specimens of *A. carinata* have a quadrate whorl cross section, and the plicae arise from a medial ridge by bifurcation. More commonly, the cross section is subquadrate, the upper surface narrowly subcarinate and the lateral slopes subparallel. The plicae are fairly uniform over the entire length of the shell and are raised, sharp crested, and continuous along the anterior slope, whereas they are lamellarly truncate in *A. aguilerae.* The amplitude of the commissure plications is proportionally greater on *A. carinata* than on *A. aguilerae*, but the rib spacing is proportionately narrower. Ribs on the type species range between 3.5 and 4.8 mm in width on the anterior margin, whereas the same measurement ranges between 5.9 and 8.7 (average 8.0 mm per rib) on *A. aguilerae.* Finally, the muscle scar of *A. carinata* is relatively closer to the hinge line than is that of *A. aguilerae. Arctostrea columbrina,* as figured by Pervinquière (1910b, p. 198), closely resembles *A. carinata* and differs from *A. aguilerae* in essentially the same respects.

Other common Upper Cretaceous European *Arctostrea* such as *A. pectinata* (Lamarck) (in part, of Woods, 1913, p. 342) are all smaller and less massive than *A. aguilerae.* Some specimens of *A. pectinata* from the Santonian approach *A. aguilerae* in size but in cross section have a narrower upper valve surface with more inclined lateral flanks (Coquand, 1869, pl. 29, fig. 7). The surface ornamentation of *A. pectinata* consists of widely spaced sharp-crested plicae extending without lateral truncation to the commissure. *Arctostrea serrata* (Defrance) (Coquand, 1869, pl. 30, fig. 5) and *A. zeilleri* (Bayle) (Bayle, 1878, pl. 146, figs. 1, 2) have a carinate upper valve surface, subovate whorl cross section, and plicae which are not truncated on the flanks of the valves.

Occurrence

Localities in Mexico:

USGS Mesozoic loc. 28181 (7039): Northeast edge of town of Cárdenas, San Luis Potosí, Mexico. *Orbitoides* zone of Wade's Cañon Cañada section.

USGS Mesozoic loc. 38323 (FE 251): Río Monte Bello, San Luis Potosí, Mexico. Collected by Ing. Felipe Mendes Munguia, May 31, 1961.

Böse (1906, p. 49) cited the type locality of *Arctostrea aguilarae* as "Cuesta de Nahual (Hacienda de la Palma, Distrito de Hildalgo, San Luis Potosí)," which lies about 20 km south of the village of Canoas on the Tampico-Cárdenas railroad. Böse also noted that the species occurs in the vicinity of Canoas. The type specimens come from what he called the lower beds, which contain *Exogyra costata*, at the "*Gryphaea vesicularis* horizon" (= Cárdenas Formation, Lower Senonian). Böse was in error in assigning this zone to the Lower Senonian, as *Exogyra costata* is restricted to the Late Campanian and Early Maestrichtian.

Imlay (1944a, p. 1084, 1106) correlated the Cárdenas Formation with the Maestrichtian and, in the same paper (p. 1138), reproduced a 5570-foot stratigraphic section of the Cárdenas Formation as measured by Bruce Wade in Cañon Cañada, about 3.22 km southeast of Cárdenas. The specimens of *Arctostrea* from the Cárdenas area studied for the present paper can be fitted into Wade's section, and all come from above his "Coon Creek horizon" of unit 9.

Collection 28181 comes from rocks equivalent to the *Orbitoides* zone of Wade's section, a unit about 650 feet thick (units 11–28 of Imlay's 1944a reproduction). This zone occurs above beds that contain a lower *Exogyra costata* zone fauna and appears to be a correlative of the Nacatoch Sand of Texas or of the Ripley Formation of the east Gulf Coastal Plain.

Fossils associated with *A. aguilerae* from USGS Mesozoic loc. 38323, such as *Veniella conradi* (Morton) and *Idonearca* cf. *I. deatsvillensis* Stephenson, are also typical of the *Exogyra costata* zone. The exact level, in terms of Wade's section, from which the type specimens were collected is not known. The associated fossils, however, tend to indicate a stratigraphic position somewhat higher (units 32–56) than that at the preceding two localities but still within the *E. costata* zone.

