of Miocene time, the ancient Tethys Sea, along which climates were fairly uniform and warm, varying from tropical to desertic. Neither climate nor land barriers existed to prevent this species from spreading the full length of the seaway.

Toward the end of Miocene time and later, tectonic events produced several land barriers across the former seaway, breaking it up into separate sea basins, gulfs, or bays. The separate populations left behind in these broken remnants of the Tethys Sea gave rise to three, or possibly more, local species of *Crassostrea: C. angulata* LAMARCK, 1819, on the shores of Spain, Portugal, and Morocco; *C. cattuckensis* (NEWTON & SMITH, 1912) [=*C. madrasensis* PRESTON, 1916] on Indian Shores; and *C. gigas* (THUNBERG, 1793), China, Japan, to Sakhalin Island (see p. *N*1037-*N*1038). At least two of these three daughter species have retained the ability to grow to extraordinary size, a feature that so characterizes their ancestor *C. gryphoides.*

The earth movements that raised the land barriers and broke up the ancient Tethys Sea were synchronous. They were part of widespread tectonic disturbances that were synchronous as far as geologic evidence indicates. Therefore, the three above-mentioned species presumably arose simultaneously. This idea is contrary to the belief that one species can give rise to three descendent species only by two successive dichotomies.

Some aspects of the geologic history of the stock of *Crassostrea gryphoides* have been discussed by DOLLFUS, DOLLFUS & DAUTZENBERG, and RUTSCH (1915; 1920, p. 465-471; 1955). Many formal species names have been proposed and are nomenclaturally available for this species. Some of the names were published in the same work by VON SCHLOTHEIM (1813). The species name used here has been selected by RUTSCH, whose decision as the first reviser must be respected according to *Code* (1961, 1964) Article 24 (a)(i).

CLASSIFICATION

CONTENTS

HISTORICAL REVIEW

LINNÉ, 1758

LINNÉ (1758) described only seven living species that today are regarded as true oysters, but he described them under three generic names: *Ostrea,* with three species of true oysters; *Anomia,* with one; and *Mytilus,* with three. On the other hand his concept of the genus *Ostrea* was very broad, including 32 nominal species now distributed among four bivalve families (DODGE, 1952).

He distinguished four subdivisions in his genus *Ostrea,* of which the fourth, namely *"Rudes vulgo Ostreae dictae"* [=the Rough ones, commonly called oysters], was obviously intended as the typical core of the genus but still contained nine species. Of these nine, only three are regarded today as true oysters, one of them is unrecognizable, and the remaining five are placed in other families. One of the three true oysters is *Ostrea edulis,* which was made the type species of the genus by ICZN Opinion 94 (Oct. 8, 1926) and placed on the Official List.

Obviously, LINNÉ's concepts of his genera *Ostrea, Anomia,* and *Mytilus* had many points needing corrections. Such corrections were made by BRUGUIÈRE and LAMARCK.

BRUGUIÈRE, 1791

Early death took the author before his work could be finished. His text is incomplete, none covering the Testacea or shelled animals, but he published 189 engraved plates. On these well-arranged plates, attempt was made to group together on each plate only those species that the author regarded as closely related. For example, pl. 187 has five figures depicting oysters that have serrate valve commissures; pl. 189 contains six figures of oysters that have a shell devoid of radial ribs but have a strongly curved left beak of either exogyroidal or gryphaeoidal spiral curvature. The pl. 178-189 have as their headings "Huitre *Ostrea*" and a line at their bottom reads: "Histoire Naturelle, Vers Testacés à Coquille Bivalve irregulaire" [Natural History, Shell-bearing Worms with irregular Bivalved Shell]. These plates depict what BRUGUIÈRE considered to be the genus *Ostrea.* It obviously included various genera of true oysters and some Malleidae and Pectinidae.

Nevertheless, BRUGUIÈRE's work foreshadows LAMARCK's (1801) classification. For instance, pl. 189 foreshadows LAMARCK's *Gryphaea,* and the species illustrated on it were given species names and listed under that genus by LAMARCK. The importance of BRUGUIÈRE's work rests on his status as a precursor of LAMARCK. His classification is based on superficial, purely external morphology.

LAMARCK, 1801

As BRUGUIÈRE's successor in Paris, LAMARCK (1801) used BRUGUIÈRE's unfinished work judiciously to propose new genera. Thus he used Plate 189 of BRUGUIÈRE (1791) to distinguish the genus *Gryphaea.* By and large, he relied on a few superficial, external features to discern genera.

Nowhere is this as apparent as in his treatment of *Gryphaea* LAMARCK, 1801. From the species described or listed by him under this genus, it is obvious that the definitive feature used to distinguish this genus from other oysters was its hooked left beak. It made no difference whether the beak was spiral gryphoidally—that is, mainly orthogyrally—or spiral exogyroidally—that is, mostly opisthogyrally. Therefore, exogyrine oysters were included in his original list of species and in his concept of *Gryphaea.*

The original list of species of *Gryphaea* Lamarck, 1801, included also *G. angulata* Lamarck, 1801, a *nomen nudum* attached to an undescribed living southern European species. It remained a *nomen nudum* until 1819. It was based on a freakish left valve (Delessert, 1841, pl. 20, fig. 3a-c) which had grown curved so that the umbonal region became curved over to the right side and was vaguely similar to the incurved left beaks of fossil Gryphaeas. This one feature led Lamarck to judge that the species must be placed in the same genus with these fossils (Fig. J71), which had been known for many years to pre-Linnean authors as *gryphites* (the postfix *-ites* was customarily used for taxa exclusively fossil). Because Lamarck thought now to have discovered a living species of *gryphites,* he decided to coin a generic name without that postfix and invented the new generic name *Gryphaea.* However, Lamarck's *"Gryphaea" angulata* is now *Crassostrea angulata* (Lamarck).

Lamarck (1801, p. 400) also described the new genus *Planospirites* and its sole species *P. ostracina,* based on a single right valve collected by Faujas Saint-Fond (1799 [1802?]) at St. Pietersberg south of Maastricht, Zuid Limburg, Netherlands, from the "tuffeau de Maestricht," a crumbly, porous lime grainstone of Maastrichtian age (see Fig. J96). There, the two valves of the species are found very rarely in natural juxtaposition, and left valves are much rarer than right ones. For that reason only a right valve was obtained and described by Lamarck, and he was so puzzled by it that he described it as a univalve shell, that is, a gastropod, under "Genres incomplètement connus." The type specimen has been figured by Faujas (1802?, pl. 22, fig. 2) and by Jourdy (1924, p. 7-8, pl. 1, fig. 1). The figure given by Faujas has been called *Ostracites haliotoideus* by von Schlotheim (1820, p. 238).

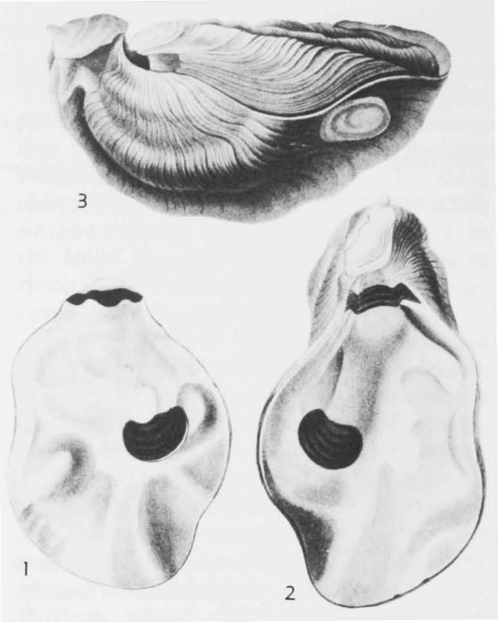

Fig. J71. *Crassostrea angulata* (Lamarck, 1819), species living on southwestern coasts of Europe, ?×1 (after Delessert, 1841). [Lectoholotype of *Gryphaea angulata* Lamarck, 1819.]—*1.* RV int.—*2.* LV int.—*3.* Both valves viewed from posterior side.

Actually left valves were probably available to Faujas and to Lamarck, but were not recognized as belonging with the right valves, because the two are so different and occur disconnected. The left valve of an exogyrine oyster figured by Faujas (1802?, pl. 28, fig. 5) under the name *"rastellum"* quite probably is a left valve belonging with *Planospirites ostracina* (see Fig. J96,*1*). These uncertainties have remained unresolved, although good topotype materials are available at Maastricht. As a consequence, authors have hesitated to use *Planospirites,* although it is a good exogyrine genus.

LAMARCK, 1819

Lamarck gave Bruguière credit for having separated the scallops from the oysters, both of which Linné had included in one taxon, *Ostrea* of Linné, 1758, and for recognizing them as natural taxa and defining their principal limits. He himself separated *Vulsella, Podopsis,* and *Gryphaea* from *Ostrea,* as defined by Bruguière, and thereby restricted *Ostrea* more closely to its natural limits. Restrictions and sharpened definitions of genera involved are indeed a major part of his accomplishments.

The oysters *(les Ostracées)* were divided by Lamarck into two subdivisions: 1) ligament semi-internal, shell foliaceous, attaining often great shell-wall thickness, and 2) ligament internal, shell thin or paper-like. Subdivision 1) contained *Gryphaea, Ostrea,* and *Vulsella;* subdivision 2) *Placuna* and *Anomia. Ostrea* itself was divided into two unnamed sections: A) Valve margins simple or undulate but not plicate and B) valve margins distinctly plicate, corresponding mainly to the Lophinae of today.

To *Gryphaea* were assigned 12 species, one living and 11 extinct; to *Ostrea* section A) 32 living and 18 extinct species; to *Ostrea* section B) 16 living and 15 extinct species. Altogether, Lamarck described or listed 94 nominal species now known to represent oysters, but many species were overnamed. For instance, *Ostrea edulis* Linné, 1758, was described under at least four species names, and *Crassostrea virginica* (Gmelin [1791]) received three names: *borealis, canadensis,* and *virginica,* all three under *Ostrea* section A). Because of the great variability of oysters, such cases of overnaming were to be expected.

More serious were errors in generic assignments. *Anomia anomialis* (Lamarck, 1819) from the Calcaire Grossier (Lutet.) near Paris, France (Clerc & Favre, 1910-18, pl. 28, fig. 102-105, and pl. 29, fig. 106-107) [=*A. tenuistriata* Deshayes, 1832, v. 1, p. 377] was originally described as *Ostrea* section A) *anomialis. Pycnodonte vesicularis* (Lamarck, 1806) from the Chalk (Campan.) at Meudon near Paris, France, was described under two names, as *Podopsis gryphoides* Lamarck, 1819 (Clerc & Favre, 1910-18, pl. 14, fig. 46-47) and as *Ostrea* section A) *vesicularis* Lamarck, 1806 (Clerc & Favre, 1910-18, pl. 26, fig. 94-95). Another oyster was described as *Chama laevigata* Lamarck, 1819 (Clerc & Favre, 1910-18, pl. 36, fig. 263); it is the same as *Ch. haliotoidea*+*Ch. conica* James Sowerby, 1813 (v. 1, p. 6, pl. 25, fig. 1-5 and p. 69, pl. 26, fig. 3) from St. Mary Donhead, Wiltshire, Eng., probably from Cenomanian beds. It is best to call it *Planospirites haliotoidea* (Sowerby). In this case, Lamarck probably was influenced in his generic assignment by Sowerby's work.

RAULIN & DELBOS, 1855

The classification proposed by Raulin & Delbos, 1855, was restricted to oysters found in the Tertiary beds of the Aquitaine region of France. It was explicitly designed to take care of the considerable number of species found there. Accordingly, they not only recognized the three widely accepted taxa *Exogyra, Gryphaea,* and *Ostrea* as subgenera, but also introduced new minor subdivisions, which they called variously *"coupures"* or *"groupes"* or *"sections,"* wherever the number of closely related species threatened to become too large and unwieldy. In this fashion, they acknowledged one of the major functions of classification, namely, to bring order out of chaos and to provide a logical hierarchy.

The criteria used by Raulin & Delbos as bases for their classification were those they judged to be least variable, if one studies a variable series of shells of a given species. They were two: 1) morphology of the ligamental area *(configuration de la surface ligamentaire)* which in their definitions they called beak *(crochet)* for short, and 2) external ornamentation of the shells. They noted that the proportions of the three subdivisions of the ligamental area maintain great constancy in a series of shells of a given series, but that these proportions are much diversified among the various species. They remarked that previous authors had attached no great importance to this feature. In discussing external ornamentation, they mentioned that the two valves have either congruent or incongruent ornamentation. Raulin & Delbos were the first to use a structural feature that is quasi-internal (i.e., the ligament) as a basis of classification within the oyster family. Their methods were quite modern in that they took into account individual variability. These methods were the first attempt among oyster paleontologists to relinquish the typological approach to classification.

Under *Ostrea (Ostrea)* only eight sections were named. Raulin & Delbos resorted to names in the plural and consistently referred to them in the plural. Because of the consistent use of the plural, these names are not available for formal nomenclature (*Code* Article 8D). For each of the eight sections they designated a type species through tautonymy, and each section was defined by a brief descriptive text. Their classification of the *"famille des Os-*

tracées," consisting of the single genus *Ostrea,* is as follows:

Classification of Ostrea *by Raulin & Delbos (1855)*

- Genus Ostrea
  - Subgenus Ostrea (Exogyra)
    - Section A: smooth species
    - Section B: plicate or costate species
  - Subgenus Ostrea (Gryphaea)
    - Section A: smooth species
    - Section B: plicate or costate species
  - Subgenus Ostrea (Ostrea)
    - Vesiculares: The two valves smooth, beak short
    - Laterales: left valve smooth, concentric growth imbrications *("plis")* on the right valve
    - Virginicae: left valve has slightly crinkled or plicated growth imbrications, beak much prolonged
    - Edules: radiating plications on the left valve, right valve smooth, beak large and short
    - Flabellulae: radiating plications on the left valve, right valve smooth, beak narrow and small
    - Cornucopiae: costae on the left valve, right valve smooth
    - Undatae: rounded costae on the two valves
    - Carinatae: angular plications on the two valves

Judging by their type species and definitions, the eight new sections of *Ostrea (Ostrea)* may be interpreted in modern terms as follows: Vesiculares, *Pycnodonte* Fischer de Waldheim, 1835; Laterales, *Gryphaeostrea* Conrad, 1865; Virginicae, *Crassostrea* Sacco, 1897; Edules, *Ostrea* Linné, 1758, *s.s.;* Flabellulae, *Cubitostrea* Sacco, 1897; Cornucopiae, *Saccostrea* Dollfus & Dautzenberg, 1920; Undatae, dubious; Carinatae, Lophinae Vyalov, 1936.

