Report of Investigations — No. 3

Successional Speciation in Paleontology: The Case of the Oysters of the *sellaeformis* Stock

By

H. B. STENZEL

1949

SUCCESSIONAL SPECIATION IN PALEONTOLOGY: THE CASE OF THE OYSTERS OF THE *SELLAEFORMIS* STOCK

H. B. STENZEL

Bureau of Economic Geology, The University of Texas, Austin

The successional mode of speciation of Julian Huxley (1942) may be defined as gradual transformation of one species into a successor species, or several of them, during the course of geologic time without primarily involving geographic, ecologic, or adaptive segregation. The purpose of this paper is to present a particular case of such a mode of speciation and to discuss problems involved therein. The example chosen is the stock of *Cubitostrea sellaeformis* (Conrad) [Mollusca, Pelecypoda], which contained 4 separate successional species of oysters and lived in Middle Eocene time in the ancient Gulf of Mexico.

STRATIGRAPHIC SUCCESSION

Only recently has it become possible to trace this succession of species, because only recently has the stratigraphic succession of the beds and localities involved been cleared up sufficiently to allow correct chronologic placing of the species involved. This modern stratigraphic information, without which satisfactory paleontologic work could not be done, we owe to the original investigative field work of geologists active in the area.

The following is a brief and simplified outline of stratigraphy involved in the **present study (compare fig. 6).**

Jackson group [Upper Eocene] : with Moodys Branch marl, a richly fossiliferous glauconite and shell marl at base.

Regional transgressive disconformity
Claiborne group [Middle Eocene] :
    Yegua formation: chiefly nonmarine, lignitic sands and shales, about 800 feet thick.

Cook Mountain formation [equivalent to Wautubbee formation in Mississippi and upper Lisbon formation in Alabama] : chiefly marine and brackish-water shales, marls, and glauconites, about 350 feet thick.

Regional transgressive disconformity
Stone City beds: brackish and marine, carbonaceous shales and glauconites, up to 80 feet thick.

Sparta sand: chiefly deltaic, cross-bedded, lignitic sands, about 250 feet thick.

Regional regressive disconformity
Therrill shale [equivalent to Zilpha shale of Mississippi] : carbonaceous shales and silts, up to 40 feet thick.

Weches formation [equivalent to Winona of Mississippi and lower Lisbon of Alabama, in part] : chiefly glauconites and clay ironstones, about 40 feet thick.

Regional transgressive disconformity
Tallahatta formation of Alabama: brackish and marine sands and silts.

Other formations, not involved in this study.

Disconformity
Wilcox group [Lower Eocene].

SPECIES SUCCESSION

The branch of the family Ostreidae [Mollusca, Pelecypoda] discussed in the present paper culminates in *Cubitostrea sellaeformis* (Conrad), which was originally described in 1832 and has been redescribed by many authors (Morton, 1833; Morton, 1834; Heilprin, 1884; De Gregorio, 1890; Clark, 1896; Clark and Martin, 1901; Harris, 1919). This showy species is a well-known, widespread, and abundant fossil oyster, useful as a marker of the Cook Mountain formation and

equivalent beds (see figs. 1 and 2). In its mature and senile stage it has a ponderous and peculiarly twisted shell. Its shape suggests a saddle *(sella* in Latin), hence the name *sellaeformis.* The long axis of the left valve (U to 8 of fig. 1), anatomically the anterodorsal-posteroventral axis of the animal, is strongly arched. Transverse to the long axis the mature left valve is concavely arched. There are two auricular flaps, one on each side of the umbo, the posterior one nearly always the larger; both are arched in a concave manner like the main body of the valve. This manifold arching of the various portions of the mature shell produces a rather high and sharp fold in the sinus located between the posterior auricle and the main shell body and a much lesser fold in the corresponding sinus between the anterior auricle and the main shell body. The right valve (fig. 2), that is, the unattached valve, conforms to the shape of the left for complete closure at the shell margins but is so thick and heavy in the senile stage that its outer face is convex along the long axis though not as much as that of the left valve. Surface sculpture consists mainly of crude, projecting, concentric growth lamellae; ribbing is either absent over most of the mature surface or shallow and faint where present.

The projecting growth lamellae are thick at their base but thin toward their free margin to a paper-thin edge, which commonly is broken off. Under each lamella is a deep chink, which is usually filled with matrix. It is obvious that shell growth was rapid and continuous to the end of each lamella. But after this period of rapid growth the fleshy portion of the animal shrank considerably in size and started to build the next lamella not in continuation of the feather-edge of the old lamella but farther back. This shrinkage in size of the fleshy portion produced the chink that is found between each lamella and its successor. Such repeated, periodical shrinkage of the fleshy portion is strongly suggestive of the shrinkage during the spawning season, which has

been observed in living oysters. Hence it is assumed that each lamella represents an annual growth and each chink, between succesive lamellae, the growth interruption during the summer spawning season. On that basis most senile shells of *Cubitostrea sellaeformis* (Conrad) are at least 8 years old (compare fig. 1). Exact determination of the age of shells that are more than 8 years old is hardly possible, because near the end of the 8th year the shell ceases to grow in length and the lamellae become closely stacked together, making them difficult to count.

Greatly different from the mature and senile shell is the immature portion preserved near the umbos (U to N of fig. 1). This stage is also known from many immature fossil shells, which are remnants of animals that died before reaching maturity. Such shells are thin, their auricles are small but show an increase from growth line to growth line; the peculiar twist of the shell is just beginning to show. The shell outline is elongate with a slight crescentic turn. The left, that is, the attached, valve is shallowly convex and regularly ribbed with radial divaricating costae; the costae are dichotomous or intercalating and about 1 to 2 mm wide at the end of the immature stage. The right valve is flat to faintly convex and devoid of ribs or with few faintly indicated radial costae; regular, concentric, and appressed growth lamellae are the only sculpture present in most cases.