As here interpreted, in the type area in San Luis Potosí, *Arctostrea aguilerae* ranges through beds that are no older than Latest Campanian and are as young as Early Maestrichtian.

Localities in Cuba (all collections by R. H. Palmer, 1929–33):

USGS Mesozoic loc. 27127 (Palmer loc. 51): Finca de Guanajita, 9 km west of Santa Clara and crossing 3 km south of Carratera, Santa Clara Province, Cuba.

USGS Mesozoic loc. 27126 (Palmer loc. 51a): La Lomita near Guanajita, Santa Clara Province, Cuba.

USGS Mesozoic loc. 27173 (Palmer loc. 907): Batey Jesús María and continuation of same hill, 2 km to west and 1.29 km southwest of Matanzas, Matanzas Province, Cuba.

USGS Mesozoic loc. 27175 (Palmer loc. 911): 1 km southwest of central Jesús María, Matanzas Province, Cuba.

USGS Mesozoic loc. 27198 (Palmer loc. 1145): Northwest of Dos Hermandos, 1 km on road to Abreus, Santa Clara Province, Cuba.

The occurrence of *A. aguilerae* in Cuba was first noted by Raymond (1925), who described it as a new species, *Arctostrea atkinsi.* Raymond's description was based on three fragmentary right valves from well spoils. The well was on the Santa Rosalia property, near the Harvard University Botanical Gardens, southeast of Cienfuegos in Santa Clara Province.

Plaster casts of the holotype are available in the collections of the U.S. National Museum. These collections also contain specimens from the Habana Formation at five additional localities in Matanzas and Santa Clara Provinces.

The age of the Habana Formation has been a matter of some dispute. Keijzer (1945, p. 150–156) summarized the problems involved in dating the formation. MacGillavry (1937) and Imlay (1944b) presented good faunal evidence for the Maestrichtian age of the formation.

The fossils associated with *Arctostrea aguilerae* from this area substantiate such an age assignment. Listed below are some of the more diagnostic associated species and their occurrence. All rudists marked by an asterisk occur in the *Titanosarcolites* limestone of Jamaica, accepted as of Maestrichtian age for many years (Chubb, 1956).

- **Bournonia cancellata* (Whitfield), USGS Mesozoic loc. 27127, 27126.
- **Plagioptychus jamaicaensis* (Whitfield), USGS Mesozoic loc. 27127, 27126.
- **Titanosarcolites giganteus* (Whitfield), USGS Mesozoic loc. 27127.
- **Praebarrettia sparcilirata* (Whitfield), USGS Mesozoic loc. 27127, 27126, 27173, 27175.
- *Parastroma guitarti* Palmer, USGS Mesozoic loc. 27127, 27126.
- *Parastroma sanchezi* Douvillé, USGS Mesozoic loc. 27127.
- *Antillocaprina annulata* Palmer, USGS Mesozoic loc. 27175.
- **Antillocaprina quadrangularis* (Whitfield), USGS Mesozoic loc. 27127.
- *Exogyra costata* Say, USGS Mesozoic loc. 27173, 27175.

In addition to the above fossils, an abundance of other pelecypods, both rudists and representatives of such genera as *Neithea*, *Idonearca*, and *Alectryonia* are associated with *A. aguilerae*. Gastropods and corals are locally common.

Exogyra costata Say is a common fossil on the Gulf Coastal Plain and occurs with *Titanosarcolites* both in Mexico and in the Southeastern United States. It ranges through the Late Campanian into the Maestrichtian. *Titanosarcolites* occurs with *Sphenodiscus* at several localities on the gulf coast.

The Cuban occurrences of *A. aguilerae* can therefore be ascribed to the Maestrichtian.

Locality in Texas:

USGS Mesozoic loc. 587: Cretaceous. Ford of the Medina River at Castroville, Texas. Collected by C. A. White, 1888.

The ventral one-half of an *Arctostrea aguilerae* is present in a collection containing a mixture of fossils from both the *Exogyra costata* and *E. ponderosa* zones. Faults in this area involve the Anacacho Limestone, Austin Chalk, Corsicana Marl, and Escondido Formation. Owing to these structural conditions, the vague nature of the locality data, and the obvious mixing of the collection, assignment of the specimen to a stratigraphic level is impossible. In spite of this, the occurrence of the species in the Upper Cretaceous of Texas is worthy of note.