It can be seen from dates given above that Raulin & Delbos were largely ahead of their time and defined but did not formally name well-founded genera, which were named by others many years later.

MISCELLANEOUS AUTHORS, 1758-1886

Several generic names that are nomenclaturally acceptable and turn out to be useful were introduced in the years following Linné's (1758) work. Nearly all of them, however, were incidental introductions, not based on any improved methods of description or discernment of generic features; thus they did nothing to advance methods employable in classifying oysters. The exceptions are *Exogyra* Say, 1820, *Amphidonte* Fischer de Waldheim, 1829, and *Pycnodonte* Fischer de Waldheim, 1835.

Planospirites Lamarck, 1801, had been the first exogyrine oyster genus to receive a name, and *Exogyra* Say, 1820, was the second one. The former remained a dubious taxon for a long time and even was considered to be a gastropod. Also, Lamarck failed to give an illustration of his genus. These facts militated against an understanding of the significance of this genus.

In contrast, *Exogyra* Say, 1820, was well described and illustrated, so that it attained acceptance right away and became the leading genus of its subfamily. Additional exogyrine genera were introduced by Bayle, 1878, but the lack of descriptive definitions of them slowed down their general acceptance by later authors.

Fischer de Waldheim was the first to note chomata on the commissural shelves of oysters. Both *Amphidonte* and *Pycnodonte* were named on the basis of chomata and their arrangement (see Fig. J80, J93). Thus he was the first to call attention to an internal shell feature important in classification. Succeeding authors paid little attention to these features until Ihering (1907) and Suter (1917).

Gryphaeostrea Conrad, 1865, was proposed in somewhat careless fashion. Only through the efforts of Meek (1876, v. 9, p. 11) was Conrad persuaded to furnish a descriptive definition. Perhaps, the situation is explainable by Conrad's rather advanced age (62 years in 1865). At the time Conrad seems to have been influenced by the theory of evolution and searching for genera that might be interpreted as evolutionary missing links. For these he used combination names such as *Gryphaeostrea* and *Ostreanomia. Gryphaeostrea* probably was so named because he believed it to be transitional between *Gryphaea* and *Ostrea.* If this was his assumption, it was erroneous. The name is rather unfortunate (see Fig. J98).

Pernostrea Munier-Chalmas, 1864, was based on material misunderstood by its author, who believed it to be related to both *Perna* and *Ostrea* or at least similar to both (see p. *N*975, N1104, Fig. J78). Nevertheless, the author must be commended for trying to use the structure of the ligamental area to discern genera and their limits.

FISCHER, 1880-87

FISCHER's *Manuel de Conchologie* furnishes a convenient summary of the efforts of conchologists and paleontologists since LINNÉ (1758) and must have been an important and very useful book in its time. His descriptions of the various taxa in the Ostreidae were careful, although the classification given by him suffered by his refusal to take note of internal shell features and by his corresponding reliance on external, conchological features in nearly every case in this family. Only in the case of *Exogyra,* which he treated as a subgenus of *Ostrea s.l.,* did he use a feature that is quasi-internal. The topography of the ligamental area in *Exogyra* was very well described.

He recognized as genera: *Ostrea, Heligmus, Naiadina,* and *Pernostrea.* The following were accepted as subgenera of *Ostrea: Ostrea, Chalmasia, Alectryonia, Gryphaea,* and *Exogyra.* His classification is vitiated by the inclusion of *Heligmus, Chalmasia,* and *Naiadina,* which are now placed in other families. His scheme overemphasized the apparent (but not real) differences between *Ostrea* and *Pernostrea* and undervalued those between *Ostrea, Exogyra,* and *Gryphaea,* which he renamed *Liogryphaea.* As long as classification was based almost exclusively on external features, too few generic characteristics were taken into account to allow proper evaluation of the taxa. Such internal features as the muscle imprints were easily available on simple inspection, and so was the vesicular shell structure, but they were ignored.

FISCHER started a new nomenclatural trend by proposing *Liogryphaea* as a new section of *Ostrea (Gryphaea).* It was erected for *Gryphaea arcuata* LAMARCK, 1801, as type species by monotypy (see p. *N*1099). The unfortunate effect was that many oyster biologists then started using *Gryphaea* for the living genus, which correctly must be called *Crassostrea* SACCO, 1897 (STENZEL, 1947; GUNTER, 1950; GUNTER, 1954). The nomenclatural question has been settled by ICZN Opinion 338 (March 17, 1955) in which *Liogryphaea* was rejected officially.

SACCO, 1897

In his great monographic treatment of the Tertiary faunas of the provinces Piemonte and Liguria in northwestern Italy, SACCO (1897a, p. 99-102, and 1897b, p. 3-30, pl. 1-9) minutely described many species and proposed four new subgenera of *Ostrea (Crassostrea, Cubitostrea, Cymbulostrea,* and *Gigantostrea),* all based on the usual external conchological features. Although RAULIN & DELBOS, 1855, had already separated the Edules from the Virginicae, SACCO made a clear distinction between *Ostrea s.s.* and *Crassostrea* by giving them formal subgeneric names and good descriptions (see Fig. J101, J109). His *Cubitostrea* is a well-defined monophyletic taxon, for which he gave a phylogenetic tree of the species from the mid-Eocene through Pliocene. *Cymbulostrea* does not differ from *Ostrea s.s.* sufficiently to deserve naming (see Fig. J111). *Gigantostrea* is the same as *Pycnodonte* except that it has a more irregular shell growth pattern than most well-known species of *Pycnodonte* (see Fig. J81). However, the two respective type species are quite similar in their shell growth pattern.

Crassostrea and *Ostrea s.s.* were distinguished by him on a subgeneric level only. Today we know that the biologic differences are much larger, making a generic distinction between them necessary. However, it is remarkable that a valid distinction between the two taxa can be made without the help of any neontological information, that is, purely on the basis of paleontological data.

Gryphaeostrea, which SACCO called *Exogyra (Aetostreon?),* was very well discussed by him (see Fig. J98). A phylogenetic tree was outlined for species from the Cretaceous to the Miocene. The phylogeny probably is correct. In other words, SACCO was the first frankly to outline phylogenetic trees for oyster species, and these phylogenies are a credit to his work.

DOUVILLÉ, 1886-1936

The features of oysters valuable in classification were reported in several papers by

Douvillé (1886-1936). In most of these studies oysters were treated only incidentally, but the results of his work turned out to be quite important.

In the first study (Douvillé, 1886), he examined the *Gryphaea* homeomorph *Aetostreon imbricatum* (Krauss, 1843) from the Neocomian of the Kingdom of Choa, now a part of Abyssinia (Fig. J63). In order to find its correct systematic position among oysters, he investigated the ligament and ligamental areas and demonstrated the structural differences in these features between *Ostrea s.l.* (=Ostreinae of today), *Gryphaea s.l.* (=Gryphaeinae), and *Exogyra s.l.* (=Exogyrinae). He traced the evolution of the exogyrine ligament and ligamental areas from the Jurassic to the Cretaceous. Thereby he laid the foundation for definition of the Exogyrinae, which has been accepted by later authors. Douvillé's (1886) conclusions concerning *Aetostreon imbricatum* (Krauss, 1843) were followed by Kitchin (1908) (see p. *N*1066-*N*1067).

In a later paper (Douvillé, 1911), he reviewed the various phyletic branches of the Exogyrinae and their stratigraphic distributions. Although this study is not strictly devoted to classification, it clearly shows his ideas of oyster taxonomy. He distinguished *Liogryphaea* Fischer (=*Gryphaea* of today) and listed species from the Hettangian to the Oxfordian. To judge from the species listed by him, he very well recognized *Pycnodonte,* but unfortunately used the then-current, emended name *Pycnodonta.*

In one of his last publications Douvillé (1936b) turned to the study of shell structure. He was the first to recognize that vesicular shell structure was an important diagnostic feature of supraspecific importance. Thus he laid the foundation for all future work on the Pycnodonteinae (see p. *N*986-*N*987, *N*1105).

IHERING, 1907; SUTER, 1917

Ihering was second after Fischer de Waldheim to pay serious attention to the chomata as a means of classifying oysters. To accommodate the many extinct and living Argentinian species of *Ostrea,* which he was studying, he proposed the subgenus *Eostrea* Ihering (1907, p. 42) to include all species of *Ostrea* having chomata on the internal valve borders. Without designating a type species he included in *Ostrea (Eostrea)* the Eogene species from Patagonia, without naming any of them specifically, and the two living Argentinian species *O. puelchana* d'Orbigny, 1842 (*Paléontologie* v., p. 162), and *O. spreta* d'Orbigny, 1846 (Mollusca v., p. 672) [=*O. equestris* Say, 1834]. Cossmann (1916, p. 12) pointed out that all species included by Ihering in *Eostrea* were really members of *Ostrea s.s.,* presumably because *Ostrea s.s.* has the same sort of chomata. Iredale (1939, p. 394) designated *O. puelchana* as the type species of *Eostrea* and since this species is doubtless well placed in *Ostrea s.s.,* Ihering's *Eostrea* is a junior subjective synonym of *Ostrea* (see Fig. J113).

Suter (1917, p. 86), who was well aware of Ihering's publication and Cossmann's criticism, sought to save the basic idea underlying Ihering's attempt at classifying *Ostrea* by proposing the subgenus *Anodontostrea* to include all species of *Ostrea* lacking chomata. Without designating a type species he included in *Ostrea (Anodontostrea)* nine species, among them *"O. angasi* [*angassi*] Sowerby," which later was designated as the type species by Finlay (1928, p. 264) (Fig. J36).

This oyster, *Ostrea angassi* G. B. Sowerby (1871, pl. 13, fig. 28), lives around Tasmania and along the south coast of Australia from the Clarence River in northeastern New South Wales to the Swan River at Perth, Western Australia. However, this species, too, has chomata (Thomson, 1954, p. 144) and falls into *Ostrea s.s.,* so that *Anodontostrea* must be a junior subjective synonym of *Ostrea s.s.* (see Fig. J113).

Just why Suter overlooked the chomata in this case is not known. The species has only a few chomata. Older specimens possibly have obsolescent chomata, easily overlooked. Thus all these efforts come to naught, although the underlying idea that chomata are a feature important to classification is sound.

JOURDY, 1924

General Jourdy gave in this monograph (Jourdy, 1924) an excellent summary of all knowledge about exogyras published before 1924.

His investigation of the hinge and ligamental areas of exogyras revealed that there are unmistakable peculiarities differentiating them from other oyster species and from individual oysters that fortuitously have spiral opisthogyral ligamental areas. The structural differences make it quite certain that exogyras differ profoundly from other oysters and must be a phylogenetic unit. They cannot be placed under *Ostrea,* as had been done by DESHAYES, D'ORBIGNY, COQUAND, and others, who recognized only one grand genus *Ostrea sensu latissimo.*

JOURDY discussed evolution of the hinge structure of the exogyras from the simpler beginnings in the Jurassic to its most evolved stage in the Late Cretaceous, which he called *"stade anodonte"* and *"stade monodonte,"* respectively. The distinction is based on the appearance of an auxiliary interlocking structure, consisting of a broad, shallow, pitted or striated depression on the left and a corresponding striated protuberance on the right valve, situated on the dorsal ends of the commissural shelves near the posterior margins of the curved spiral ligamental areas. This structure had been described by STEPHENSON (1914, p. 47) (see Fig. J90).

JOURDY emphasized the structural unity of all exogyras and thereby laid the foundation for regarding them as a distinctive taxon, ultimately to be recognized as a subfamily by VYALOV (1936).

In adding information on Jurassic Exogyrinae to the seven *"groupes"* which PERVINQUIÈRE (1912, p. 173-174) had distinguished among Cretaceous Exogyrinae of France and North Africa, JOURDY came to the conclusion that eight phyletic branches are discernible among the Exogyrinae. For these he did not propose any formal names, but showed where the older names *Aetostreon, Rhynchostreon,* and *Ceratostreon* would fit in, and for each phyletic branch he named several member species.

JOURDY (1924, p. 31, 96-97, pl. 4, fig. 2 and pl. 11, fig. 1, left row), without mentioning the genus *Gryphaeostrea* CONRAD, listed and discussed a few Miocene species of that genus, particularly *G. ricardi* (COSSMAN & PEYROT, 1914) from early Burdigalian beds at Saucats, Gironde, France. He called them all *Exogyra* and claimed that they showed generic features of *Exogyra s.l.* clearly enough to prove that they should be included in *Exogyra,* although their generic position has been contested.

ORTON, 1928; NELSON, 1938; GUNTER, 1950

For many years, oyster biologists were so preoccupied with their studies of local biological phenomena in living commercial oysters that they did not participate in discussions of generic classification. Rather, they remained content to classify all oyster species as *"Ostrea."* However, during that period, one after another biological difference between the common commercial oyster species was encountered. Finally, it became obvious that numerous biological differences demonstrated the presence of two distinct groups of species and that these demanded recognition in classification as separate taxa.

ORTON (1928) was first to enumerate the biological differences between the two groups. He recognized that these differences were profound enough to demand separate generic or subgeneric names. He distinguished a "Type I" taxon and stated that it has a subcircular shell outline, large eggs, larviparous propagation [he meant incubatory, instead], and monoecious sexuality, that it spawns at temperatures around 15°C., and that its several species flourish in temperate regions. He listed only three species under "Type I," one of which was *Ostrea edulis* LINNÉ. "Type II" oyster species, he noted, have a dorsoventrally elongate shell, small eggs, and nonlarviparous adults [he meant nonincubatory]; individual oysters are dioecious (hermaphroditic) and spawn around 20°C.; the various species flourish in tropical or subtropical regions. Under "Type II" he listed three species, of which one was *O. virginica* GMELIN.

By now it has been shown that both groups are dioecious and protandric alternating hermaphrodites. However, among incubatory oysters their successive sex phases overlap so much that at first it was difficult to prove that sex phases are successive and overlap very much, rather than that they are contemporaneous throughout (see p. *N*961).

NELSON (1938, p. 55) pointed out that *Crassostrea virginica* lives in the Gulf of St. Lawrence region of Canada, where individuals growing in intertidal situations freeze solid for four to six weeks in the winter. Therefore, "Type II" oysters could not all be called tropical to subtropical. Although the geographic distributions were very poorly stated by ORTON, some real, fundamental differences distinguish geographic ranges of the two groups (see p. *N*1037-*N*1038).

ORTON was so impressed by these differences that he proposed radical changes in names for the species: *Ostrea edulis* to *Monoeciostrea europa* and *O. virginica* to *Dioeciostrea americana.* IREDALE (1939, p. 394) designated *O. edulis* as the type species of *Monoeciostrea,* making this taxon a junior objective synonym of *Ostrea.* STENZEL (1947, p. 173) designated *O. virginica* as the type species of *Dioeciostrea,* thus fixing it as a junior objective synonym of *Crassostrea.* In this fashion ORTON's radical nomenclature was eliminated.