The immature shells are an indication of the true affinities of this oyster within the family Ostreidae. They are very similar to the immature shells of European fossil oysters of the genus *Cubitostrea* Sacco (1897). If one compares immature specimens of *Cubitostrea sellaeformis* (Conrad) with those of *C. cubitus* (Deshayes) and *C. plicata* (Solander) (Brander, 1766; Cossmann, 1887; and Cossmann and Pissarro, 1906) one is at once impressed by the great similarity in all morphologic and anatomic features of the shell including costae, hinge, and position and shape of the adductor and pedal muscle imprints.
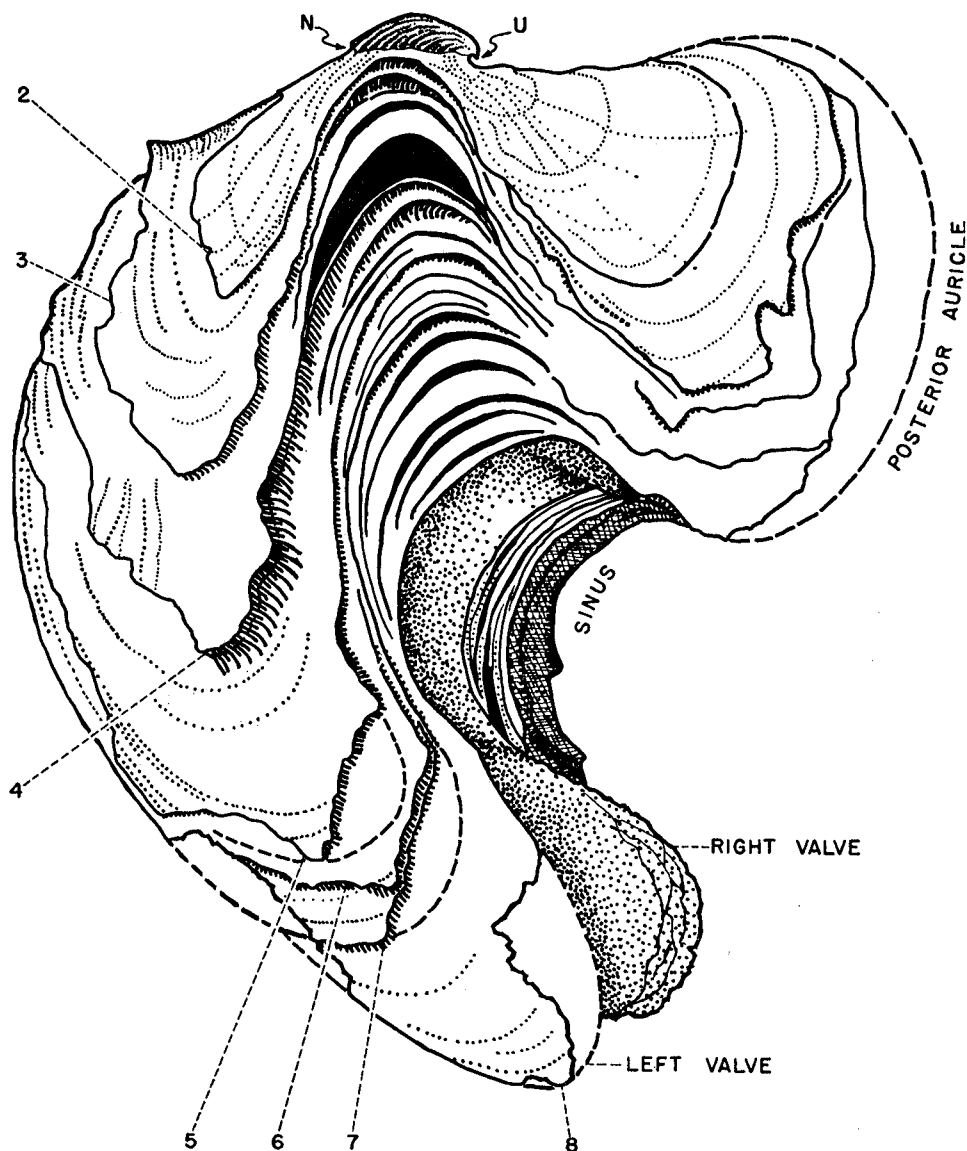
FIG. 1.   Senile shell of *Cubitostrea sellaeformis* (Conrad), × 5/6, from the Archusa marl of the Cook Mountain (Wautubbee) formation in cut of New Orleans & Northeastern Railroad, 1 mile north of Wautubbee or 0.4 mile north of highway overpass, Clarke County, Mississippi.

This individual probably reached an age of 8 years as indicated by the 8 abruptly terminated major growth stages, each of which forms a growth squama and a sharp step. These growth stages are shown on the figure by N, 2, 3, 4, 5, 6, 7, and 8; the ribbed neanic stage ends at N; the umbo and very small attachment scar are at U.

This is an oblique posterior view seen at approximately 45° to the hinge axis showing the twisted valve commissure and the large posterior auricular flap.   The right valve is largely hidden from view by the left; the right valve is stippled.   Compare text figure 2.
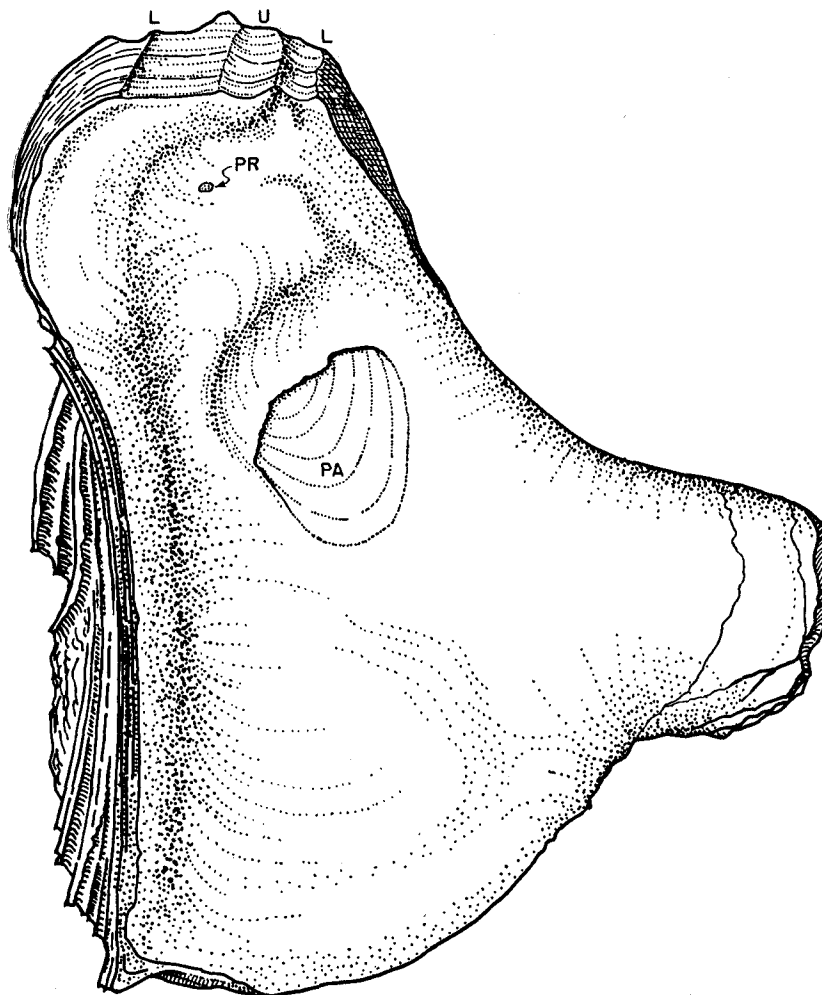
FIG. 2. Senile right valve of *Cubitostrea sellaeformis* (Conrad), same individual as figure 1, × 5/6.

This is an oblique anterior view of the inside of the right valve seen at approximately 45° to the hinge line showing the warping of the valve. The posterior adductor muscle imprint is seen straight on, hence is shown without perspective distortion, but its thin shelly cover at the upper margin is broken off, thus modifying its reniform outline somewhat. Abbreviations: L = ligament, PA = posterior adductor muscle imprint, PR = pedal retractor muscle imprint, U = umbo.

The similarity in youth is so obvious that one can but conclude that *sellaeformis* (Conrad) is a near relative of the two European species or, to put this conclusion into systematic terminology, *sellaeformis* is a *Cubitostrea* too or closely related to that genus. This conclusion is merely an example of the procedure Garstang (1922) had in mind in his critical discussion of the Biogenetic Law.