Localities in Mississippi and Alabama:

USGS Mesozoic loc. 25509: Upper Cretaceous. Ripley Formation, Chiwapa Member. Roadcuts of Mississippi Route 30 in north-facing slope of Wilhite Creek valley from 0.7 to 1.7 miles south of Keownville, Union County, Miss., from SE¼SW¼NE¼ to SE¼ of sec. 30, T. 6 S., R. 4 E. Collected by L. W. Stephenson and N. F. Sohl, 1955.

USGS Mesozoic loc. 28712: Upper Cretaceous. Ripley Formation, Chiwapa Member. Bluffs south of Okanatie Creek about 50 yards above bridge on secondary road, near center west edge sec. 16, T. 8 S., R. 3 E., Union County, Miss. Collected by Mid-South Earth Science Club, 1962.

USGS Mesozoic loc. 25498: Upper Cretaceous. Prairie Bluff Chalk. Shell Bluff on Shell Creek, sec. 36, T. 14 N., R. 6 E., Wilcox County, Ala. Collected by L. W. Stephenson, N. F. Sohl, and W. H. Monroe, 1955.

In Mississippi, *Arctostrea aguilerae* (Böse) occurs in the Chiwapa Sandstone Member of the Ripley Formation at two localities. Its occurrence at USGS Mesozoic locality 25009 has been noted in a measured section by Sohl (1960, p. 35, unit 13). Here it occurs abundantly in a 5-foot unit that also contains *Sphenodiscus lobatus* (Tuomey) of Hyatt, *Exogyra costata* Say, and other typical Ripley Formation invertebrates. One specimen assigned to *Titanosarcolites* sp. was also found in this section at a level 39 feet higher than *A. aguilerae*, near the top of the formation.

Specimens of *A. aguilerae* from USGS Mesozoic locality 28712 are embedded in the same sandy limestone matrix and are assumed to have come from about the same position.

The occurrence of *Sphenodiscus* alone is sufficient to indicate a probable Maestrichtian age. Its proximity to the species of *Titanosarcolites* further strengthens the assignment.

The Alabama specimens occur near the type section of the Prairie Bluff Chalk at Shell Bluff on Shell Creek Here the formation is only about 12 feet thick. *Arctostrea* occurs near the base of the formation. The associated molluscan fauna (USGS Mesozoic loc. 25498) is as follows:

Pelecypoda:
- *Idonearca capax* (Conrad)
- *Inoceramus* sp.
- *Ostrea tecticosta* Gabb
- *Gryphaea mutabilis* Morton
- *Exogyra costata* Say
- *Trigonia thoracica* Morton?

Pelecypoda—Continued
Plicatula urticosa Morton
Lima reticulata Forbes
Anomia argentaria Morton
Paranomia scabra (Morton)
Liopistha protexta (Conrad)
Veniella conradi (Morton)
Crassatella vadosa Morton
Legumen ellipticum Conrad
Gastropoda:
Turritella vertebroides Morton
Xenophora leprosa (Morton)
Anchura cf. *A. abrupta* Conrad
Pugnellus densatus Conrad
Euspira rectilabrum (Conrad)
Gyrodes abyssinus (Morton)
Gyrodes petrosus (Morton)
Sargana stantoni (Weller)
Pyrifusus sp.
Napulus octoliratus (Conrad)
Pyropsis sp.
Volutomorpha cf. *V. retifera* Dall
Longoconcha sp.
Anisomyon cf. *A. centrale* Meek
Anisomyon sp.
Cephalopoda:
Eutrephoceras perlatus Morton
Baculites columna Morton
Baculites carinatus Morton
Baculites cf. *B. ovatus* Morton
Discoscaphites conradi petichiolus Morton
Discoscaphites conradi qulosus Morton?
Discoscaphites cf. *D. roanensis* Stephenson
Coahuilites sp.

In addition to the above, various species of echinoids, bryozoa, serpulid worms, boring sponges, corals, and the brachiopod *Terebratulina floridana* (Morton) also are present.