ORTON's proposals had been based on an erroneous philosophy of nomenclature. Generic names need not be coined in manner reflecting generic descriptions. After all, they are merely devices for information retrieval from the scientific literature. Actually the names proposed by ORTON turned out to be misleading, because it is now known that all oysters are dioecious [=hermaphroditic], as was pointed out by GUNTER (1950, p. 440).

In summary, ORTON's work was the first attempt, and a successful one, to infuse biological information into the pool of basic data on which classifications are based. As such it was very important, and incidental data and ideas of his that turned out to be unacceptable are unimportant and were corrected very soon. To the surprise of many, the conchological and paleontological differences between the two taxa noted before ORTON's work (1928) was published were found to be quite reliable guides to classification. The result of this experience was to produce considerable confidence in the reliability and validity of conchological and paleontological investigation methods.

The chief result of ORTON's studies, namely, that oyster species are divisible into two natural groups was fully supported by NELSON, who added to it by showing that "Type I" oysters lacked a promyal passage, whereas "Type II" oysters have such a passage, which he called promyal chamber. He believed that the differences between the two deserved recognition in taxonomy on the genus level (NELSON, 1938, p. 55) and suggested *Ostrea* for "Type I" of ORTON and *Gryphaea* for "Type II." In selecting the latter name he followed FISCHER (1880-87). At this stage, the question of proper generic names came to the fore.

GUNTER (1948, 1950) extensively discussed this question and several other problems concerning the family with STENZEL, who had just published his nomenclatural synopsis of the Ostreidae (STENZEL, 1947) and was in a position to help. GUNTER (1948) checked STENZEL's conclusions independently and published his concurrence with them. GUNTER (1950) reiterated these nomenclatural conclusions and added much information on features that separate the two groups of oyster species. In a table he contrasted the two with the aid of ten characters, also adding several more species to "Type I" and "Type II." Through STENZEL (1947) and GUNTER (1950) the correct generic name, *Crassostrea,* for *C. virginica* (GMELIN) became widely known to oyster biologists and has now been adopted by most of them.

ARKELL, 1934; ARKELL & MOY-THOMAS, 1940

In a study of oysters of the Fuller's Earth (Jur.) in western Europe, ARKELL (1934) proposed a new, experimental system of classification and nomenclature for some of the Jurassic and Cretaceous oysters. His revolutionary system was based on then-prevailing ideas of phylogeny of *Gryphaea* and its descendants. His premise was that "it has long been realised that all the Mesozoic species of oysters conveniently called *Gryphaea* do not form a monophyletic group or genus in the ordinary sense of the word" (ARKELL, 1934, p. 58). He fully approved the ideas concerning *Gryphaea* as a polyphyletic form-genus propounded by KITCHIN and TRUEMAN (compare p. *N*1062-*N*1078). ARKELL considered

Experimental "Rationalised" Classification of Jurassic and Cretaceous Oysters Proposed by Arkell (1934)

OLD NAMES	"RATIONALISED" NAMES
Pycnodonta marcoui (HILL & VAUGHAN)	*Ostrea (Marcoui) gryphaea*
Pycnodonta wardi (HILL & VAUGHAN)	*Ostrea (Marcoui) catinula*
Gryphaea dilatata SOWERBY	*Ostrea (Dilatata) gryphaea*
Ostrea (Catinula) alimena COSSMANN	*Ostrea (Dilatata) catinula*
Gryphaea bilobata SOWERBY	*Ostrea (Bilobata) gryphaea*
Ostrea (Catinula) matisconensis LISSAJOUS	*Ostrea (Knorrii) catinula* mut. *matisconensis*
Ostrea (Catinula) knorrii VOLTZ	*Ostrea (Knorrii) catinula*
Ostrea (Liostrea) subrugulosa MORRIS & LYCETT	*Ostrea (Acuminata) catinula*
Ostrea (Liostrea) hebridica var. *elongata* DUTERTRE	*Ostrea (Acuminata) virgula* mut. *elongata*
Ostrea (Liostrea) hebridica FORBES	*Ostrea (Acuminata) virgula* mut. *hebridica*
Ostrea (Liostrea) acuminata SOWERBY	*Ostrea (Acuminata) virgula*
Gryphaea incurva SOWERBY	*Ostrea (Incurva) gryphaea*
Ostrea (Liostrea) irregularis VON SCHLOTHEIM	*Ostrea (Incurva) catinula*
Ostrea (Liostrea) liassica STRICKLAND	*Ostrea (Incurva) virgula*
Pycnodonta corrugata (SAY)[1]	*Ostrea (Corrugata) gryphaea*[1]

[1] Added by ARKELL & MOY-THOMAS (1940, p. 404).

it needful to reconcile nomenclature of various Jurassic and Cretaceous gryphaeas with these ideas by proposing experimental nomenclature which he claimed to be "rationalised" (ARKELL, 1934, p. 64) and better than the conventional one. His scheme is outlined in the tabulation above.

This experimental nomenclature did away with the hierarchy of old names that followed the *Code* and consisted of names for genus, subgenus, and species. The "rationalised" names proposed in their stead, admittedly under disregard of the *Code,* consisted of trinomina: 1) the single genus *Ostrea,* 2) a name representing lineages, written as a subgenus of *Ostrea*, and 3) a stage-designation. Only three stage-designations were admitted: *virgula, catinula,* and *gryphaea,* based merely on external shell form. ARKELL was convinced that the phylogeny of every lineage progressed in this fashion: Shape like *virgula* (an exogyrine species) to shape resembling that of a *Catinula,* to shape similar to a *Gryphaea.* However, no real proofs of such iterative phylogenies exist. The idea was strictly an assumption.

ARKELL & MOY-THOMAS (1940) are the only authors who gave serious consideration to ARKELL's (1934) scheme, even adding one more "rationalised" name. No other authors adopted or explicitly approved the scheme. The new subgeneric names were declared unavailable by STENZEL (1947), because they did not fulfill Article 13(a) of the *Code* in that (after 1930) the two authors failed to give characters differentiating the taxa.

The basis of the ARKELL revolutionary system of oyster classification is presumed iterative evolution in the Gryphaeidae. Such iterative evolution never was more than an assumption, however, and therefore, it furnished an insecure basis for an elaborate classificatory system. If it can be shown that the concept of iterative evolution does not apply, the whole system collapses. It is better to stay with the conventional system, because the latter is by experience very flexible and adaptable to various interpretations of phylogeny and evolution. Rather use an imperfect but adaptable conventional system than propose a scheme that at the moment seems less imperfect, but requires profound reconstruction whenever one conceives new ideas of phylogeny and evolution.

VYALOV, 1936, 1937, 1948a

VYALOV (1936, 1937) deliberately set out to resolve the major problems of oyster classification. The principal taxonomic character which he selected for use is structure of the upper valve. In addition, he planned to distinguish sculpture patterns, form of the beaks, and general shape of the shell. Accordingly, he divided oysters into four subfamilies: 1) Ostreinae—both valves convex, lower valve smooth or costulated, upper valve smooth, containing 2 genera, 14 subgenera, and 11 sections; 2) Gryphaeinae—lower valve convex and smooth or costulated, upper valve flat or concave, containing 2 genera, 5 subgenera, and 6 sections; 3) Lophinae—both valves radially sculptured, valve commissure plicate or undulate, containing 1 genus, 3 subgenera, and 7 sections; 4) Exogyrinae—umbones of both valves spirally inrolled, umbonal spire of upper valve not produced beyond valve outline and turned downward, forward, or upward, containing 3 genera, 3 subgenera, and 4 sections. All together he recognized 61 taxa above species rank and below that of subfamily. Of these, 27 taxa were given new names.

Vyalov (1936, 1937) provided each taxon with a very short descriptive definition and a type species, so that his 27 new names were available immediately. However, for two of the older taxa, *Crassostrea* and *Gryphaeostrea,* he listed wrong type species. The former was corrected by him later (Vyalov, 1948a, p. 23, footnote).

Vyalov succeeded in collecting quite a few obscure generic names that had entered the literature before 1936. However, a few such names were omitted (viz., *Alectryonella, Odontogryphaea, Planospirites, Saccostrea*). Omission of obscure names hidden somewhere in the literature cannot be criticized severely, for no matter how thorough a search may be no assurance can be given that one has found all available names. A serious omission, however, was *Pycnodonte,* which he did not mention in 1936, because he concluded, unfortunately incorrectly, that it is a junior subjective synonym of *Gryphaea s.s.,* as explained in a later work (Vyalov, 1948a, p. 28).

Vyalov did not follow the *Code* in every case. For example, he placed *Ostreonella* Romanovskiy, 1890, as a section under the genus *Liostrea* Douvillé, 1904, and arranged *Sokolowia* Böhm, 1933, as a section under the genus *Fatina* Vyalov, 1936. In the latter case, he evidently realized the close affinities of the two respective type species, but presumably he wished to conserve his *Fatina,* instead of subordinating it under *Sokolowia,* which has clear priority as a name. In my opinion the two taxa are synonyms not separable even on the section level.

Vyalov's major classification method was ingenious in a way, for his use of the upper valve to diagnose major divisions of oysters is eminently effective in certain cases. For example, some exogyrine forms have spiral lower valves which are confusingly similar to those of some gryphaeine oysters; among them the upper valves are the key to their distinction. However, this diagnostic feature by itself is insufficient in other cases.

Vyalov used too few diagnostic attributes, and for that reason his classification became quite uncertain on generic and lower levels. He did not make serious use of the structures of hinges and of ligamental areas. Although he discussed outlines of muscle imprints in his later work (Vyalov, 1948a, p. 9, 17-18), he never mentioned them in his earlier work and did not recognize them as a diagnostic character, nor did he use vesicular shell structure. The chomata of oysters and vermiculate wrinkles of the Pycnodonteinae, as well, were disregarded. He interpreted the latter as "not a generic, and in the majority of the cases not even a specific character" (Vyalov, 1948a, p. 27), in spite of the fact that these features had already been discussed and used successfully by others.

Small wonder that the Pycnodonteinae were not recognized by Vyalov as a taxon and that the various genera of the Pycnodonteinae were scattered about: *Gigantostrea* as a subgenus of *Ostrea; Labrostrea* as a section of *Liostrea (Liostrea); Biauris, Circogryphaea,* and *Phygraea* as sections of *Gryphaea (Gryphaea);* and *Pycnodonte* suppressed as a junior subjective synonym of *Gryphaea s.s.*

In several other cases, disruption of a well-definable genus or of a set of related genera ensued from his classification. The genus *Crassostrea* was broken into *Ostrea (Crassostrea)* and *O. (Angustostrea).* The very closely related genera *Flemingostrea* and *Odontogryphaea* were widely separated as *Ostrea (Flemingostrea)* and as the new section *Sinustrea* of *Liostrea (Liostrea).*

The Gryphaeinae, as defined by Vyalov on the basis of external valve morphology, without regard as to vesicular shell structure, vermiculate wrinkles, and outline and position of the muscle imprint, are obviously a polyphyletic collection of various gryphaeine oysters, *Gryphaea* homeomorphs, and *Gryphaea* descendants. In this subfamily he placed *Sokolowia (=Fatina),* which is a *Gryphaea* homeomorph and an ostreine oyster. *Sokolowia* is closely related to *Turkostrea,* which VYALOV placed correctly as a subgenus of *Ostrea.* The placements of *Sokolowia* and *Turkostrea,* far apart, are another one of many dislocations of evolutionary lineages. Although polyphyletic origins were a well-known problem already in 1936, no attempt was made to unravel any of them. Such wide separations of phylogenetically closely related lineages are the real test of validity of a classification. The more severe they are and the greater their number, the more does a classification producing them differ from a natural or phylogenetic arrangement. Separations of phylogenetically closely related taxa normally should become eliminated and their total number, both those recognized as such and those yet undiscovered, should become smaller as successive authors improve classification by using more and more criteria and by perfecting the methods they employ. It is desirable to discern more criteria of classification, but VYALOV reduced their number in comparison with preceding authors.

VYALOV actually increased the number of disruptions because 44 percent of the taxonomic names recognized by him were newly established ones and because he used an insufficient number of criteria and failed to use internal or structural criteria so that too great a weight came to rest on purely external shell features. The fact that he distinguished 79 percent more taxa than had been recognized before him and that he had to resort to sections to subdivide subgenera clearly indicate that he made too many taxonomic divisions.

Because of the great number of taxa distinguished and newly proposed by him, VYALOV's classification was received without enthusiasm (BEURLEN, 1958; RANSON, 1943b, p. 162; 1948b, p. 2-3). Indeed, several of the type species selected by VYALOV for new taxa are insufficiently known species, so that the taxa based on them are in doubt.

In defense of VYALOV's classification it must be pointed out that he (VYALOV, 1948a, p. 5) was not at all convinced that he had succeeded in taking into account all peculiarities of the oysters or that no modifications of his classification would be required in future. According to him, the ultimate, unshakable classification cannot be built by a single investigator in a few years of study.

To summarize, VYALOV deserves credit for recognizing for the first time that taxonomic differences among the oysters are profound enough to require breaking the family into subfamilies. However, the basic philosophy of his work, namely that a single feature can serve as principal criterion for subdividing oysters, cannot stand the test.

Because VYALOV's early work (1936) was so brief (only four pages), need for amplification was obvious, and was given later (VYALOV, 1948a). The two cited works are similar in all essential features. However, the later publication included two additional taxa: *Rygepha* VYALOV, 1946, a section of *Gryphaea s.s.* and *Solidostrea* VYALOV, 1948c, supposedly a subgenus of *Ostrea.* Here VYALOV (1948a, p. 33) gave a compelling reason for including *Gryphaeostrea* in the Exogyrinae. Although other authors before him had placed that genus either near *Exogyra* or even included it in the latter, *Gryphaeostrea* had remained dubious as to systematic position. VYALOV emphasized that the umbonal part of the upper valve is spiral in an exogyroidal fashion in this genus.

STENZEL, 1947

At the beginning of his studies on oysters, STENZEL set out to acquire the nomenclatural tools needed for thorough work. He endeavored to collect all names that various authors had applied to supraspecific taxa among oysters and to ascertain their type species, as well as where these had been found and described (STENZEL, 1947). Although handicapped by poor library facilities, he managed to round up 116 such names.

Many of these were found to be vitiated on purely nomenclatural grounds, because they had been proposed in a nomenclaturally illegal fashion or because they were homonyms of earlier names, unjustified emendations of earlier names, or junior objective synonyms. All together, objections of these sorts reduced the list to 80 nomenclaturally available and potentially usable names.