The conclusion as to the affinity of *C. sellaeformis* (Conrad) to typical Cubitostreas can be repeated with all other species of the *sellaeformis* stock, and clearly the earlier species of the stock are more similar to and less divergent from the typical branch of *Cubitostrea*. The earliest species of the stock, *Cubitostrea perplicata* (Dall), cannot be distinguished from the typical branch of *Cubitostrea;* it is a
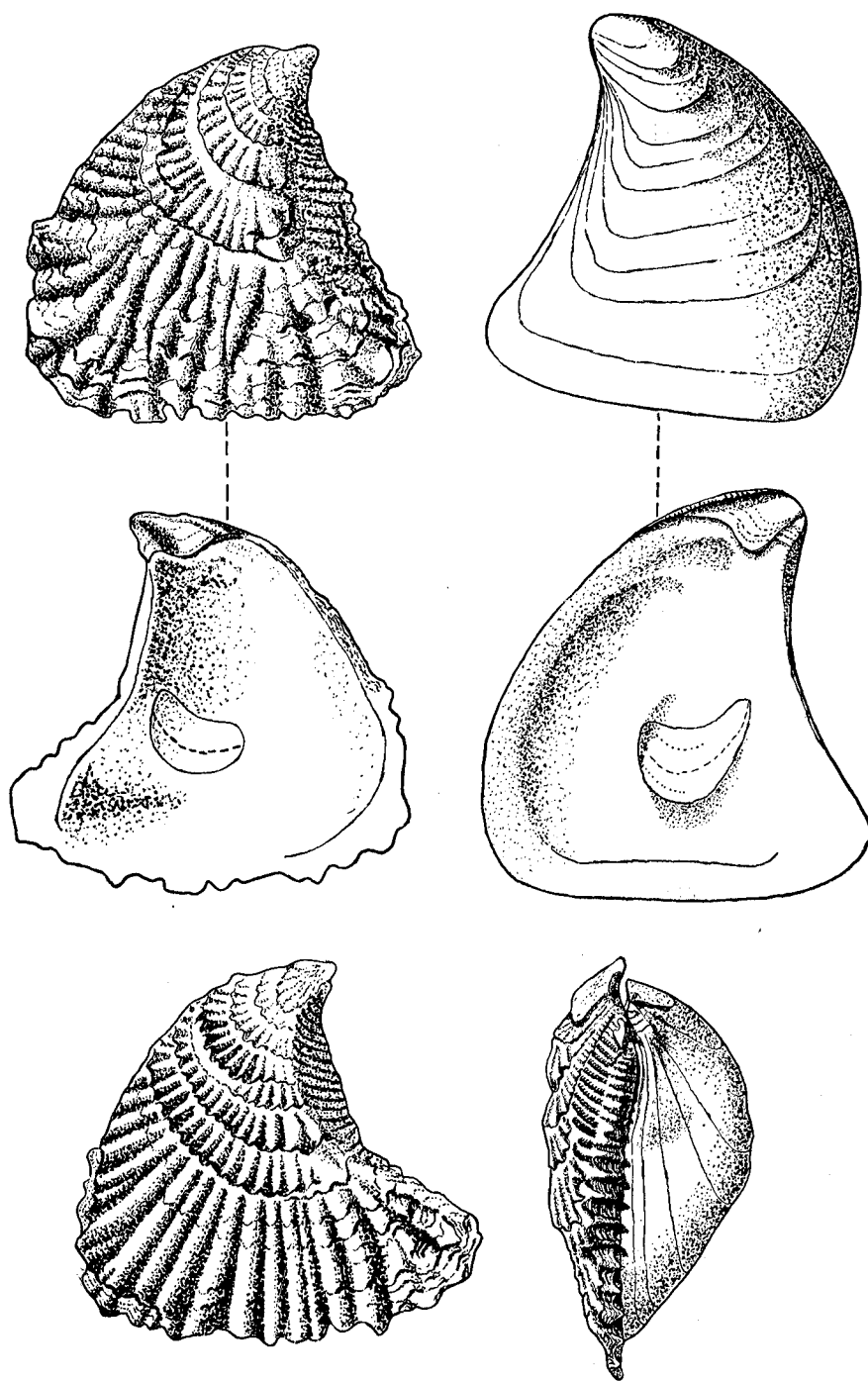
FIG. 3. Valves of *Cubitostrea perplicata* (Dall), ×1, topotypes. Costate left valves in left column; smooth right valves, upper two figures in right column; complete shell in lower right.

Cubitostrea s.s. But the species descendent from it are a more and more divergent off-branch of the typical branch; in other words, they are a subgenus of *Cubitostrea* s.l. as yet unnamed. This subgenus comprises *Cubitostrea lisbonensis* (Harris)—*C. smithvillensis* (Harris)—*C. sellaeformis* (Conrad). The *sellaeformis* stock includes in addition to these 3 species their ancestor species, the *C. perplicata* (Dall).

The chain of species culminating in *C. sellaeformis* appears first in the Middle Eocene as *C. perplicata* Dall (Dall, 1898; Harris, 1919) from the Tallahatta formation of Alabama (fig. 3). This species has a strongly costate left valve and smooth right valve; it lacks the auricles entirely and for that reason its umbonal region is more pointed than in the other species of this stock. In youth its outline is oval to crescentic, but on maturing it expands along the anterior margin so that the shell assumes gradually a curved-triangular outline with one part of the margin nearly straight. The ribbing of the left valve is weak in youth but becomes stronger with maturity, and at that stage the costae are wider than their interspaces. The valves are thick as in *C. lisbonensis* (Harris).

The *C. perplicata* (Dall) possesses several primitive features. Primitive is the comparatively small size of the shell. The largest left valve at hand is 64 mm high; the corresponding right valve is smaller as is the case in all members of the family Ostreidae. Mature shells of *perplicata* are 45 to 60 mm high. All succeeding species of the phylogenetic series stemming from *C. perplicata* are larger, and the increase in size is progressive from species to species so that the last species, *C. sellaeformis*, is very large. Left valves up to 182 mm high are known in the latter species.

Primitive is also the complete lack of **auricles at any stage of growth. All later** species of this evolutionary chain have well-developed auricles. The auricles increase in proportionate size from species to species and develop to such an extreme

in the last species of the chain, *C. sellaeformis* (Conrad). Auricles appear suddenly for the first time in *C. lisbonensis* (Harris). This sudden appearance of auricles in the evolutionary chain coincides with the regional disconformity separating the Tallahatta formation from the overlying lower Lisbon formation. The *Cubitostrea perplicata* (Dall) occurs at the very top of the Tallahatta formation and lacks auricles; the *C. lisbonensis* (Harris) is found in many places at the very base of the overlying Lisbon formation and has already well-developed auricles. The fact that the sudden appearance of auricles coincides with the break between the two formations emphasizes the hiatus of time represented by the disconformity, which is also demonstrable from other evidence.

Primitive in *C. perplicata* is also the strength of the costae and their retention in strength to the end of growth in senile left valves. The chain of species shows a progressive weakening of the costae (see fig. 7). The second species, *C. lisbonensis,* retains its costae throughout shell growth but they are weaker than in *C. perplicata.* The next species, *C. smithvillensis,* has greatly subdued costae after maturity is reached, but they are retained throughout growth of the left valve. The last species, *C. sellaeformis,* may lack costae in the later, post-neanic stages of growth or may have sporadic and obsolescent costae. However, in distinction to the mature and senile portions of the left valves the immature portion is regularly costate in all species of the chain.