The fauna is typical of the chalk facies and of the Prairie Bluff Chalk. The ammonites indicate a high Maestrichtian level. *Baculites columna* occurs only in the highest part of the Cretaceous section, in beds above the first occurrence of *Sphenodiscus* from New Jersey to Texas, and has recently been found in the Fox Hills Sandstone of South Dakota (W. A. Cobban, written communication, March 1963). *Coahuilites* is common in the Maestrichtian of Mexico. The remainder of the ammonites are similarly restricted to the highest Cretaceous formations.

Summary of Stratigraphic Range

All the known specimens of *Arctostrea aguilerae* are associated with fossils indicating latest Cretaceous age (fig. 2). In the type area in Mexico, the species may occur as low as the uppermost Campanian; but in Cuba, Mississippi, and Alabama, it seems to be restricted to beds of Maestrichtian age.

Types

Illustrated hypotypes from Cuba, USNM 132075, 132076, 132078, 132079, 132080. Illustrated hypotype from Mexico, USNM 132072. Illustrated hypotypes from Mississippi, USNM 132069–132071, 132074, 132077. Illustrated hypotypes from Alabama, USNM 132073, 132081, 132082. Mentioned hypotype from Texas, USNM 132341. Measured unfigured hypotypes from Mississippi, USNM 132068 (four specimens).

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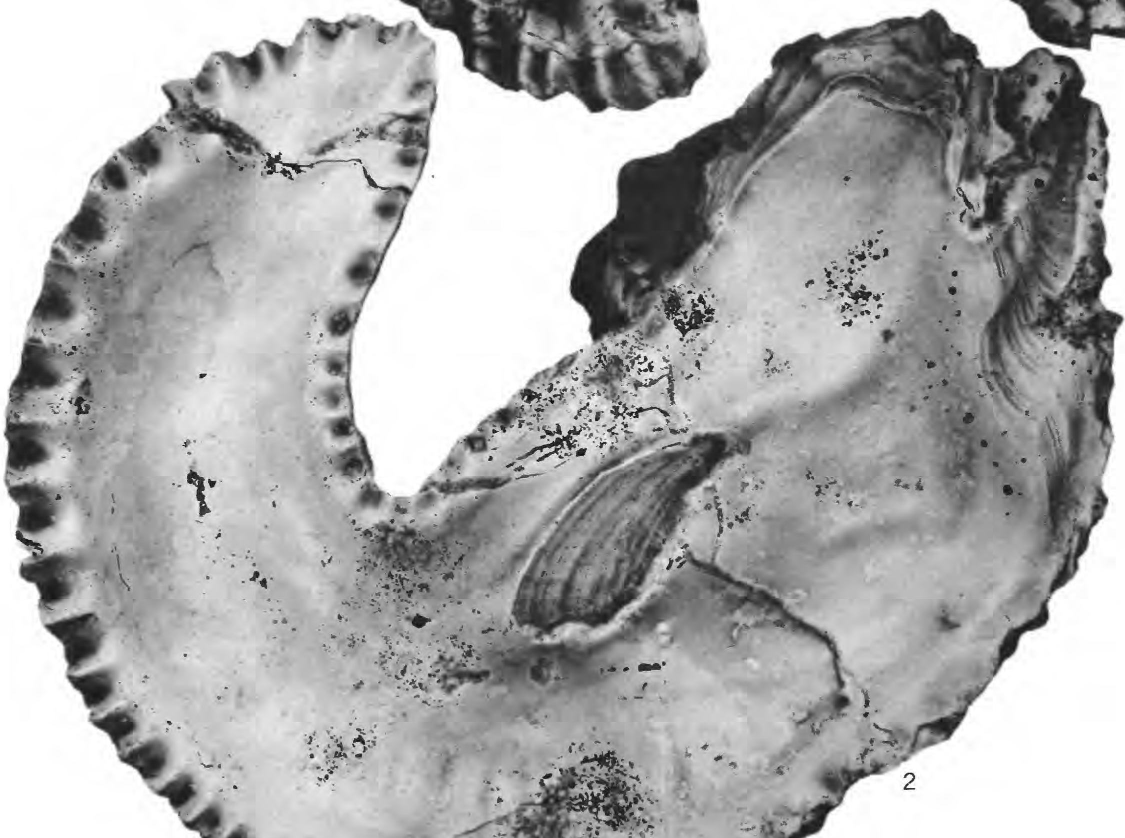
PLATES 1–5

PLATE 1

FIGURES 1, 2. *Arctostrea aguilerae* (Böse) (p. H14).