Jaworski (1951) reviewed Stenzel's synopsis favorably and corrected his own conception of *Heterostrea* Jaworski, 1913, pointing out that it was not applied to an oyster, instead was a subjective synonym of *Myoconcha* Sowerby, 1824 (see Fig. J147). Beurlen (1958) criticized both Vyalov (1936, 1948a) and Stenzel (1947) for their extreme splitting of the Ostreidae into many supraspecific taxa. Evidently he misunderstood the intent of Stenzel's synopsis. Stenzel (1947, p. 165) had made it clear that his synopsis was intended to provide no more than the nomenclatural tools and not to judge which names were justified or not from a biological point of view. In spite of Beurlen's objection to the surfeit of available names, he added one more (*Nanogyra* Beurlen, 1958) to the 116 names.

At that, Stenzel failed to find about eight names published before 1947 and misinterpreted the type species of *Aetostreon*. Also, by following Francis Hemming's (1944) interpretation of what constitutes definition, description, or indication of a generic name, Stenzel withheld nomenclatural priority from *Lopha* Röding, 1798, in favor of *Alectryonia* Fischer de Waldheim, 1807. The new *Code* does not allow this conclusion.

THOMSON, 1954

In his study of living Australian oyster species, Thomson (1954) furnished modern descriptions and a classification founded on both purely conchological features of the hard parts of the mantle/shell and biological features of the soft parts. Internal anatomy, as far as known, was discussed, and two identification keys—one founded on soft parts and another one on shell features (Thomson, 1954, p. 162-163)—were constructed. The interdisciplinary approach made the study modern and highly informative.

In classifying materials at hand Thomson followed Ranson (1943) and distinguished only three genera: *Ostrea* Linné, *Crassostrea* Sacco (for Ranson's *Gryphaea*), and *Pycnodonte* Fischer de Waldheim (for *Pycnodonta*). If one makes allowance that the classifications of Ranson and of Thomson are dedicated to "lumping," they are quite correct and informative.

An important part of Thomson's (1954) paper was correction of generic names proposed by Iredale: The type species of *Saxostrea* was given as *Crassostrea commercialis* (Iredale & Roughley, 1933), now regarded as a geographic subspecies of *Saccostrea cucullata* (von Born, 1778). The type species of *Pretostrea* was given as *Ostrea folium* Linné, 1758 (=*O. bresia* Iredale, 1939), and it was shown that *O. folium* and *Mytilus crista galli* Linné are one and the same polymorphic species. Thus *Pretostrea* is a junior subjective synonym of *Lopha* and *Dendostrea* (Fig. J47; see Fig. J129, J130).

METHODS AND PRINCIPLES

Many authors have expressed dismay when they noticed that they were unable to identify and classify oysters readily and correctly. Most of them had been accustomed to use only a few selected specimens per species, that is, to employ typological methods of classification, so that they failed to have at hand sufficiently large and diverse samples of species they were studying. Several such situations gave rise to embarrassing errors. A case in point is Finlay's (1928a,b) proposal of the generic name *Notostrea* (see Fig. J144) introduced either without enough material at hand to describe both valves or perhaps not caring to describe more than one valve. At any rate he confounded one side with the other (Boreham, 1965). No wonder that *Notostrea,* 40 years later, remains doubtful and valueless. The first prerequisite in oyster classification is availability of ample material.

Even when specimens are numerous, problems of species identification generally remain. An example is the question posed by Thomson (1954): Are the morphs commonly called *Lopha cristagalli* (Linné, 1758), *Dendostrea folium* (Linné, 1758), and *Ostrea (Pretostrea) bresia* Iredale, 1939, really three separate species representing different genera or are they merely morphs of one and the same polytypic species, as THOMSON maintained? The first two of these three are quite common, and study specimens of them abound in most museums. THOMSON (1954) claimed to have seen transitional morphs linking the three, whereas other authors have either not seen any or overlooked them, in spite of abundant materials available. The question is not yet settled, although I am inclined to assume that THOMSON's idea of only one polymorphic species is sound, because his careful work is based on more extensive local observations made under favorable conditions. Similar suspicions have been voiced by other authors concerning other supposedly separate species.

Questions of species identity and synonymy are only too numerous among the oysters. Some questions have major importance in generic classification. In particular, the type species must be elucidated fully first, else the genus would remain obscure. Examples of such questions are the three species discussed above (see also under *Lopha,* p. *N*1157) and *Striostrea procellosa* ("VALENCIENNES" in LAMY), the type species of *Striostrea* VYALOV, 1936. Credit for solving the latter problem must be given to RANSON (1949, 1951). The case was reinvestigated by me at Paris and RANSON's conclusion as to the identity of *Ostrea procellosa* with *O. margaritacea* LAMARCK, 1819 (p. 208), was fully confirmed (see Fig. J107, J108). Only then it was possible to form an opinion as to the taxonomic status and morphologic features of *Striostrea,* which had been proposed in 1936 without sufficient knowledge of its morphology and of the synonymy of its type species. It is hoped that ultimately, through the concerted efforts of various authors, all type species of oysters will become well described so that then it will become possible to allocate firm taxonomic positions to all generic names and genera involved. However, the *Code* allows new genera to be introduced with much less effort than it takes to elucidate the taxonomic features of their type species, so that an early end to this task is not in sight.

Classification and taxonomy of oysters, on the various hierarchical levels above species and superspecies, seems extraordinarily difficult and open to divergent interpretations. For this reason, it cannot be claimed that the classification proposed here is unshakably correct. In support of it, however, is the fact that more data, particularly of neontological and phylogenetic sorts, were gathered and built into it than in any other classification.

To improve on any extant classification one must adduce more observational data, gain knowledge of more taxonomic characters, and be able to make a keener evaluation of their significance and reliability. The best way to obtain more data is to use both paleontological and neontological observations to limits of present-day knowledge.

Not all observational taxonomical characters are equal in usefulness or importance to classification. However, one cannot know in advance which characters are more important than others. Only trial and error can establish their relative importance, which really is arranged in a hierarchy, largely obscure at the beginning, as complicated as the taxonomy that is to be built from the characters. The great problem is to guess at their respective importance before one has built a system of classification on them. Certain rules are of some help in evaluating the importance of a taxonomic character. Those used by me in study of oysters are as follows.

1) A feature is judged to gain in importance, the more its changes require shifts in the position of internal organs. For example, shifts of the intestine with respect to the pericardium seem to have great significance. All oysters in which the intestinal tract runs through the pericardium and ventricle of the heart (viz., *Hyotissa, Neopycnodonte*) must differ considerably from oysters in which the intestinal tract bypasses the ventricle and pericardium at their dorsal side (viz., all other living oysters).

2) Internal features are commonly more important than external ones. As example, the shape and position of insertion of the adductor muscle are internal features and therefore probably quite important. The reason is that a given relative position of the insertion could not be accomplished originally without other internal organs having to change shapes or outlines or having to shift their positions to make room. In other

words, rule 2) is an extension or application of rule 1). In classification of oysters, the shape and position of insertion of the posterior adductor muscle is judged to have great importance.

3) Shell structure is more important than most other features. For instance, all oysters with vesicular shell walls (viz., Pycnodonteinae) must form a closely knit taxon, whether defined as a single genus or a subfamily. Shell structure outranks other taxonomic characters. For example, *Hyotissa* has a plicate valve commissure and vesicular shell-wall structure. The former character would appear to entitle it, so to say, to be placed in the Lophinae, all of which have plicate commissures. This is rejected because shell-wall structure is considered to outrank and overrule the plicate commissure. The shell wall, vesicular in *Hyotissa,* requires that this genus be placed in the Pycnodonteinae, as RANSON (1941) has demonstrated.

4) Correlated features, that is, characters that constantly or prevailingly make appearance together, are more important than noncorrelated ones. For example, the group of oysters, mostly fossil, which are now called Pycnodonteinae, have several apparently unrelated characters that always show up together. These are: vesicular shell walls, vermiculate chomata on both valves, orbicular outline of adductor muscle insertion, and a rather high position of the muscle insertion between hinge and opposite valve margin. These various characters are unrelated in the sense that apparently no reason can be cited to explain why one character should entrain others. For instance, why should vesicular shell-wall structure have any influence on shape of the insertion of the adductor muscle? Because these characters appear to be independent of each other, although making their appearance together, they are regarded as good indicators of monophyly.

OUTLINE OF CLASSIFICATION

The following outline summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each suprageneric group of oysters from suborder to subfamily. A single number refers to genera; where two numbers are given, the second indicates subgenera additional to nominotypical ones.

Main Divisions of Ostreina

- Ostreina *(suborder)* (52;13). *U.Trias.-Rec.*
  - Ostreacea (superfamily) (52;13). *U.Trias.-Rec.*
    - Gryphaeidae (22;6). *U.Trias.-Rec.*
      - Gryphaeinae (6;2). *U.Trias.(Carn.)-U.Jur.(Portland.).*
      - Pycnodonteinae (4;3). *L.Cret.-Rec.*
      - Doubtful genus (1). *Paleog.*
      - Exogyrinae (11;1). *M.Jur.(Bajoc.)-Mio.*
    - Ostreidae (27;4). *U.Trias.-Rec.*
      - Ostreinae (14;1). *L.Cret.-Rec.*
      - Lophinae (6;3). *U.Trias.-Rec.*
      - Doubtful genera (7). *U.Cret., low.Oligo.-Eoc.*
    - Chondrodontidae[1] (1;3). *L.Cret.(Alb.)-U.Cret.(Campan.).*
    - ?Lithiotidae[1] (2). *L.Jur.(L.Lias.).*

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[1] Included in Ostreacea for convenience.

SYSTEMATIC DESCRIPTIONS

INTRODUCTION

For the first time, it is now recognized that oysters, as commonly understood (Ostreidae AUCTORUM), are not a monophyletic family, but are very probably diphyletic. Accordingly, two families are distinguished in the *Treatise:* 1) Ostreidae *(sensu stricto),* emended here to exclude the subfamilies Gryphaeinae VYALOV, 1936, Pycnodonteinae STENZEL, 1959, and Exogyrinae VYALOV, 1936, and 2) Gryphaeidae VYALOV, 1936, which is composed of the three above-mentioned subfamilies.

The Gryphaeinae, furthermore, are revised as shown by STENZEL (1959). For the second family listed above the designation Gryphaeidae VYALOV, 1936, must be used according to the *Code,* although VYALOV (1936) merely proposed Gryphaeinae.

The distinction between the two families is based on 1) hinge structure of the prodissoconch, 2) shape and position of the imprint of the posterior adductor muscle, and 3) the course of the intestine with reference to the heart. Characters 2) and 3) are linked, as explained above (p. N1095).

Suborder OSTREINA Férussac, 1822

[*nom. correct.* Newell, 1965 (*ex* order Ostracés Férussac, 1822)] [Diagnosis by N. D. Newell]

Monomyarian; foot and byssus lacking in adults; generally cemented by LV; shell chiefly, but not exclusively, calcitic, foliaceous; gills eulamellibranch; pallial line entire. *U.Trias-Rec.*

Superfamily OSTREACEA Rafinesque, 1815

[*nom. transl.* Schweigger, 1820, p. 712 (*ex* family Ostreacia Rafinesque, 1815)] [Diagnosis and other materials for this superfamily prepared by H. B. Stenzel (except Chondrodontidae, furnished by †L. R. Cox and H. B. Stenzel, and Lithiotidae, which was prepared by †L. R. Cox)]

Mantle open all along margins except at point of palliobranchial fusion, devoid of a pallial line except one genus (*Saccostrea,* see p. *N*1134), which has a disjunct line of pallial muscle insertions. Outer edge of gills fused to mantle; shell cemented to a firm substratum by left valve except in the case of a few species which never become attached to a firm substratum (see p. *N*995-*N*996); postlarval shell foliaceous, inequivalve ranging from extremely inequivalve in some genera to slightly so in others, edentulous, ligamental area divided into three parts, resilifer in middle. *U.Trias.-Rec.*

Family GRYPHAEIDAE Vyalov, 1936

[*nom. transl.* Stenzel, herein (*ex* Gryphaeinae Vyalov, 1936, *emend.* Stenzel, 1959)]

Nonincubatory. Prodissoconch hinge on planktonic larvae carries uninterrupted alternating series of equal tooth precursors and corresponding sockets (Fig. J72). Promyal passage extensive, reaching close to pallial isthmus; intestine passing through pericardium and ventricle of heart. Posterior adductor muscle orbicular in cross section placed closer to hinge than to opposite valve margin, ventral border of its insertion on LV elevated above general surface of valve. Valves highly unequal in most genera to subequal in others. Radial posterior groove on LV absent, more or less deep, or reduced to a mere flexure of growth lines, or obscured in later forms. Attachment area of LV tiny to small in most genera, average to large in some. Umbonal cavity of LV very shallow except in Exogyrinae; LV beak of highly inequivalve forms filled with solid shell matter, no chambers except in Exogyrinae. Prismatic shell layer thin in most genera, absent in a few. Ligamental area of lower valve never very high except in Exogyrinae. [Strictly euhaline and stenohaline; most genera never form true oyster reefs in which conspecific individuals grow mainly on one another.] *U. Trias.-Rec.*

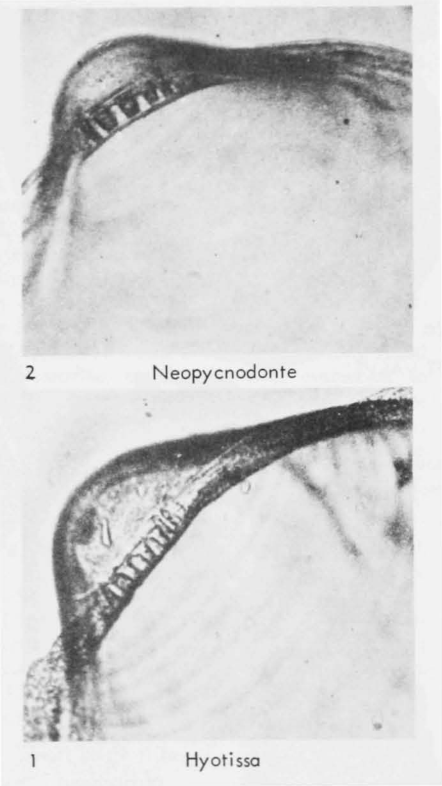

Fig. J72. Prodissoconch hinges of the Gryphaeidae, ×240 (Ranson, 1967).—*1. Hyotissa hyotis* (Linné, 1758), living, IndoPacific. — *2. Neopycnodonte cochlear* (Poli, 1795), living, Atlantic, Mediterranean, and IndoPacific.