Primitive is also the triangular shell outline of *C. perplicata.* The second species, *C. lisbonensis,* is moderately triangular in outline. There are individuals of this species that come rather close to *C. perplicata* in triangularity of outline; beginning with these shells one may group others in a variation series that goes from crescentic-triangular to crescentic with only a slight indication of triangular outline. Of the next species, *C. smithvillensis,* many shells have a roundedly project-
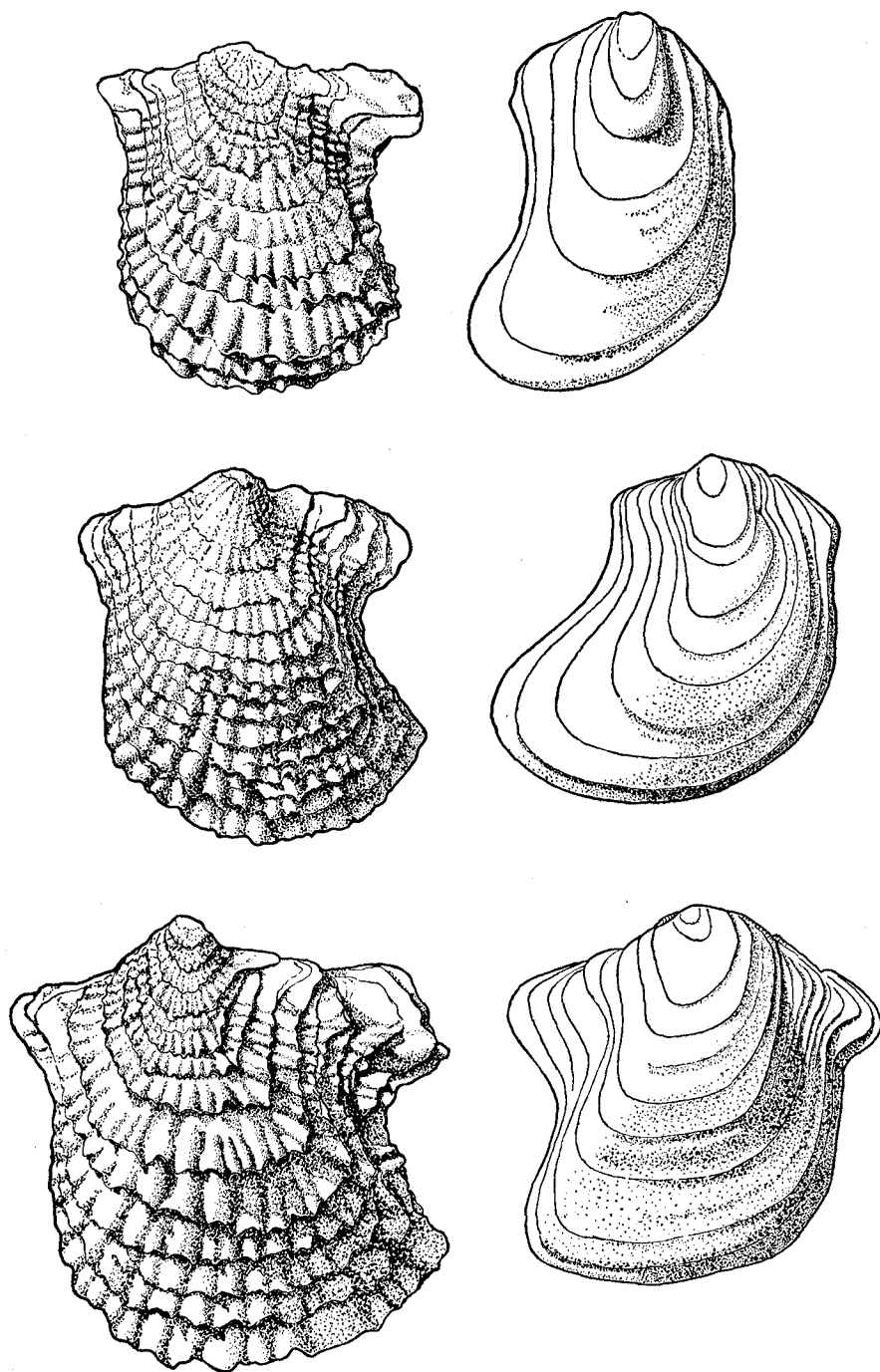
FIG. 4. Valves of *Cubitostrea lisbonensis* (Harris), × 1, from Texas. Costate left valves and smooth right valves of 6 individuals; outside views.

ing anterior margin that is suggestive of a remnant of triangular outline; but as a whole the shell outline of this species is ovate. In the last species of the chain the triangular outline has been completely submerged in the ovate outline. As a whole the chain shows a progressive reduction of the triangular projection in the shell outline and a gradual change from pronouncedly curved-triangular to moderately triangular to ovate outlines.

Primitive in *C. perplicata* (Dall) is also the complete lack of arching of the valves; the commissure of the two valves lies in a plane. Shells of the succeeding species are arched. Those of *C. lisbonensis* and *C.*

smithvillensis are only slightly arched; in fact they are arched so little that were one not searching for this feature one might easily overlook its presence. The shell of *C. sellaeformis* is highly arched so that the commissure between the two valves is not a plane but arched so much that the rise is about 0.50 of the chord of the arch.

The second species of the chain is *Cubitostrea lisbonensis* (Harris) from the lower Weches formation and its equivalents (fig. 4). This species is widespread, in Alabama, Mississippi, Louisiana, and Texas. It is very similar to *C. perplicata.* The shell is thick. The umbonal region is wider, because auricles are present.
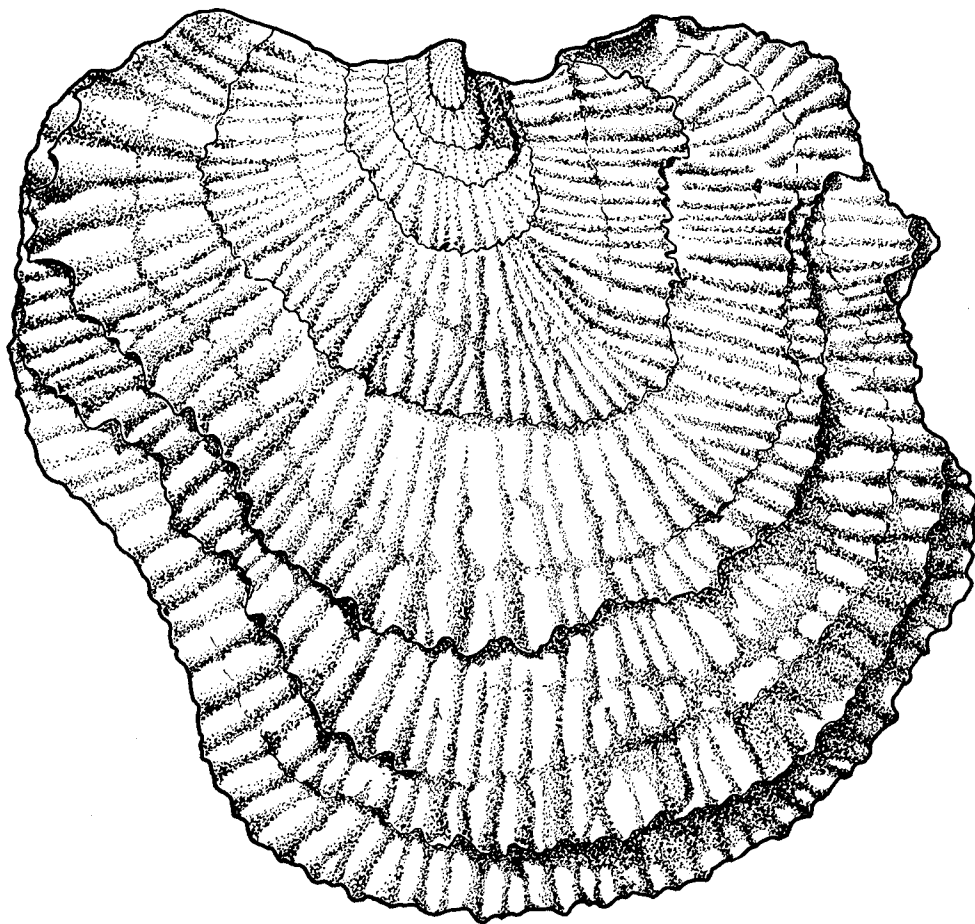