1. Lateral view (× 1) of a typical left valve, from the Prairie Bluff Chalk, Wilcox County, Ala. (USGS Mesozoic loc. 25498), illustrating nature of the ornamentation, valve outline, position of the attachment scar, and development of the posterior auricle. A hypotype, USNM 132082.
2. Interior view (× 1) of the specimen illustrated in figure 1, showing position and development of the deeply incised posterior adductor muscle scar, the crenulate commissure, structures of the cardinal area, and interior of the posterior auricle and the overlapping lamellae at its margin. Hypotype (USGS Mesozoic loc. 25498), USNM 132082.

1



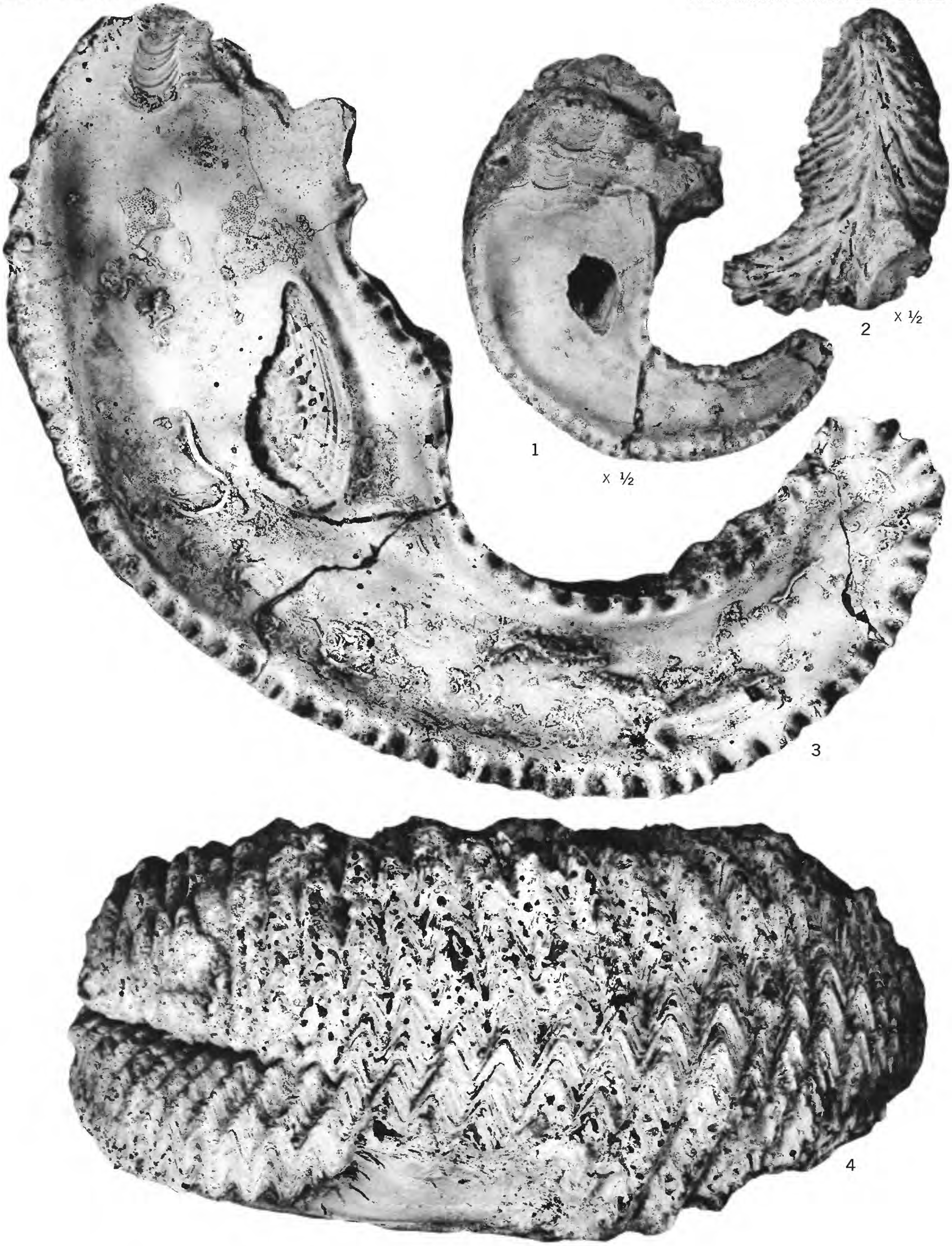
2

ARCTOSTREA AGUILERAE (BÖSE)