Subfamily GRYPHAEINAE Vyalov, 1936

[Gryphaeinae Vyalov, 1936, p. 19, *emend.* Stenzel, 1959, p. 16; Gryphaeinae Vyalov, 1937 was placed on Official List by ICZN, Opin. 356; evidently Gryphaeinae Vyalov, 1936, had been overlooked]

Commissural shelf less well defined than in Pycnodonteinae, lacking chomata; no vesicular shell structure. *U.Trias.(Carn.)-U.Jur.(Portland.).*

Gryphaea Lamarck, 1801, p. 398 [Official List, ICZN Opin. 338] [**G. arcuata;* SD ICZN, Opin.

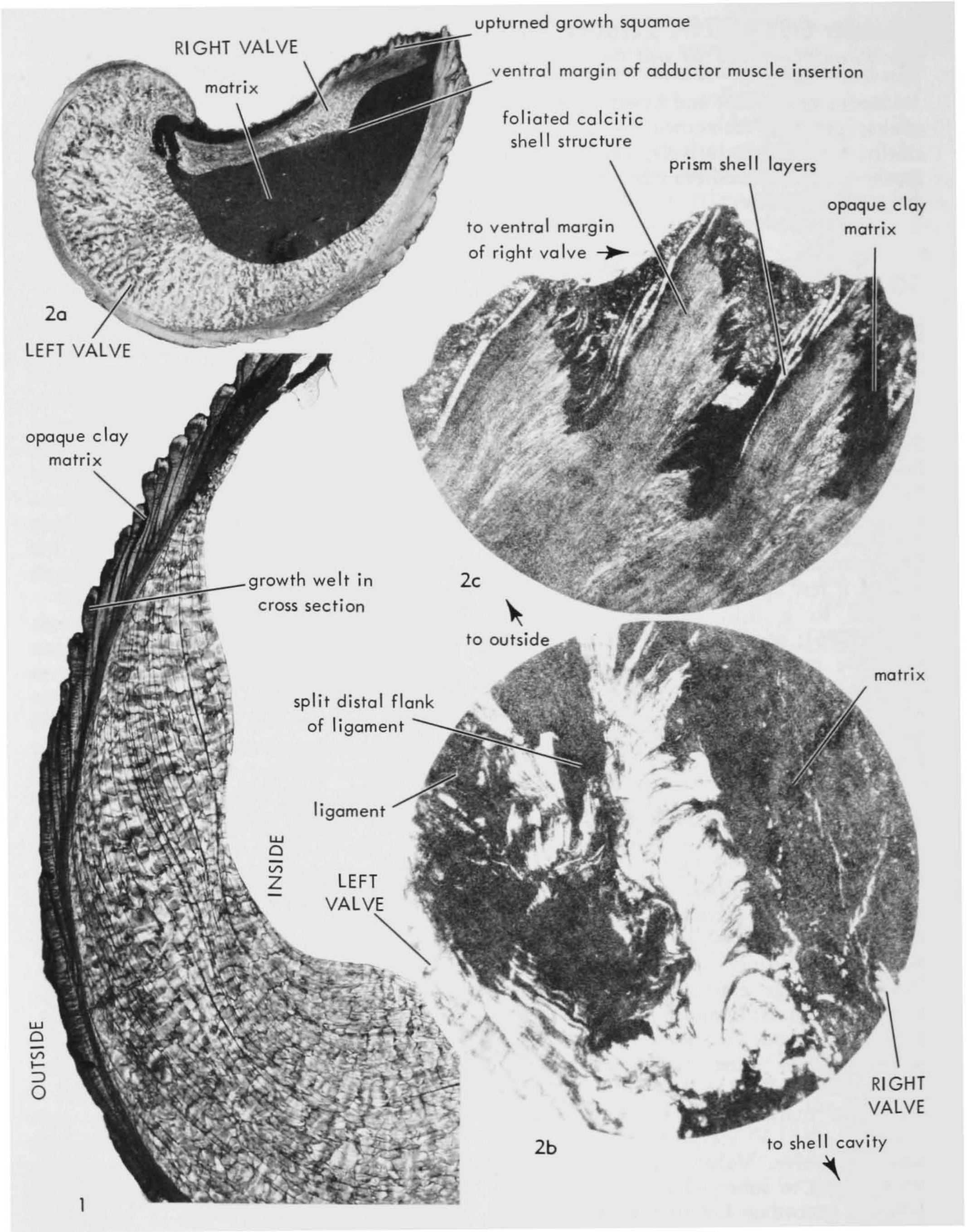

FIG. J73. Shell structures in *Gryphaea (Gryphaea) arcuata* LAMARCK (1801), from Lower Jurassic (Lias.) of England (Stenzel, n).

1. Appressed growth squamae ending in terminal expansions that produce concentric growth welts on LV; thin section at right angles to hinge axis and commissural plane in ordinary light, showing irregular foliated shell structure on inner part and calcitic crossed-lamellar structure on outer part of valve, ×2.

2a. Thin section of shell cut at right angles to hinge

338] [=*Gryphoea* Bosc, 1802, p. 307 *(nom. van.)*; *Gryphaeigenus* Renier, 1807, p. 7 (rejected ICZN, Opin. 427); *Gryphites* von Schlotheim, 1813, p. 52 *(nom. van.)*; *Griphaea, Griphoea* de Blainville, 1821, p. 533 *(nom. null.)*; *Griphea* Brongniart, 1822, in Cuvier & Brongniart, *(nom. null.)*; *Gryphea* Brongniart, 1823, p. 10 *(nom. null.)*; *Liogryphaea* Fischer, 1886, p. 927 (rejected ICZN, Opin. 338) (obj.); *Gryphaae* White, 1887, p. 20 *(nom. null.)*; *Liogryphea* Douvillé, 1904a, p. 273 *(nom. null.)* (rejected ICZN, Opin. 338); *Ghyphaea* Scalia, 1912, p. 21 *(nom. null.)*; *Lyogryphaea* Couffon, 1918, p. 116 *(nom. null.)*; *Jurogryphaea, Incurva* Arkell, 1934, p. 62 *(nom. neg.)*; *Gryphaca* Jaworski, 1935, p. 885 *(nom. null.)*; *Rygepha* Vyalov, 1946, p. 34 (type, *Gryphaea skuld* Böhm, 1904, p. 17; OD); *Liogriphaea* Vyalov, 1948a, p. 36 *(nom. null.)*; *Liographaea* Charles, 1949, p. 35 *(nom. null.)*; *Liogryphanaea* Krach, 1951, p. 355 *(nom. null.)*; *Gruphea, Griphea* Ćirić, 1951, p. 65 *(nom. null.)*; *Cryphaea* Zaprudskaya, 1953, p. 23 *(nom. null.)*] [*non Gryphaea* Fischer, 1886, p. 927 (=*Crassostrea* Sacco, 1897)]. Shell medium-sized to large (up to 16 cm. long and 14 cm. high), LV ranging from high and narrow (*H* [height] about 178 percent of *L* [length]) in some species to orbicular to horizontal-oval *(H* about 70 percent of *L)* to bilobate-oval *(H* about 80 percent of *L)* to bilobate-triangular in others, orthocline to very slightly opisthocline, convex and capacious, ranging from highly convex to broadly convex in horizontal cross section; not compressed and devoid of median radial keel. LV with radial posterior sulcus ranging from evanescent to deeply sunken, posterior flange poorly or well set off from main body of valve (bilobate forms), and beak small, pointed, opisthogyral to nearly orthogyral, highly inrolled with tiny attachment scar in some species to less inrolled and with large attachment scar in others; LV smooth or with low smooth irregular concentric growth welts or with low smooth regularly spaced concentric undulations, mostly with appressed or rarely nonappressed growth squamae, either devoid of radial ribs or furnished with them (Fig. J74). RV concave, vertical-oval to spatulate, orbicular, horizontal-elliptic, or bilobate, truncated by hinge, without ribs or having few narrow radial gashes or threads, and having appressed or nonappressed growth squamae. Resilifer ranging in size from as long as to 5 times length of each bourrelet of ligament, excavate in LV and flat to very slightly excavate in RV. Umbonal cavity beneath hinge plate on inside of LV largely filled in by thickened shell (Fig. J73, *2a*); commissural shelf well developed but without chomata. Adductor muscle imprint orbicular to oval, with dorsal margin clearly convex and ventral edge projecting obliquely upward into shell cavity. *U.Trias.,* Boreal Prov.(B.C.-Can.Arctic-Bear I.-Far NE.Sib.)-USA(Nev.); *L.Jur.(Hettang.)-U.Jur.(Kimmeridg.),* worldwide.

G. (Gryphaea). Small to large. LV lacking radial ribs, costellae, or threads, with evanescent to shallow radial posterior sulcus and posterior flange not detached. *U.Trias.,* Boreal Prov., Nev.; *L. Jur.(Hettang.)-U. Jur.(Oxford.),* worldwide. ——Fig. J74,*3*. **G. (G.) arcuata* Lamarck, L. Jur.(Lias.), Eng.; *3a-d,* RV, various views, aragonite of adductor muscle pad leached, ×1; *3e-g,* entire shell, various views, ×1 (Stenzel, n). [Specimens by courtesy of P. C. Sylvester Bradley.] (*See* also Fig. J60.)

G. (Africogryphaea) Freneix, 1965, p. 32 [**Liogryphaea costellata* Douvillé, 1916, p. 58; OD] [=*Africogryphaea* Freneix & Busson, 1963, p. 1632 *(nom. nud.)*]. Small to medium-sized, outline tending to higher than long and truncate at umbo because of large attachment area and earlike extension of valves at posterior flank of hinge line. Radial posterior sulcus broad and deep; posterior flange well detached, ending in small projecting divergent lobe. LV with somewhat irregular, strong and large radial ribs. *M. Jur.(Bathon.)-U. Jur.(Callov.),* N. Afr.(Alg.-Tunisia)-Sinai Penin.-Ethiopia-Arabia.——Fig. J74,*1*. **G. (A.) costellata* (Douvillé), M.Jur.(Bathon.), Massif of Moghara, Sinai Peninsula; *1a,b,e,* LV, both sides and ext.; *1c,d,* RV int. and ext. views, all ×0.7 (Douvillé, 1916).

G. (Bilobissa) Stenzel, **n. subgenus,** herein [**G. bilobata* J. de C. Sowerby, 1840, p. 4; OD] [=*Bilobata* Arkell, 1934, p. 64 *(nom. nud.)*]. Small to medium-sized. Radial posterior sulcus deep; posterior flange well detached. No radial ribs, costellae, or threads. [*Bilobissa* is possibly ancestral to *Texigryphaea.*] *M.Jur.-U.Jur.,*Eu.——

Fig. J73. *(Continued from facing page.)*

axis and commissural plane viewed under crossed nicols, showing umbonal region solidly filled, ×1.

2b. Lithified ligament from same thin section (*2a*) under ordinary light, ×20. [The ligament remains attached to LV but has pulled away from RV, allowing sediment to ooze between ligament and RV.]

2c. Upturned growth squamae near ventral margin of RV in same thin section (*2a*) in ordinary light, showing foliated calcitic shell structure ending in thin strips of prismatic shell layers (light-colored), ×20. [Black areas are opaque mineral aggregates, possibly pyrite or black clay.]

[Specimens courtesy of P. C. Sylvester-Bradley, Univ. Leicester, England. Thin sections made under supervision of Otto Majewske, Shell Development Co., Houston, Texas.]

Fig. J74,2. **G. (B.) bilobata* J. de C. Sowerby, M.Jur.(Bajoc.), Inferior Oolite, Eng.; *2a-d,* several views of holotype, ×0.7 [photographs by courtesy of British Museum (Natural History)].

Catinula Rollier, 1911, p. 272 [**Ostrea knorri* Voltz, 1828 (=*O. knorrii* Voltz, 1828, p. 60) (*non O. knorri* Defrance, 1821, p. 27, suppressed ICZN, Opin. 360, =*O. knorrii* Voltz, ICZN Official List, Opin. 360); SD Arkell, 1932, p. 149, 180] [=*Catinulus* Lissajou, 1923, p. 142 *(nom. van.), O. (Knorrii)* Arkell, 1934, p. 64 *(nom. van.)*]. Very small (up to 35 mm. high). LV deep, capacious, scoop-shaped, orthocline to opisthocline at 70 degrees to hinge axis, commonly

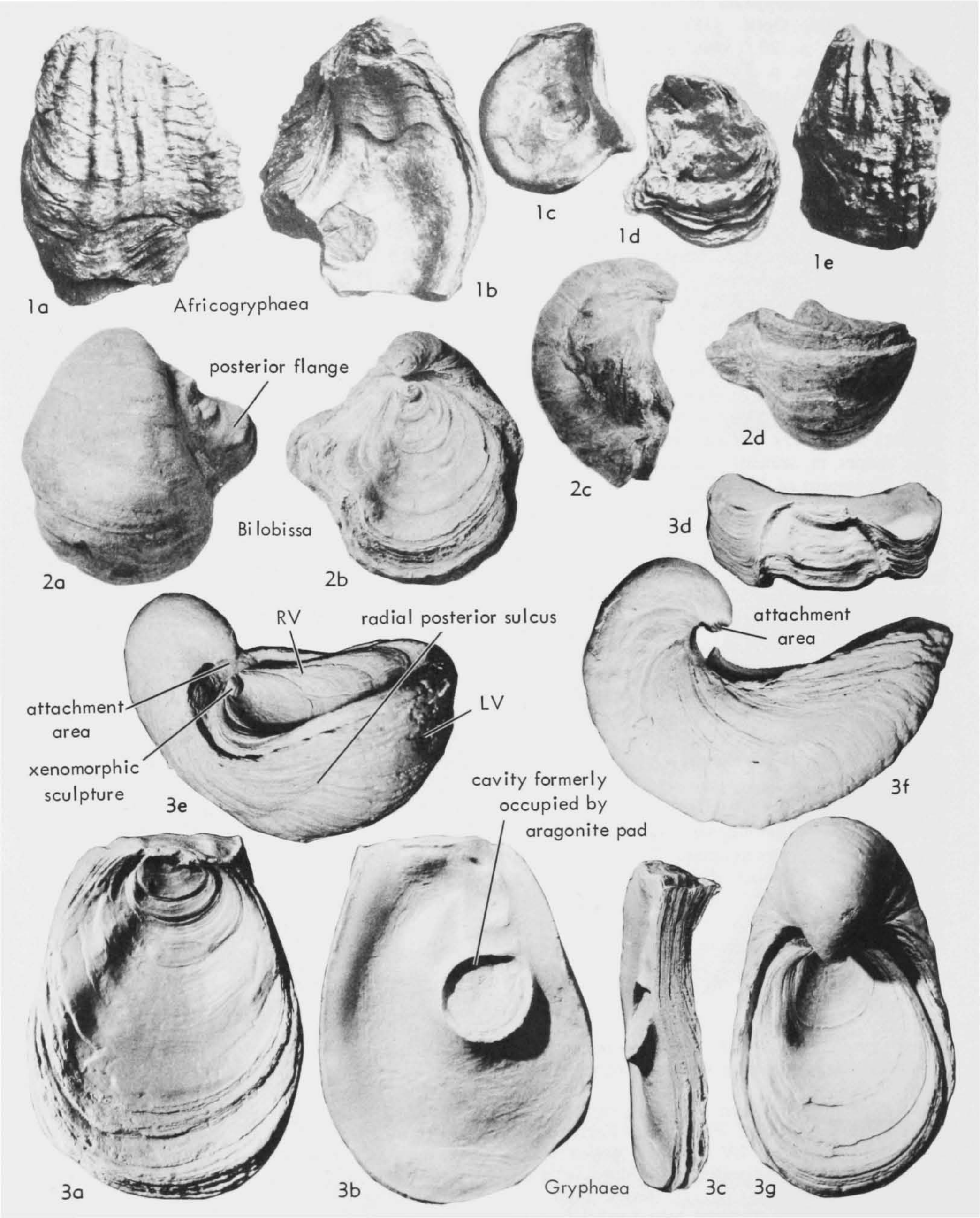

Fig. J74. Gryphaeidae (Gryphaeinae) (p. *N*1097, *N*1099).