FIG. 5. Outside view of left valve of adult *Cubitostrea smithvillensis* (Harris), × 1, from Choctaw County, Alabama.
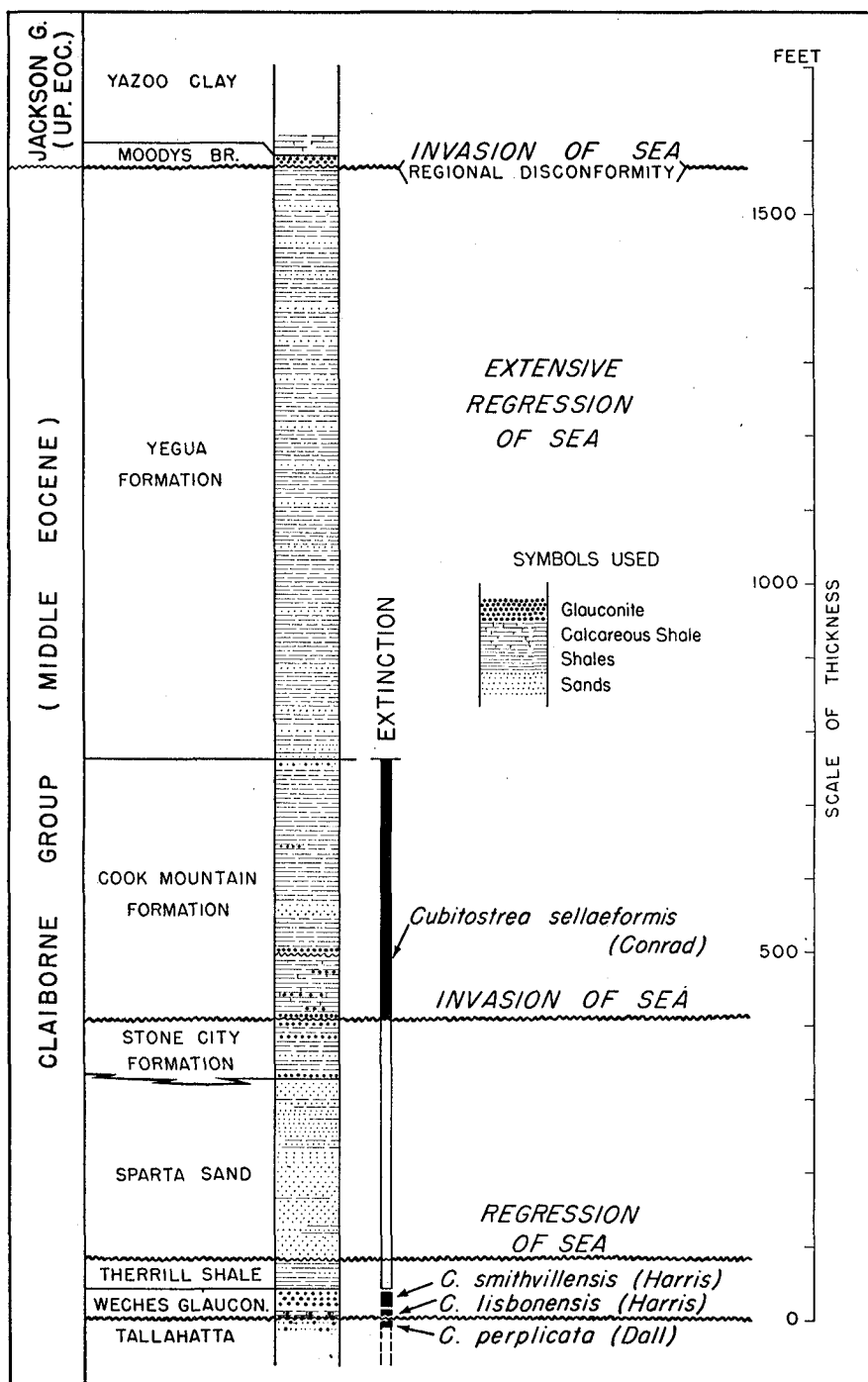
FIG. 6.   Stratigraphic ranges of the chain of species composing the *Cubitostrea sellaeformis* (Conrad) stock in the Gulf Coastal Plain.

Some specimens have very prominent auricles while others have small ones, but never is this feature missing. The valve outline is crescentic to ovate with a triangular extension of the shell margin similar to but less prominent than in *C. perplicata* (Dall). The ribbing of the left valve is very similar to *C. perplicata* (Dall), but the interspaces are as wide as or wider than the costae. The shell commissure is slightly arched; the rise of the arch is 0.10 of its chord.

The third species of the chain, *Cubitostrea smithvillensis* (Harris), too is found in the Weches formation, but it is restricted to Texas and Alabama and occurs always in a higher level than *C. lisbonensis* (Harris) (fig. 6). No signs of intergradation between *C. lisbonensis* (Harris) and *C. smithvillensis* (Harris) are found. This lack of intergrading forms is explained by a scarcity of any oyster remains between the two respective levels occupied by the two species and by a well-defined depositional hiatus separating the top of the *C. lisbonensis* level in the lower Weches formation from the succeeding beds of the upper Weches formation. Similarly there are no intergrading populations between any of the four species discussed here. All four species are precisely limited at the top and bottom of their stratigraphic ranges by gaps of the record that eliminate intergrading forms.

Cubitostrea smithvillensis (Harris) differs from *C. lisbonensis* (Harris) in several respects of which the most diagnostic is the presence of a few low costae radiating from the umbo of the right valve. This species as it grows large assumes an ovate outline, and its costae become wider and lower; the auricles are large but in many cases poorly set off from the main body of the valve. The gradual loss of the crescentic shell outline and the change into an ovate one, as the shell grows, is an advanced character. So is the gradual widening and weakening of the radial costae on the left valve. A newly added character is the faint radial ribbing of the right valve. The shell commissure is

slightly arched; the rise of the arch is 0.11 of its chord in large shells.

The strata between the Weches and the Cook Mountain formations are largely fluviatile and nonmarine; hence oysters cannot be found in them. However, the Stone City beds contain brackish and marine deposits and some oysters have been found in them, but among the oysters no representatives of the *sellaeformis* stock have been discovered to date.

The *Cubitostrea sellaeformis* (Conrad) from the Cook Mountain formation and its equivalents is still larger than *C. smithvillensis* (Harris) and has in addition a ponderous habit and a twisted shell with large auricular flaps. Owing to the twist of the shell the flaps are rather well set off from the main shell body. As the shell grows, the costae of the left valve become more and more obscure. All-in-all its features are accentuations or exaggerations of the characters found already
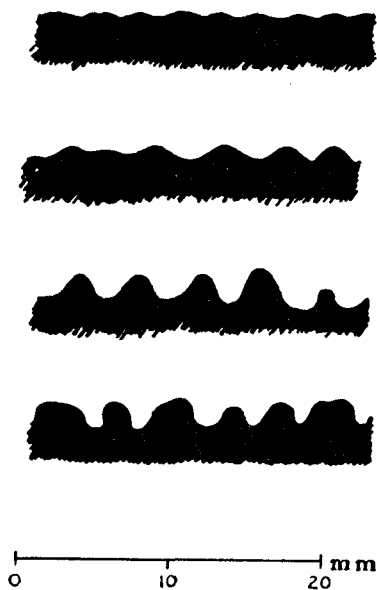

FIG. 7. Sections across radial costae of left valves, mature stage, at a distance of 6 cm from the umbo, × 2 of natural size. Top: *Cubitostrea sellaeformis* (Conrad) ; second from top: *C. smithvillensis* (Harris) ; second from bottom: *C. lisbonensis* (Harris); bottom: *C. perplicata* (Dall).

in *C. smithvillensis* (Harris). The twist or arching of the shell, so prominent in this species, is nevertheless present in *C. lisbonensis* and *C. smithvillensis* but is very faint in these two.

The features which show progressive evolutionary changes from species to species in this chain are:

(1) increase in size of shell (compare fig. 8)

(2) increase in proportionate size of auricles (compare fig. 8)

(3) decrease in strength of costae (compare fig. 7)

(4) disappearance of triangular shell outline (compare fig. 8)

(5) appearance of twist in shell.

These features can be expressed in numerals with the aid of measurements. Below is a tabulation of approximate data. It is recognized that more reliable and exact data might be obtained by extended statistical work. However, the material at hand does not seem to warrant such work.

Cubitostrea

	perplicata (Dall)	*lisbonensis* (Harris)	*smithvillensis* (Harris)	*sellaeformis* (Conrad)
(1)	64	86	147	182
(2)	0.00	0.33	0.41	0.51
(3)	0.45	0.42	0.30	0.13
(4)	0.90	0.79	0.58	0.55
(5)	0.00	0.10	0.11	0.50

(1) is the maximum size attained by each species as measured by the distance in millimeters from the umbo to the opposite margin of the left valve [or the height of the left valve].