PLATE 2

FIGURES 1–4. *Arctostrea aguilerae* (Böse) (p. H14).

1. Interior view (× ½) of a right valve, from the Prairie Bluff Chalk, Wilcox County, Ala. (USGS Mesozoic loc. 25498), illustrating the development and position of the deep posterior adductor muscle scar and the crenulate commissure. Note the abnormally massive cardinal area with offset resilifer and broad lateral cardinal plates. A hypotype, USNM 132073.
2. Lateral view (× ½) of a small right valve, from the Chiwapa Member, Ripley Formation, Union County, Miss. (USGS Mesozoic loc. 25509). This specimen is closely comparable to Böse's syntype of the species (1906, pl. 2, fig. 2). A hypotype, USNM 132070.
3. Interior view (× 1) of a large right valve, illustrating characteristic development of the valve outline, crenulate commissure, and posterior auricle, which bears well developed denticles. Structures of the cardinal area are typically developed, but the area itself is smaller than average. The well-developed posterior adductor muscle scar, generally incised in thick-shelled specimens, is raised on a platform and surrounded by a raised rim in this thin-shelled form. A hypotype from the Prairie Bluff Chalk, Wilcox County, Ala. (USGS Mesozoic loc. 25498): USNM 132081.
4. Anterior view (× 1) of paired valves, illustrating the convexity of the shell, zig-zag nature of the commissure, flattering of the plicae on the steep anterior flank of both valves, and the chevron-shaped trace of the lamellae at their intersection with the anterior flank. A hypotype from the Chiwapa Member, Ripley Formation, Union County, Miss. (USGS Mesozoic loc. 25509); USNM 132069.