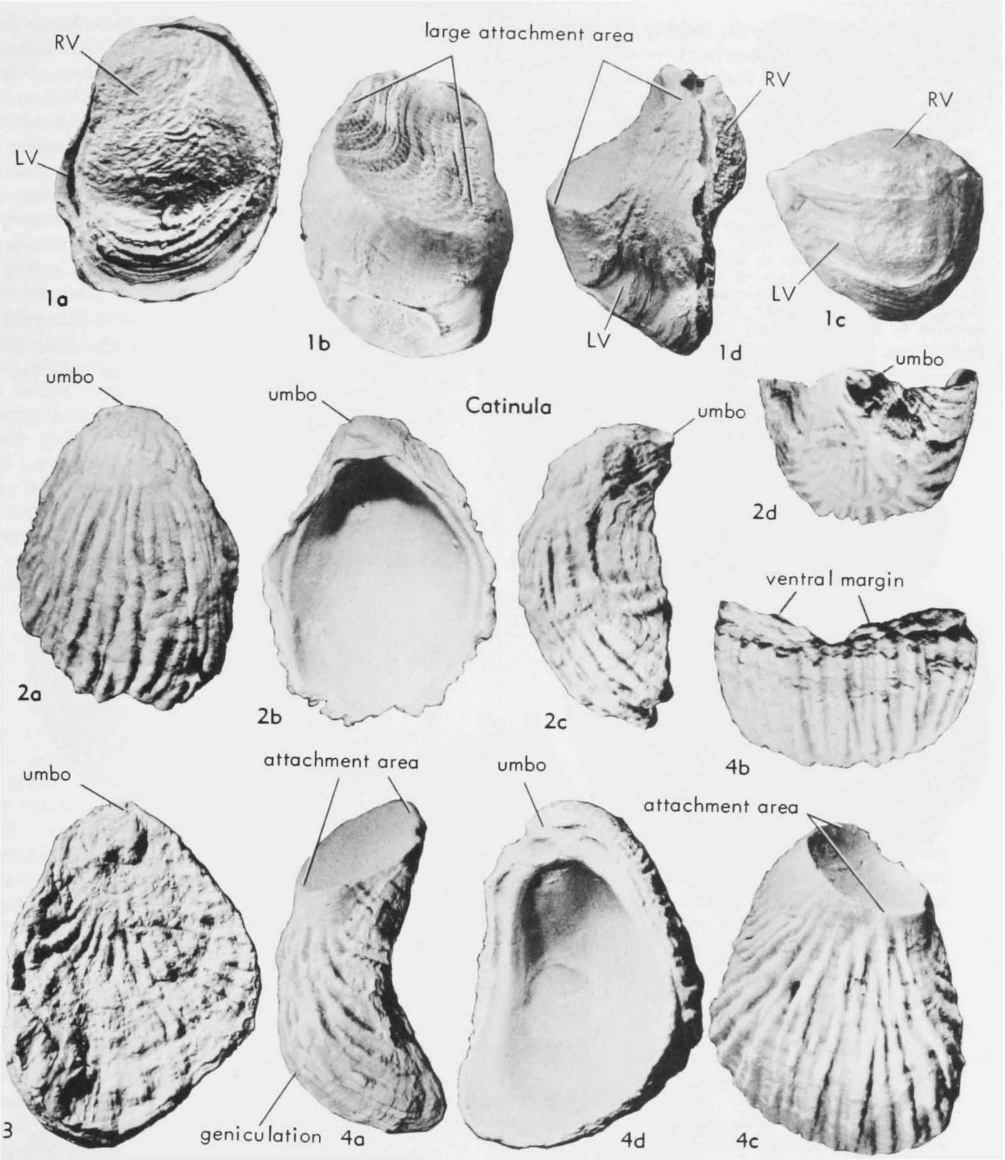

FIG. J75. Gryphaeidae (Gryphaeinae) (p. *N*1100-*N*1102).

higher than long (*H* 95 to 170 percent of *L*, averaging 125 percent); commonly less wide than high (*W* [width] 20 to 75 percent of *H*, averaging 45 percent); attachment area tiny to very large (10 by 11 mm., even up to 17 mm.); LVs with large attachment area growing steeply upward from substratum to form straight or convex profile without geniculation, others with tiny attachment area higher, less deep, obliquely spatulate, and less scoop-shaped, growing out at first fairly flat, but later bending abruptly and convexly to attain convex, geniculate profile; LV with many narrow, crowded, rounded, divaricating, irregular to fairly regular, discontinuous to subcontinuous, radial costae and some nonappressed growth squamae. RV flat, operculiform, fitting into LV, elliptic in those with large attachment area, grading to oblique-spatulate, pointed at umbo, smooth to ribbed, though less prominently than LV. Resilifer about twice length of each bourrelet; ligamental area mostly less high than long (2-3 mm.). Adductor muscle imprint orbicular to only faintly convex at its dorsal margin. Commissural shelf well developed, extending all around valves in some individuals, lacking chomata. *M. Jur.*, Eu.-N.Am.(La. subsurface).——FIG. J75,*1-4*. *C. knorri (VOLTZ), Bathon., Schönmatt near Basel, Switz.; *1a-d,* specimen with both valves, various views; *2a-d,* LV, various views; *3,* RV, ext.; *4a-d,* LV, various views, all ×3 (specimens courtesy Naturhistorisches Museum, Basel. Stenzel, n).

[Nomenclature has been discussed by STENZEL (1947, p. 171) and SYLVESTER-BRADLEY (1952). Species lacking ribs have been included in *Catinula* by some authors, but presumably they belong to a subgenus of *Catinula* as yet unnamed. *Catinula* probably evolved through neoteny from a costellate *Gryphaea*. SYLVESTER-BRADLEY (1958) gave a statistical description of the type species.]

Deltoideum ROLLIER, 1917, p. 566 [*Ostrea sowerbyana BRONN, 1836, p. 316 (*nom. subst. pro O. deltoidea* J. SOWERBY, 1816, p. 111, in SOWERBY & SOWERBY, *non* LAMARCK, 1806, p. 160, =*O. delta* SMITH, 1817, p. 18); SD ARKELL, 1932, p. 149 (footnote)]. Medium-sized to large (to 17 cm. long and 21 cm. high), shell very flat, bilaterally much compressed (to 5.5 cm. wide), outline spatulate to triangular, pyriform, or crescentic; many individuals with narrow, prominent branchitellum pointed toward rear in less extreme spatulate forms, but turning up toward dorsum in extreme more crescentic forms. LV as flat as RV, with low broad smooth irregular concentric undulations and few poorly appressed growth squamae; attachment area small to large, covering much of valve. RV very similar to LV, but in some spe-

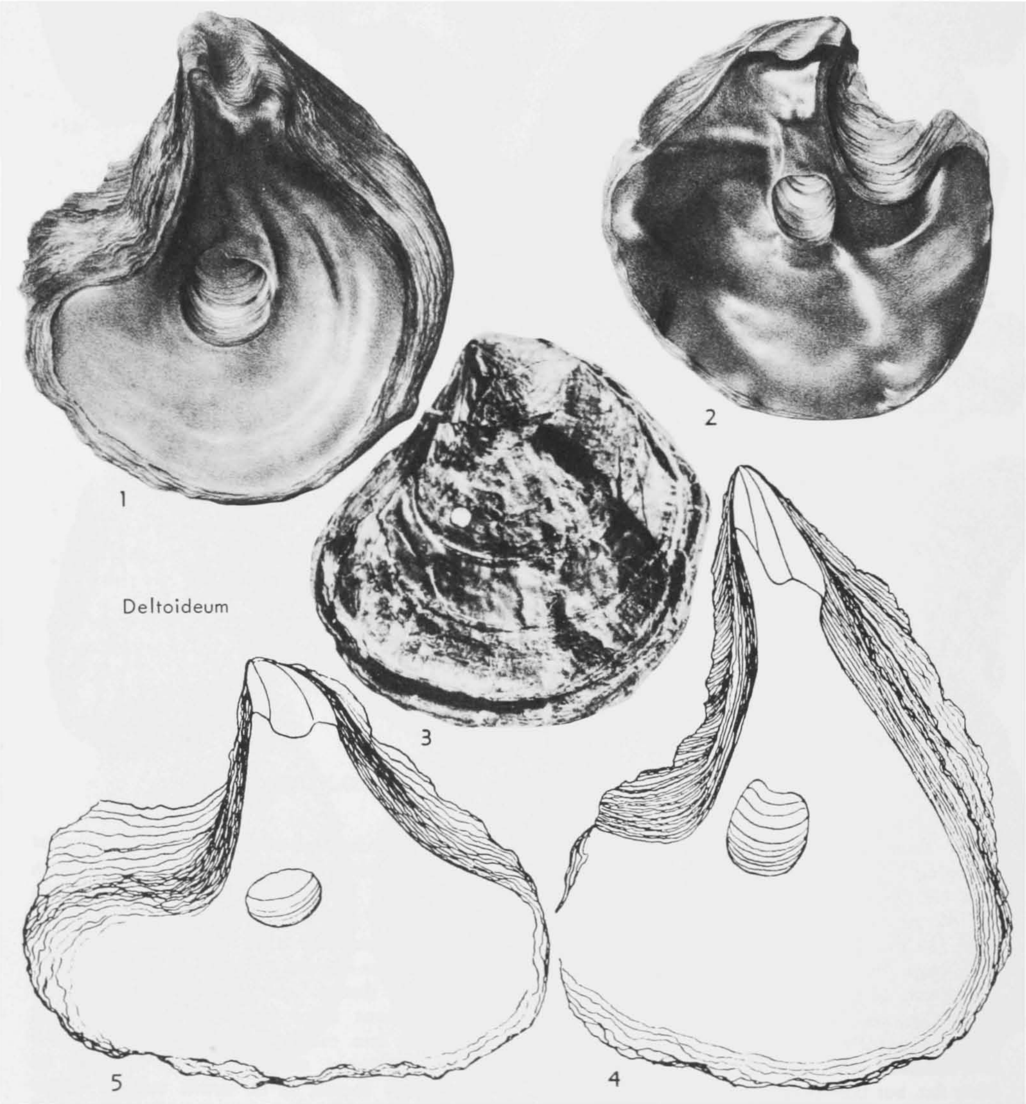

FIG. J76. Gryphaeidae (Gryphaeinae) (p. N1102-N1103).

cies having short (7 mm.), narrow (0.5 mm.), rounded radial threads separated by flat wide (1.6 mm. or more) interspaces. Ligamental area flat; LV and RV resilifers very shallowly excavate; anterior bourrelet generally flatter and longer (by as much as 50 percent) than posterior one. Adductor-muscle imprint in some individuals with very slightly concave dorsal margin flanked by well-rounded convexities; position of imprint close to posterior valve margin and closer to hinge than to ventral valve margin. No chomata. Ligamental area of older individuals rather high, with subparallel anterior and posterior margins, but in many shrinking in length as age advances, so that area constricts as it grows. Some old individuals no longer grew as to size of shell cavity but merely shifted it in ventral direction leaving behind many growth foliations which flank anterodorsal and posterodorsal valve margins. [ROLLIER's claim that *Deltoideum* was attached by its RV is in error as ARKELL (1935, p. xvi) pointed out. Specimen figured by BAYLE (1878, pl. 132, fig. 1, as *Ostreum subdeltoideum* PELLAT), examined by me at the École des Mines, Paris, has large attachment area on LV and corresponding xenomorphic features on RV. ORIA (1933, p. 71-72) believed that *Deltoideum delta* and *Gryphaea dilatata* J. SOWERBY, 1816, occurred together and had to be regarded as variants of one species. Thus *Deltoideum*, if accepted as a genus, presumably would be a descendant of *Gryphaea*. ARKELL (1932-36, p. xvi-xvii) did not agree with these conclusions, but regarded *Deltoideum* as a synonym of *Liostrea*. *Liostrea, Pernostrea,* and *Deltoideum* are probably close relatives.] *M.Jur.(Bathon.)-U.Jur.(Portland.),* Eu. (Eng.-France-Ger.-Pol.-USSR)-Saudi Arabia.——FIG. J76,*1-5*. **D. delta* (SMITH) (=*Ostreum subdeltoideum* PELLAT in BAYLE, 1878), U.Jur.(low.Kimmeridg.), LeHavre, France; *1,2,* LV int., RV int., ×0.5 (Bayle, 1878); *3,* RV with LV, ext. (holotype of *Ostrea laeviuscula* J. DE C. SOWERBY, 1825), ×0.5; *4,5,* LV ints., ×0.5 (*3-5,* Arkell, 1932-36).