(2) is the proportion of the height of the posterior auricle to the height of the valve, measured on the left valves of specimens with large auricles.

(3) is the average proportion of the height to the width of a costa on the left valve, measured at a distance of 6 cm from the umbo.

(4) is the proportion of the length to the height of the right valve in adult specimens.

(5) is the proportion of the rise of the arch made by the left valve to the height of the left valve.
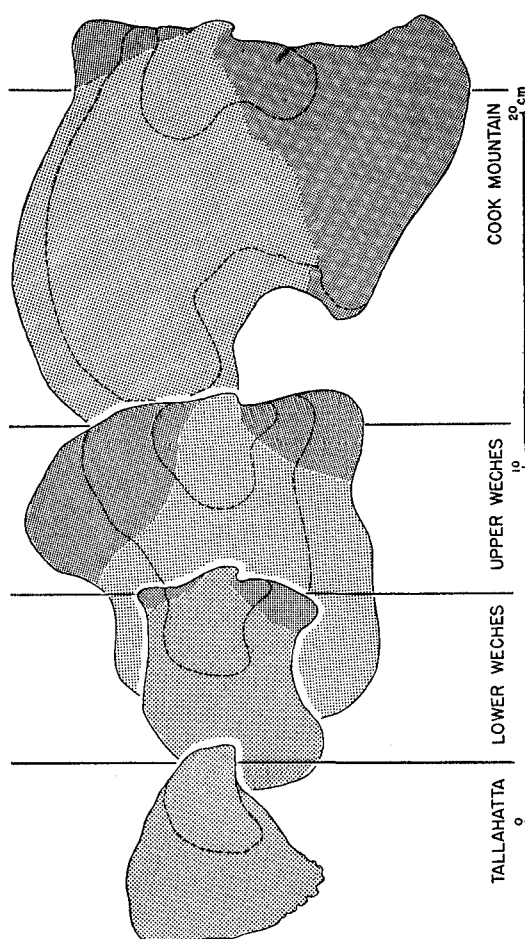

FIG. 8. Left valves of species composing the *Cubitostrea sellaeformis* (Conrad) stock, × ½ of natural size.

These are outlines of the left valves of large specimens of each species. They show the development of auricles and increase in shell size from species to species. The species are arranged with the earliest at the bottom and the latest at the top. Horizontal bars are the extensions of the hinge axes. Auricles are shaded differently than the main shell body. Some growth lines are indicated by dashed lines.

EXTINCTION OF THE STOCK

The *C. sellaeformis* (Conrad) and the stock it represents disappeared from the Gulf Coast Tertiaries with the close of Cook Mountain time. The end of Cook Mountain deposition in the Gulf Coast was marked by a regional, extensive, and long lasting withdrawal of the sea, and the

North American Distribution of Cubitostrea

Cubitostrea (unnamed- sub genus):

sellaeformis (Conrad)	Cook Mountain formation and its equivalents, Maryland to Mexico
smithvillensis (Harris)	upper part of Weches formation and its equivalents, Texas and Alabama
lisbonensis (Harris)	lower part of Weches formation and its equivalents, Alabama to Mexico

Cubitostrea (Cubitostrea):

divaricata (Lea)	Weches and Cook Mountain formations and their equivalents, Alabama to Texas
imdescribed species	lower Cook Mountain formation, Texas
perplicata (Dall)	Tallahatta formation, Alabama

formation succeeding the largely marine Cook Mountain is a nonmarine, largely lignitic series of beds known as the Yegua formation (Stenzel, 1940). The withdrawal of the sea during Yegua time was certainly of long duration for the formation is a thick one and contains ancient soils with tree roots *in situ.* The withdrawal of the sea had also a long reach in a gulfward direction for the formation can be traced a considerable distance underground and down dip toward the Gulf before its facies changes to near-shore marine. These extensive shifts in the location of the ancient Middle Eocene Gulf shores wiped out the *Cubitostrea sellaeformis* stock. When finally the Gulf sea readvanced in late Yegua and early Jackson time, it returned without a descendant of this ostreid stock. In distinction to the Claiborne group the deposits of the succeeding Jackson group in the Gulf Coastal Plain have not yielded any species of *Cubitostrea.* Common and leading oysters of the Jackson group belong to the genus *Gigantostrea* and to other genera but not to *Cubitostrea.*

GEOGRAPHIC DISTRIBUTION

The chain of species, *Cubitostrea perplicata* (Dall)—*lisbonensis* (Harris)—*smithvillensis* (H a r r i s)—*sellaeformis* (Conrad), evolved in a restricted area, the Tertiary Gulf of Mexico. With the exception of *C. sellaeformis* (Conrad) they did not spread beyond the confines of this sea. The *sellaeformis,* however, spread along the Atlantic shore of the Tertiary continent northward and is found as far

north as Virginia and Maryland. Tertiary deposits of the same age in England and France, well explored for fossils, have not produced any fossil of this branch of the Ostreidae, although *Cubitostrea* s.s. is common there. South American deposits are equally devoid of them. Outside of their home province there are no forms directly traceable to or closely comparable with these Gulf Coast species. The Gulf Coast chain of species is a purely provincial off-branch of the genus *Cubitostrea* s.l. This point is of importance in the discussion given below, because it precludes the assumption of extensive migrations into or from regions outside of the Tertiary Gulf of Mexico as explanations of some of the evolutionary features of the chain.

On the other hand, it is important to note that there existed in the Tertiary Gulf of Mexico, simultaneous and side by side with this chain, species of oysters that are true representatives of *Cubitostrea* s.s. The *sellaeformis* stock of *Cubitostrea* was never geographically separate from the typical branch of *Cubitostrea.*

The listing of the three species given above under *Cubitostrea (Cubitostrea)* does not imply a sequence of descent, but merely close relationship. The species *divaricata* (Lea) is not regarded as descended from *perplicata* (Dall), but both these species are regarded as derived from other, earlier Cubitostreas.

ECOLOGY AND POPULATION SIZE

Generally oysters are regarded as brackish water animals, and very little

thought is given to possible difference of salinity tolerance in the various species and genera of the family. Actually the range of salinity tolerance and optimum in which the oysters thrive are different for the various living species. There are species that inhabit brackish waters and species that do not. The former are more conspicuous, better known, and more **populous than the latter. Therefore, it** is not possible to conclude that the fossil species were brackish water inhabi**tants without investigating their geologic** occurrence and associations.

In many cases where data are available to the writer, the fossil oysters of the genus *Cubitostrea* are associated with fossils which were most probably truly **marine. Among these associates are com**pound and single corals, such as *Amphihelia, Balanophyllia, Endopachys, Flabellum, Madracis, Turbinolia,* etc., and echinoids such as *Fibularia texana* (Twitchell) and the sand dollar *Proscutella mississippiensis* (Twitchell). A similar observation was made by J. Gardner (1945), who observed *Cubitostrea sellaeformis* (Conrad) associated with many solitary corals referable to *Balanophyllia* and *Flabellum* in Mexico. Possibly some of the corals could endure brackish water temporarily, but it seems improbable that they thrived in a brackish water environment. These associates indicate that the environment was either truly marine or only slightly brackish or only temporarily brackish. Locally one or another of the associates is quite abundant in the oyster-bearing beds. They are not everywhere abundant, but at least a few specimens always can be found in the same bed in which the oysters are common. Another characteristic of these **beds is that they are not true oyster beds,** that is, beds composed overwhelmingly of one oyster species with hardly any admixtures of other fossils. On the contrary, in nearly all instances the oyster beds containing *Cubitostrea* are multispecific, that is, they contain a rich and varied faunule in which many different biologic groups are represented. It is

almost axiomatic that brackish water oyster beds are paucispecific, that is, composed of a very few species some of which may be represented by great hordes of individuals. Brackish water environment is a highly specialized environment into which only a few hardy species can penetrate. These few species are comparatively free of competition and enemies and they can multiply enormously. Paucispecific oyster beds are, of course, known from the Tertiary of the Gulf Coastal **Plain, but none of the beds under discus**sion are of this type.