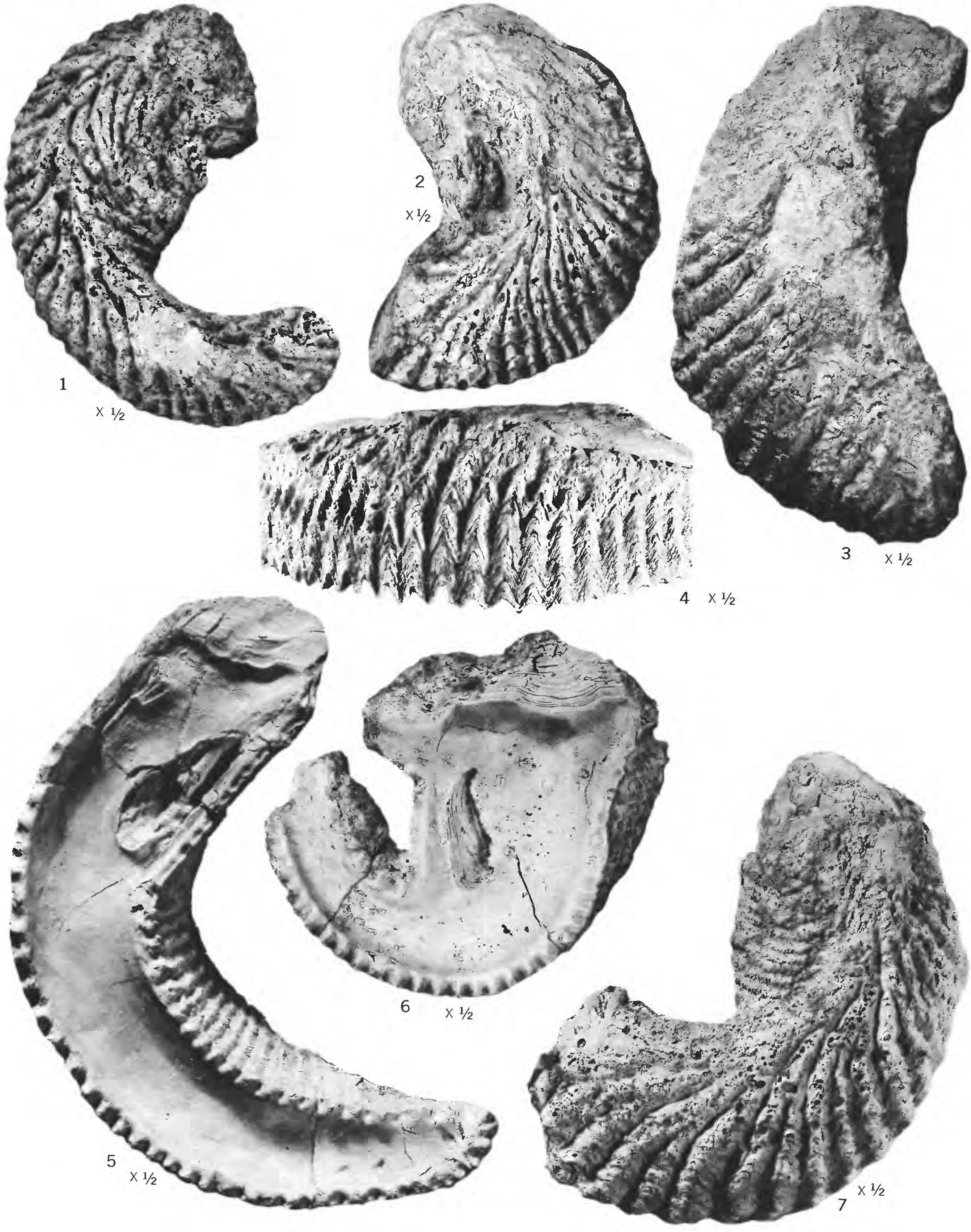


ARCTOSTREA AGUILERAE (BÖSE)

PLATE 3

FIGURES 1–7. *Arctostrea aguilerae* (Böse) (p. H14).

1. Lateral view of a left valve (× ½), showing characteristic outline and ornamentation of species. A hypotype from the Chiwapa Member, Ripley Formation, Union County, Miss. (USGS Mesozoic loc. 25509), the specimen illustrated on plate 2, figure 4; USNM 132069. Compare with Böse's syntype (1906, pl. 6, fig. 1).
2. Lateral view of a right value (× ½) from Cárdenas Formation, San Luis Potosí, Mexico (USGS Mesozoic loc. 28181); USNM 132072.
3. Lateral view of a left valve (× ½) from Santa Clara Province, Cuba (USGS Mesozoic loc. 27198), showing narrow umbonal ridge and steep dorsoposterior slope; slope flattened at the margin and bears straight subparallel plicae. A hypotype, USNM 130280.
4. A partial anterior view of a right valve (× ½), showing zig-zag nature of the commissure, flattening of the plicae on the steep anterior slope, and chevron-shaped trace of lamellae intersecting anterior slope. A hypotype from Santa Clara Province, Cuba (USGS Mesozoic loc. 27198); USNM 132078.
5. Interior view (× ½) of the right valve from Cuba, illustrated in figure 4 (USGS Mesozoic loc. 27198). A hypotype showing the crenulate commissure and the outline and deeply incised nature of the posterior adductor muscle scar on thick-shelled forms; resilifer unusually shallow; USNM 132078.
6. Interior view (× ½) of a right valve with abruptly recurved ventral part of shell, characteristic structures of the cardinal area (resilifer, lateral cardinal plates), posterior auricle, commissure, and posterior adductor muscle scar. A hypotype from the Chiwapa Member, Ripley Formation, Union County, Miss. (USGS Mesozoic loc. 25509); USNM 132071.
7. Lateral view of a right valve (× ½) from Santa Clara Province, Cuba (USGS Mesozoic loc. 27127), showing characteristic valve outline and ornamentation. Note subparallel, gently curved plicae of flattened part of dorsoposterior flank. A hypotype, USNM 132075, comparable to one of Böse's syntypes (1906, pl. 6, fig. 2).



ARCTOSTREA AGUILERAE (BÖSE)

PLATE 4

FIGURES 1–4, 6–8. *Arctostrea aguilerae* (Böse) (p. H14).