Liostrea DOUVILLÉ, 1904b, p. 546 [**Ostrea sublamellosa* DUNKER, 1846; OD] [=*Liostrea* DOUVILLÉ, 1904a, v. 3, pt. 4, p. 273 *(nom. imperf.)* (type, *O. lamellosa* DUNKER, *nom. nud., err. pro sublamellosa;* OD)] [=*Lioster* VOLKOVA, 1955, p. 146 *(nom. null.)*]. Small (up to 3 cm. long and 5 cm. high), subequivalve but preponderantly inequivalve; outline irregular but tending to spatulate, margins tending to converge toward umbo; some individuals slightly crescentic. LV variable, mostly capacious and highly convex in anteroposterior direction, much less so dorsoventrally; attachment area fairly large for so small a shell, correspondingly large bulging xenomorphic area on RV umbo. RV variable, gently convex to flat or slightly concave beyond xenomorphic area. Both valves carry low concentric swellings and simple irregularly spaced growth squamae, very poorly or not at all appressed. Radial posterior sulcus of LV absent in some but present in many individuals, well developed, deep, and broad; posterior flange not detached. Sulcus appearing rather early in some individuals, that is, near attachment area. Resilifer about twice as long as each bourrelet. [Type species is highly variable and long-ranging stratigraphically (Rhaet.-Sinemur.). The following names are believed to be synonyms (SCHÄFLE, 1929, p. 16-20): *Ostrea hisingeri* NILSSON, 1832 (p. 354, pl. 4, fig. 2,3); *O. irregularis* MUNSTER in GOLDFUSS, 1833 (v. 2, pt. 4, p. 20, pl. 59, fig. 5); *O. sublamellosa* DUNKER, 1846 (p. 41, pl. 6, fig. 27-30); *O. anomala* TERQUEM, 1855 (p. 329, pl. 25, fig. 4-4b, not 5-5c); *O. liassica* STRICKLAND in TATE & BLAKE, 1876; and possibly *O. bristovi* RICHARDSON (*ex* ETHERIDGE, MS.), 1905 (p. 422, pl. 33, fig. 4). The first name has clear priority. The species has thin shell walls in northern parts of its geographic range and thick ones in the southern parts (France). Orbicular muscle adductor imprint, radial posterior sulcus on LV, lack of chomata, and absence of umbonal cavity place the genus firmly in the Gryphaeinae. It is perhaps a descendant of *Gryphaea* rather than its ancestor, as commonly assumed.] *U.Trias.(Nor.),* Far E.Sib.; *U.Trias.(Rhaet.)-Jur.,* Eu.(Mesogaean region).——FIG. J77,*1*. *L. hisingeri* (NILSSON, 1832) (=*Ostrea anomala* TERQUEM, 1855), Lias., Lux-

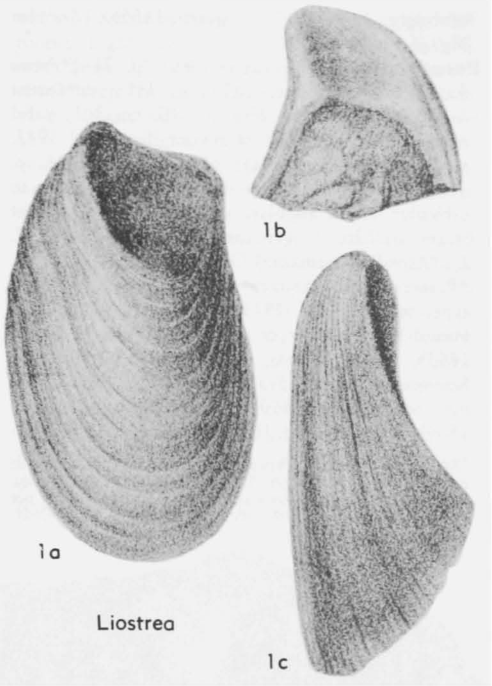

FIG. J77. Gryphaeidae (Gryphaeinae) (p. N1103).

embourg; *1a-c,* ×1.4 (Terquem, 1855). [*See* also Fig. J61.]

Pernostrea MUNIER-CHALMAS, 1864, p. 71 [**Perna bachelieri* D'ORBIGNY, 1850, p. 341 (=**Ostrea luciensis* D'ORBIGNY, 1850, p. 315, no. 341; valid name determined by first reviser, STENZEL, 1947, p. 180, Code Art. 24a); SD FISCHER, 1864, p. 364]. Size medium to large. Outline oval to orbicular to rectangular. Similar to *Liostrea* but larger and has longer cardinal area. *M.Jur.,* W. Eu.(Alps-Pol.-Rumania)-Greenl.——FIG. J78,*1-3*. **P. luciensis* (D'ORBIGNY); *1,* Bathon., Luc, France; type, ×0.3 (Boule, 1913); *2a,b,* Forest Marble of Pound Pill, Eng.; types of *P. wiltonensis* (LYCETT, 1863), ×0.3 (Lycett, 1863); *3a-d,* Callov., St. Scolasse-sur-Sarthe, France; types of *Perna bachelieri* (D'ORBIGNY, 1850), ×0.3 (Munier-Chalmas, 1864). [*See* also Fig. J15.]

[Because of page precedence *P. luciensis* is the preferred name of the type species. The fact that the generic name is constructed on the basis of a misconception should not mitigate against its use, see Article 18 (a) of Code. Compare discussion under Multiple Resilifers, p. *N*974. If *Liostrea* and *Pernostrea* were synonymous as claimed by ARKELL (1932-36), *Liostrea* would have to fall as a junior synonym.]

Praeexogyra CHARLES & MAUBEUGE, 1952b, p. 118 [**Ostrea acuminata* J. SOWERBY, 1816, v. 2, p. 82; OD]. Shell tiny to small (largest diameter to about 7 cm.), outline variable, but commonly much higher than long (common proportion 2.5:1 or 3:1), crescentic or ovate to strap-shaped with zigzag edge along their heights in some. LV slightly convex, RV flat to slightly concave; both covered on outside by many straight very fine radial threads, which may be absent, however, and by fairly even-spaced prominent concentric growth squamae separated by wide smoother interspaces. Attachment area at umbonal tip of LV rather small. [ARKELL (1934) described the type species and corrected its involved synonymy. Because of its numerous affinities to *Catinula* CHARLES & MAUBEUGE regarded *Praeexogyra* as a subgenus of *Catinula.* They assumed that *Prae-*

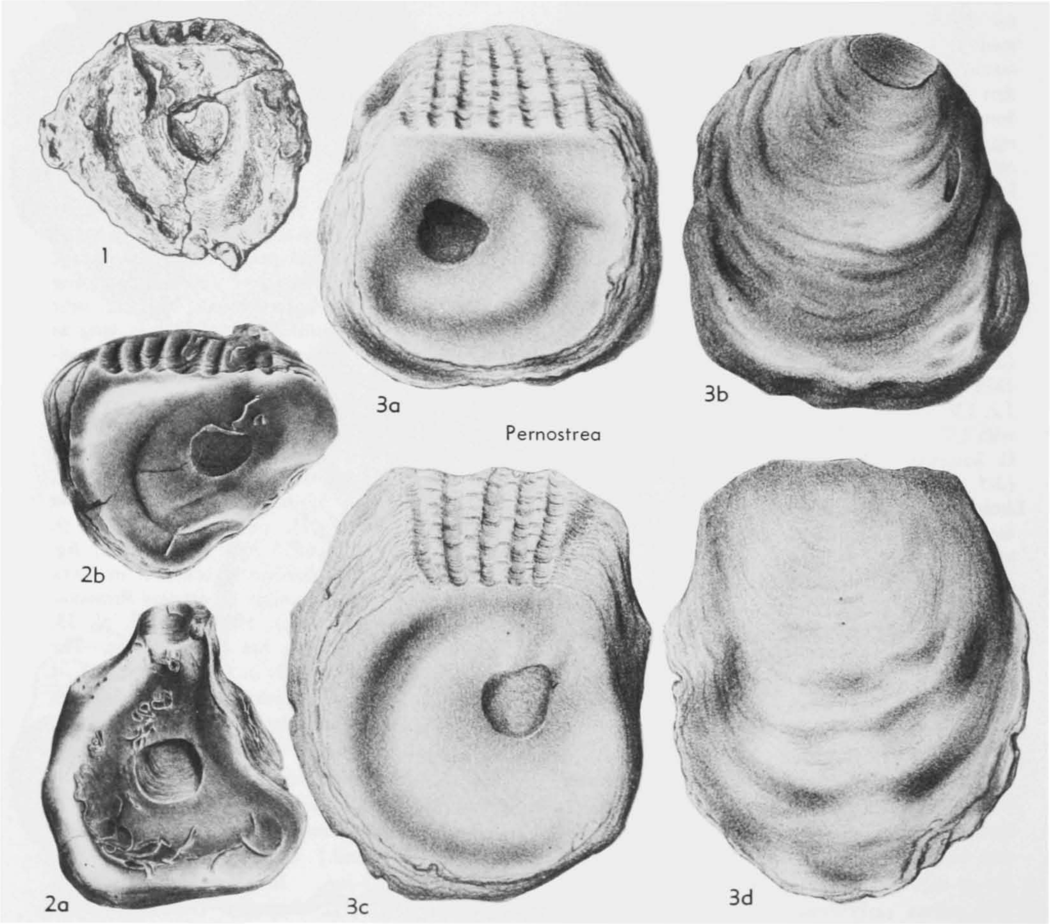

FIG. J78. Gryphaeidae (Gryphaeinae) (p. *N*1104).

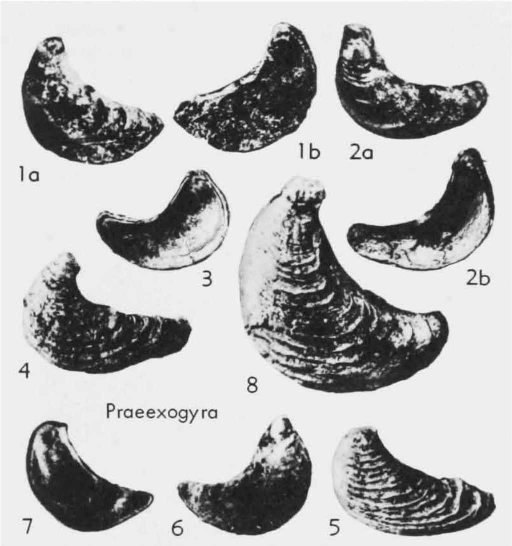

FIG. J79. Gryphaeidae (Gryphaeinae) (p. *N*1104-*N*1105).

exogyra formed the transition between *Catinula* and true *Exogyras* of the Upper Jurassic. They pointed out that *Praeexogyra* has a resilifer that is generally arched opisthogyrally, but never twisted.] *M. Jur. (Bajoc.-Bathon.),* Eu. (Eng.-France-Ger.-Switz.).——FIG. J79,*1-8*. **P. acuminata* (J. SOWERBY), Bathon.(Lower Fullers Earth), Eng.; *1-5,8,* LV views, *6,7,* RV views (Arkell, 1934). [*1* and *2* are syntypes of J. SOWERBY Collection, British Museum (Nat. History)].

Subfamily PYCNODONTEINAE Stenzel, 1959

[Pycnodonteinae[1] STENZEL, 1959, p. 16]

Commissural shelf well defined, delimited proximally by circumferential curb; chomata short to long, branching and vermiculate; vesicular shell structure present. No prismatic shell layer except in *Neopycnodonte. L.Cret.-Rec.*

Pycnodonte FISCHER DE WALDHEIM, 1835, p. 118-119 [**P. radiata;* OD] [=*Pycnodonta* G. B. SOWERBY, JR., 1842, p. 35 (*nom. van.*); *Pycnodontes* HERRMANNSEN, 1849, p. 373 *(nom. null.); Pycnodunta* G. B. SOWERBY, JR., 1852, p. 259 *(nom. null.); Pycnondota* COSSMANN & PISSARRO, 1906, pl. 45 *(nom. null.); Cretagryphaea* ARKELL, 1934, p. 62 (*nom. nud.,* not available according to *Code* Art. 11d, *nom. subst. pro Pycnodonta* FISCHER); *Pychnodonta* ROMAN, 1940, p. 355 *(nom. null.)*]. Small to large (up to 16 cm. long). LV mostly highly convex; attachment area small to quite large; LV umbo incurved, either rises barely above hinge line or well above it, species with low umbo subcircular or semicircular in outline, some have long straight dorsal margins continuing in auricles (as in type species), species with prominent raised umbo vertical-oval or prosocline oblique-oval to horizontal-oval in outline and lack auricles, species with either of 2 last-mentioned outlines have concave geniculate posterodorsal margins. Commissural shelf prominent; chomata either long and straight (as in *Crenostrea*) or short to long (up to 13 mm.) and arborescent and vermiculate. Radial posterior sulcus ranges from absent to broad and shallow or broad and deep. Growth squamae nonappressed to very closely appressed. Radial ribs on LV may be absent, gently undulatory and short in some species, or small irregular unequal round-topped and well defined (as in *Costeina*). Concentric

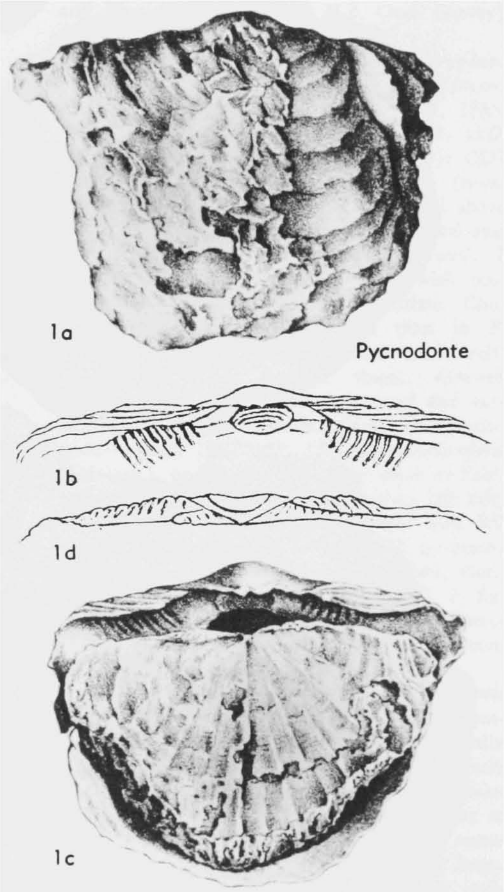

FIG. J80. Gryphaeidae (Pycnodonteinae) (p. *N*1105, *N*1107).

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[1] Pycnodonteinae STENZEL, 1959, is derived from *Pycnodonte*. The form enjoined by the zoological *Code* (Art. 29), Pycnodontinae, was avoided because the names Pycnodontidae and Pycnodontinae already were used in the Pisces. To avoid confusion and homonymy STENZEL (1959) adopted the pattern given as example accompanying *Code* Art. 55a, in this way deriving the name Pycnodonteinae.