The distribution of *Cubitostrea lisbonensis* **(Harris) is particularly interesting.** This species ranges from the typical, heavy-shelled form to a thin-shelled, more irregular form. The forms grade into each other laterally in the strata but never occur side by side in the same bed. Each **is geographically restricted. The heavy-**shelled form occurs in the lower Weches formation from central Leon County in east Texas eastward; the thin-shelled form occurs in the same beds westward from central Leon County. Also, as one ascends the stratigraphic column of the lower Weches formation, the heavy-shelled form grades upward into the thin-shelled form, but again the two do not occur together in the same bed. The heavy-shelled form occurs only in the lower part of the Weches formation, the strata of which are transgressive over the Queen City formation and rest on that formation with a widespread disconformity.

The typical, heavy-shelled form of *Cubitostrea lisbonensis* (Harris) occurs in the basal, transgressive strata of the Weches formation that show obvious traces of ancient wave action. There are well-rounded boulders of limestone up to 7 inches in diameter with molluscan bore holes, layers of rolled and worn fossil shells, and coarse glauconite grains. The **strata tend to be massive, showing few** traces of bedding. This seems to indicate that the sediments were repeatedly **disturbed, being reworked by waves and** by burrowing benthonic shore animals.

The robust build, the thickness of the

valves, the simplicity of rib pattern, the usual absence of fine, thin, squamate imbrications on the shell of the typical, heavy-shelled form of this oyster are apparently adaptations to life in the zone of wave action and shifting sediments. In this connection it should be noted that the attachment scar of the left valve of this oyster is small or missing. Evidently many individuals were not attached to anything but were lying free on or partly in the bottom sediment. The specimens with small attachment scars were fixed to objects in their youth, but in later life these objects were not sufficiently large and heavy to anchor the shells firmly and the animals assumed a virtually free position of repose. Similar conditions are found today among some living oysters.

Wherever the lower Weches strata merge upward into sediments which lack obvious signs of wave action, the heavy-shelled form of *Cubitostrea lisbonensis* (Harris) is replaced by the thin-shelled form. The beds which enclose this form are usually shaly and thinly bedded; the glauconite grains are fine. The thin-shelled form is usually associated with other delicate species, such as thin-shelled pectens and fragile bryozoans. Its surface ornamentation consists of fine, thin, squamate imbrications that would not have been preserved had the shell been exposed to wave action. Among its associates are corals, echinoids, and crabs, but these are usually represented only by a few specimens.

By comparison with the typical, heavy-shelled form of *Cubitostrea lisbonensis* (Harris), the thin-shelled form looks immature. The former is usually larger, and in a given stratum and locality the proportion of large adults to small juveniles is much greater for the heavy-shelled than for the thin-shelled form. A striking feature of the populations of the thin-shelled form in any one exposure is the great number of very young and juvenile shells. These individuals either were buried by sediment before reaching their full size and maturity or died from other natural causes without being incorporated into

the sediment immediately. The latter seems more probable because there are no signs of excessively rapid sedimentation in these beds and because in case of quick burial old and fully grown shells should be fairly abundant too. The scarcity of old and fully grown shells of this thin-shelled form is a most striking feature. It seems that the thin-shelled form lived on the fringes of the geographic range of the species where conditions were so unfavorable that only a few individuals reached adult size.

The chief ecologic distribution of this oyster species must have been in the zone of prevalent wave action and in normal marine waters. However, the thin-shelled ecologic form of this species must have lived in quiet waters which may have been slightly less saline than normal marine waters. At no place did even the thin-shelled form enter brackish water lagoons extensively and build large flourishing oyster beds.

Similar observations may be made on the other species of *Cubitostrea* of the *sellaeformis* stock. Hence it seems to the writer that the oysters of this stock did not enter brackish waters to a great extent and flourished chiefly in shallow truly marine waters in the lower part of the zone of wave action in front of the barrier beaches which separated the Tertiary Gulf of Mexico from its lagoons (Stenzel, 1945).

The oysters of the *sellaeformis* stock are found in great quantities at many localities, and these localities have a wide geographic distribution. For instance, the species *sellaeformis* is found from Mexico to Maryland. Geological field evidence indicates that these oyster-bearing layers are continuous, and their oyster content is always a large one. Hence there were at these times large populations present in an almost unbroken and continuous belt along the ancient shore. Whether these large populations were living continuously during the entire geologic time range of the *sellaeformis* stock, i.e., from Tallahatta time to the end of Cook Mountain time, it is not possible to

state definitely, because the chronologic record is incomplete. It is conceivable that during those times which left no geologic record of these oysters their populations had shrunk to small size. No evidence can be adduced to prove such an assumption or to make it likely. On the contrary, there must have been an ancient Gulf of Mexico shore at all times no matter where it was located owing to shore line shifts and no matter whether or not its shore deposits are now accessible to fossil collecting at the surface of the ground. Also this shore line must always have been a long one and must always have had plenty of locations favorable to these oysters. Wherever deposits made long ago seaward of the barrier beaches are exposed today at the surface of the ground, the oysters of the *sellaeformis* stock show large populations, and equally large populations should be assumed to have been present during all times of the evolution of this stock.

CONCLUSIONS

During the evolution of the *sellaeformis* stock the following features emerge or undergo progressive change: (1) size of shell increases, (2) thickness of shell increases, (3) auricles appear and increase in size, (4) shell outline changes from pronouncedly curved-triangular to moderately triangular to ovate, (5) valve commissure changes from plane to slightly arched to highly arched, and (6) costae gradually fade out on the adult shell portion. Some of these features clearly go hand in hand in their changes, for instance, shell size and shell thickness. In such cases a logical explanation of the changes can probably be found. Among other features interrelation is more obscure and explanations are more difficult to realize. All-in-all, explanations offered here must remain speculative owing to the nature of the material at hand. In the following paragraphs a discussion is given of the possible origins or causes of some of these changing characters.

Shell size and shell wall thickness go hand in hand to some extent in this group.

The entire chain of species has a tendency to thick shell walls except *C. smithvillensis* (Harris). Even the smallest of the four species, *Cubitostrea* (*Cubitostrea*) *perplicata* (Dall), is unusually thick-walled for an oyster. But the last species of the chain, *C. sellaeformis* (Conrad), is not only large but very thick-shelled; it is ponderous. Shell size and shell wall thickness must go hand in hand for structural strength of the shell at least in some cases; the shell must be thicker if it is to be larger and able to withstand similar mechanical stresses. The ponderous habit of *C. sellaeformis* (Conrad) therefore may be merely an end product of the process of size increase.

Paleontologists have recorded many instances of gradual progressive increase in the size of adults among various phylogenetic lives. It is a common trend[1] among various kinds of animals. In fact this evolutionary trend is so common and in many instances so obvious that it was noted by early observers and is now considered somewhat of a law of evolution. Cope and Deperet (1908) were the first to call attention to this trend. Most of the observations of this trend are on terrestrial vertebrates, and observations of that kind on mollusca are not as common. Newell (1942, pp. 19-20) called attention to it in his study of late Paleozoic Mytilacea [Mollusca, Pelecypoda], among which the genus *Myalina* admirably exemplifies this trend. Although Newell pointed out certain observational difficulties inherent in his material, he did come to the conclusion that progressive size increase of individuals in his material is so marked that it can be reasonably attributed to evolution. The size increase in the genus *Cubitostrea* also is regarded as an evolutionary feature, and the possibility that this size increase is merely

---

[1] Trend is used here as a summation of observable features showing progressive change in one direction only observable in a given chronologic chain of species. No connotation of momentum or drive is implied. Trend is merely a summation of observable or measurable properties.

due to chance ecological or habitat differences among the four species of *Cubitostrea,* as represented in the collections, is regarded as very small indeed. The importance of these confirmations of this evolutionary trend among mollusca, as shown by Newell and in the present paper, lies first in the extension of the presence of this evolutionary trend not only in terrestrial vertebrates, but also in mollusca, and second in the fact that in the mollusca this trend was active in enormously large interbreeding populations.