1. Lateral view of a left valve (× ½), illustrating exceptionally well-developed subparallel plicae on the dorsoposterior slope and well-defined posterior auricle. A hypotype from Santa Clara Province, Cuba (USGS Mesozoic loc. 27198); USNM 132079.
2. Enlarged photograph (× 4) of a weathered fragment from a left valve, showing structure of subnacreous shell layer. Note major flat lamellae composed of prominent vertical calcite plates transected by finer horizontal calcite laminae. A hypotype from the Ripley Formation of Union County, Miss. (USGS Mesozoic loc. 25509); USNM 132077.

3, 4. Lateral and internal views (× ½) of a crushed palmate right valve, showing that despite subsequent flattening, shape and position of interior valve margins identifies specimen as having been narrow and strongly curved. A hypotype from Santa Clara Province, Cuba (USGS Mesozoic loc. 27127); USNM 132076.

6. Natural section (× 1) through a left valve fragment, the specimen illustrated in figure 2, showing typical valve cross section and structure of the subnacreous shell layer—major horizontal plates composed of prominent vertical calcite crystals. A hypotype from the Ripley Formation in Union County, Miss. (USGS Mesozoic loc. 25509); USNM 132077.
7. Posterior adductor muscle scar (× 1) from a massive left valve, showing incised nature and characteristic ornamentation of scar. A hypotype from the Chiwapa Member, Ripley Formation, Union County, Miss. (USGS Mesozoic loc. 25509); USNM 132074.
8. Interior view (× ½) of a typical left valve showing well-developed cardinal features: resilifer, lateral cardinal plates, marginal cardinal troughs. The specimen illustrated in figure 1; a hypotype from Santa Clara Province, Cuba (USGS Mesozoic loc. 27198); USNM 132079.

5, 9, 10. *Crassostrea cusseta* Sohl and Kauffman n. sp. (p. H7).

5. Dorsoposterior margin (× 1) of a right valve, illustrating the elongate trace of the denticles. A paratype from the Cusseta Sand just below Woolridge landing, Chattahoochee River, Ala. (USGS Mesozoic loc. 5396); USNM 132061.

9, 10. Interior and lateral views of a typical right valve (× ½), showing valve outline, strong posterior curvature of the valve, well-defined cardinal structures (midcardinal fold, lateral cardinal troughs), caved shell layers over site of covered posterior adductor muscle scar, and characteristic exterior ornamentation of overlapping lamellae. A paratype from the Cusseta Sand below Woolridge landing, Chattahoochee River, Ala. (USGS Mesozoic loc. 26027); USNM 132060.

ARCTOSTREA AGUILERAE (BÖSE) AND *CRASSOSTREA CUSSETA* SOHL AND KAUFFMAN N. SP.

PLATE 5

[All pictures × ½]

FIGURES 1–4. *Crassostrea cusseta* Sohl and Kauffman n. sp. (p. H7).

1. Interior view (× ½), dorsal part of a large right valve showing well-developed posterior auricle and cardinal structures (midcardinal fold, lateral cardinal troughs). A paratype from the Cusseta Sand at Woolridge landing, Chattahoochee River, Barbour County, Ala. (USGS Mesozoic loc. 28451); USNM 132058.
2. Interior view (× ½), dorsal part of a large left valve showing well-developed resilifer, lateral cardinal folds, subcardinal cavities, posterior auricle, and the surface of the posterior adductor-muscle scar, here exposed by removal of numerous calcite lamellae on the floor of the valve. A paratype from the Cusseta Sand, Barbour County, Ala. (USGS Mesozoic loc. 26029); USNM 132059.

3, 4. Internal and lateral views (× ½) of the holotype, a large left valve, characteristic of the species, illustrating the marginal outline, lack of exposed muscle scar on large adult valves, well-defined resilifer, lateral cardinal folds, denticulate commissure, attachment scar, and lamellate exterior ornamentation. Specimen from the Cusseta Sand, below Woolridge landing, Chattahoochee River, Barbour County, Ala. (USGS Mesozoic loc. 26027); USNM 132057.

CRASSOSTREA CUSSETA SOHL AND KAUFFMAN N. SP.