Assuming for the present that the evolution of the *Cubitostrea sellaeformis* stock took place in a series of successive and large interbreeding populations, the ideas developed by W. E. Castle (1932) assume added significance. Castle indicated that phylogenetic size increase may be caused by competition among individuals of the same species in a given population. The larger, or stronger, individuals or those obtaining a large size earlier in life than others are favored in competition with other individuals of the same neighborhood. Although the examples given by Castle were rabbits and mice, he regarded this consideration as equally well applicable to other kinds of animals. It is indeed probable that early attainment of large size may be quite advantageous among oysters living in a group or in a given vicinity, although it may not be possible to state definitely wherein the competition between the individuals may lie. This is then an example of the intraspecific competition of Huxley (1942) as opposed to extraspecific competition, that is, the competition between different species. Where intraspecific competition is strong and outweighs extraspecific competition, those features will be favored that are of advantage to the individual rather than to the species as a whole. Such individuals will have a greater survival value and will transmit their special distinctive features to succeeding generations. This may be the mechanism by which a gradual progressive size increase is accomplished in an evolving stock. It is also likely that intraspecific competition is fiercer in species with large contiguous populations than in those that have only small interbreeding populations. This then possibly is the significance of the combination of phylogenetic size increase and large interbreeding populations. Normally there is in each species some degree of intraspecific competition as well as the ever-present extraneous competition, and a species in a balanced condition, that is, one with a stabilized interbreeding population size, has a fine balance between effects and features of intraspecific and extraneous competition. The degree of intraspecific competition that can be tolerated without pernicious effect must depend on a multitude of factors, one of which may very well be the size of the interbreeding population.

It has been pointed out by Huxley (1942) that intraspecific competition favors features that are of advantage to the individual but not necessarily to the species as a whole. Long continued evolution under strong intraspecific competition may then lead to the appearance of features and their diffusion in the species that are either deleterious to the species as a whole or make the species vulnerable to extinction. It is possible that the great size attained by *Cubitostrea sellaeformis* (Conrad) was such a feature and predisposed the species to extinction as soon as rapidly changing conditions of one sort or another were encountered. The *C. sellaeformis* (Conrad) disappeared with the extensive shore line shifts at the end of Cook Mountain time and did not survive into Jackson group time.

SUMMARY

The fossil oyster *Cubitostrea sellaeformis* (Conrad) from the Middle Eocene of the Gulf Coast is a peculiarly shaped end member of a provincial and divergent off-branch of the genus *Cubitostrea.* The successional evolution of this off-branch can be traced through four separate species, which lack intergrading populations owing to gaps in the geologic record.

This off-branch evolved in the ancient Gulf of Mexico, where it existed in large

interbreeding populations, and became extinct with the extensive withdrawal of the sea at the end of the Middle Eocene. Peculiar features of this off-branch, culminating in the *C. sellaeformis* (Conrad), are increasing shell size and shell wall thickness, development of increasingly large shell auricles, increasing obliteration of the costae of the left valve, disappearance of the triangular shell outline, and development of a highly twisted shell.

The progressive increase in size in this off-branch recalls similar observations in other animal groups. It is considered probable that early attainment of large size may be quite advantageous among oysters living in a group or in a given vicinity due to intraspecific competition. Individuals which attain large size early in life may have greater survival value and may transmit their distinctive features to succeeding generations. This may be the mechanism by which a gradual progressive size increase is accomplished in an evolving stock. Intraspecific competition is probably fiercer in species with large contiguous populations than in those that have only small interbreeding populations. This may possibly be the significance of the combination of phylogenetic size increase and large interbreeding populations.

LITERATURE CITED

BRANDER, GUSTAV. 1766. Fossilia Hantoniensia collecta et in Musaeo Britannico deposita, pl. 8, figs. 84–85.

CASTLE, W. E. 1932. Body size and body proportions in relation to growth rates and natural selection. Science, 76: 365.

CLARK, W. B. 1896. The Eocene deposits of the middle Atlantic slope in Delaware, Maryland, and Virginia. U. S. Geol. Survey, Bull. 141: 87 and pl. 35, figs. 1a–d; pl. 36, figs. 1a–b.

CLARK, W. B., AND MARTIN, G. C. 1901. Systematic Paleontology, Eocene, Mollusca. Maryland Geol. Survey, Eocene: 192–193 and pls. 48–49.

CONRAD, T. A. 1832. Fossil shells of the Tertiary formations of North America, 1, no. 2: 27 and pl. 13, figs. 1 and 2.

COSSMANN, MAURICE. 1887. Catalogue illustré des coquilles fossiles de l'Eocène des environs de Paris, etc., fasc. 2. Soc. Royal Malac. Belgique Ann., 22: 199.

COSSMANN, M., AND PISSARRO, G. 1906. Iconographie complète des coquilles fossiles de l'Éocène des environs de Paris, 1: pl. 44, figs. 135–31.

DALL, W. H. 1898. Contributions to the Tertiary Fauna of Florida, etc. Wagner Free Inst. Sci. Trans., 3, pt. 4: 678.

DEGREGORIO, ANTOINE. 1890. Monographie de la faune éocènique de l'Alabama et surtout de celle de Claiborne de l'étage Parisien. Ann. Geol. Pal., livr. 7 & 8: 175–176 and pl. 18, figs. 15–20; pl. 19, figs. 1–6, 11–12; pl. 20, fig. 5.

DEPERET, CH. 1908. Les transformations du monde animal: 192–210.

GARDNER, JULIA. 1945. Mollusca of the Tertiary formations of northeastern Mexico. Geol. Soc. America, mem. 11: 80.

GARSTANG, WALTER. 1922. The theory of recapitulation: A critical restatement of the Biogenetic Law. Linnean Soc. Jour., 35, no. 232: 81–101.

HARRIS, G. D. 1919. Pelecypoda of the St. Maurice and Claiborne stages. Bull. Amer. Paleontology, 6, no. 31: 10–14 and pl. 6, figs. 2–12; pl. 7; and text fig. 1.

HEILPRIN, ANGELO. 1884. North American Tertiary Ostreidae. U. S. Geol. Survey, 4th Ann. Rept., appendix 1: 310–311 and pl. 62, figs. 1 and 2; pl. 63, fig. 1.

HUXLEY, JULIAN. 1942. Evolution, the modern synthesis. Harper & Brothers, Publishers, 386.

MORTON, S. G. 1833. Supplement to the "Synopsis of the organic remains of the Ferruginous Sand Formation of the United States." Amer. Jour. Sci. Arts, ser. 1, 24: 130.

MORTON, S. G. 1834. Synopsis of the organic remains of the Cretaceous group of the United States: 52.

NEWELL, N. D. 1942. Late Paleozoic Pelecypods: Mytilacea. Univ. Kansas, State Geol. Survey Kansas, 10, pt. 2: 19–20.

SACCO, FEDERICO. 1897. I molluschi dei terreni terziarii del Piemonte e della Liguria, 23: 12.

STENZEL, H. B. 1940. The Yegua problem. Univ. Texas Pub. 3945: 847–910.

STENZEL, H. B. 1945. Paleoecology of some oysters. Rept. Comm. on marine ecology as related to paleontology, 1944–1945, Div. Geol. Geogr., Nat. Res. Council, Washington, D. C.: 37–46. [Mimeographed.]