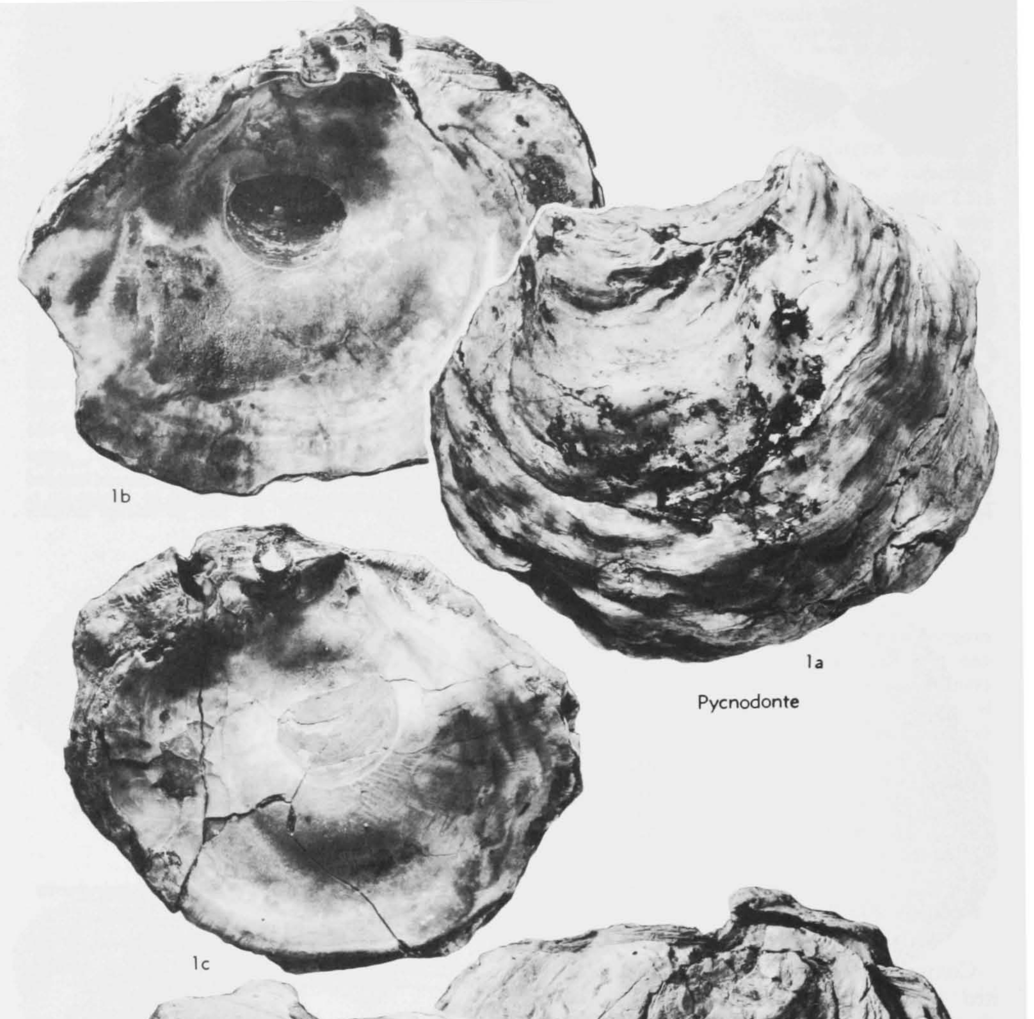

Fig. J81. Gryphaeidae (Pycnodonteinae) (p. N1105, N1107).

puckers or welts parallel to growth lines present or absent on LV. A few Paleogene species have 1 to 3 sharply raised hyote spines on otherwise smooth LV. RV flat to concave, commonly carries sharp radial gashes. [Many authors have assumed that *P. (Pycnodonte) radiata* (U.Cret., Crimea) is the same species as *P. (Phygraea) vesicularis* (LAMARCK) (1806a, p. 160) from the Chalk (Campan.) at Meudon, near Paris, France. In outline, shape, and sculpture they are so dissimilar that this conclusion seems to be erroneous.] *Cret.-Mio.*, cosmop.

P. (Pycnodonte) [=*Ostrea (Gigantostrea)* SACCO, 1897, p. 14 (type, *G. gigantica* (SOLANDER) in BRANDER, 1766, p. 36; OD); *O. (Gigantostraea)* SACCO, 1897, p. 15 *(nom. null.)*; *O. (Biauris)* COSSMANN, 1922, p. 211 (type, *O. (B.) subhippopodium* (ARCHIAC), 1850, p. 439; OD); *Gryphaea (Gryphaea) sec. Circogryphaea* VYALOV, 1936, p. 19 (type, *G. sinzowi* NECHAEV, 1897, p. 53; OD); *Biaurus, Circographaea* HAAS, 1938, p. 294 *(nom. null.)*; *Circogryhaea* VYALOV, 1948a, p. 36 *(nom. null.)*]. LV umbo rising barely above long straight dorsal margin; auricles present; outline subcircular to semicircular; chomata arborescent and vermiculate; radial ribs absent to low, short, and gently undulatory; concentric puckers and welts absent or present; no well-defined radial riblets. *Cret.-Mio.*, worldwide.——FIG. J80,*1*. **P. (P.) radiata* FISCHER DE WALDHEIM, 1835, U.Cret., Crimea; *1a*, LV ext.; *1b*, LV umbo and hinge; *1c*, both valves seen from right side; *1d*, RV umbo and hinge; all ×0.5 (Fischer de Waldheim, 1835).——FIG. J81,*1,2*. *P. (P.) gigantica* (SOLANDER in BRANDER, 1766) (=*"Ostrea (Gigantostrea)"* SACCO, 1897), Eoc.(Barton.); Barton Cliff, Eng.; *1a,b*, LV ext. and int. views; *1c*, RV int.; *2a,b*, both valves, ext.; all ×0.5 [photographs courtesy of †L. R. Cox, British Museum (Nat. History)].——FIG. J82,*1,2*. *P. (P.) subhippodium* (D'ARCHIAC, 1850) (=*"Ostrea(Biauris)"* COSSMANN, 1922), Eoc.(Barton.), Trabay, France *(1a,b)* and Biarritz and vicinity, SW.France *(2a-h)*; *1a,b*, RV int., ext., ×1 (d'Archiac, 1850); *2a,b,e*, RV int., ext., edge view; *2c,d*, RV int., ext.; *2f,g*, LV ext., int.; *2h*, RV int.; all ×1 (Cossmann, 1922).——FIG. J82,*3*. *P. (P.) sinzowi* (NECHAEV, 1897) (=*"Gryphaea (Gryphaea)* section *Circogryphaea"* VYALOV, 1936), Paleoc. below Kamyshin on Volga R., USSR; *3a-c*, LV ext., int., section along mid-axis, ×1 (Nechaev, 1897).

P. (Costeina) VYALOV, 1965, p. 5 [**P. (C.) costei* COQUAND, 1869, p. 108; OD] [*nom. subst. pro Avia* VYALOV, 1936, p. 19, *non* NAVAS, 1912]. As *P. (Pycnodonte)* but has many long, narrow, discontinuous, dichotomous, rounded radial riblets on LV only. *Cret.*, USA(Texas)-Eu.(France)-N.Afr.——FIG. J83,*2*. **P. (C.) costei* (COQUAND), U.Cret.(Campan.), Maadid, Alg.; LV ext., ×0.9 (specimen collected and donated by C. W. DROOGER, Rijks-Universiteit te Utrecht, Neth. Stenzel, n).

P. (Crenostrea) MARWICK, 1931 [**Ostrea (Crenostrea) wuellerstorfi* ZITTEL, 1864, p. 54; OD]. LV umbo prominent, rising well above hinge line; no auricles; LV outline vertical-oval; posterodorsal valve margin not geniculate; chomata strong, straight, most not branching; radial ribs short, gently undulatory; many variable prominent concentric puckers and welts on LV. [When MARWICK established *Ostrea (Crenostrea)* he gave *O. wuellerstorfi* as type species. The type specimen of that species has arborescent and vermiculate chomata so that it must fall into *Pycnodonte*.] *Oligo.*, N.Z.——FIG. J84,*1*. **P. (C.) wuellerstorfi* (MARWICK), up.Oligo.(Duntroon.), North Island *(1a)*, Oligo.(Forest Hill Ls.), Southland (Snowdrift quarry) *(1b-d)*; *1a*, holotype, LV int., ×0.5 (cast of holotype furnished by courtesy of O. PAGET, Naturhistorisches Mus., Wien, Austria); *1b-d*, LV ext., int., post., ×0.6 (specimen by courtesy of C. A. FLEMING and Mrs. A. U. E. SCOTT, N.Z. Geol. Survey) (Stenzel, n).

P. (Phygraea) VYALOV, 1936, p. 19 [**Gryphaea (Gryphaea)* sec. *Phygraea frauscheri* VYALOV, 1936 (=*Ostrea (G.) escheri* FRAUSCHER, 1886, p. 53, *non* MAYER-EYMAR, 1876, p. 29, =*G. pseudovesicularis* GÜMBEL, 1861, p. 659); OD] [=*Phrygaea* STENZEL, 1947, p. 180 *(nom. null.)*]. LV umbo prominent, rising well above hinge line, no auricles, LV outline vertical-oval or procline oblique-oval to horizontal-oval, 2 last-mentioned outlines inequilateral, with posterodorsal margin concave and geniculate. Chomata shorter and less elaborate than in *P. (Pycnodonte)*. Concentric puckers and welts feeble; radial ribs few or absent. Growth squamae mostly very closely appressed and surface of LV rather smooth. *Cret.-Mio.*, worldwide.——FIG. J83,*1*. **P. (P.) pseudovesicularis* (GÜMBEL), up.Paleoc., Haunsberg north of Salzburg, Aus.; *1a-g*, LV ext., both valves left side, right side, both valves left side, right side, RV ext., RV int., ×0.9 (Stenzel, n). [All specimens by courtesy of FRANZ TRAUB, München, Ger.; *1b-c* are plaster cast of specimen of pl. 2, fig. 1a,b of TRAUB, 1938.] [=*Gryphaella* CHELTSOVA, 1969, p. 62 (type, *Gryphaea similis* PUSCH, 1837, v. 1, p. 34; OD).]

Hyotissa STENZEL, **n. genus**, herein [**Mytilus hyotis* LINNÉ, 1758, p. 704, no. 207; OD]. Medium-sized to large (up to 28 cm. long and equally high), valves tending to be subequal and similarly sculptured, LV slightly more convex and capacious than RV, outline variable, mostly suborbicular to vertical oval, more rarely subspatulate and somewhat falcate; attachment area large to very large. Shell commissure plicate in free-growing individuals, commissural plications originating from crude irregularly dichotomous strong radial plicate ribs, tops of which are mostly well rounded and crossed by prominent nonappressed growth

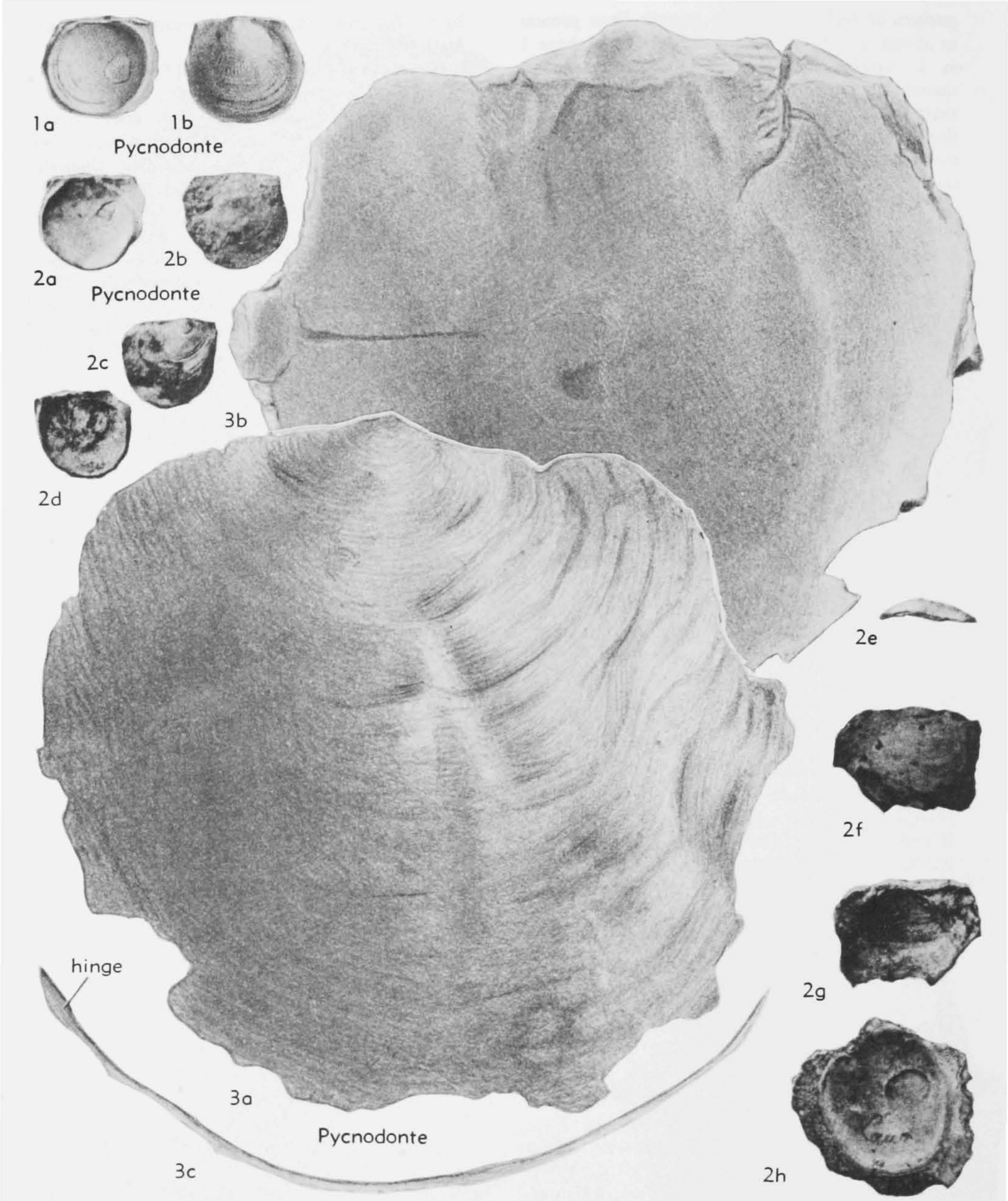

FIG. J82. Gryphaeidae (Pycnodonteinae) (p. *N*1105, *N*1107).

squamae rising here and there into prominent hyote spines. Chomata long, vermiculate, and arborescent, in many places breaking up into tubercles. Distortions of shell shape and sculpture caused by large attachment area common and extensive. [The oldest known species is *H. semiplana* (J. DE SOWERBY, 1825) (v. 5, p. 144, pl. 489, fig. 3), U.Cret., W.Eu., common at Ciply, Belg. The genus is strictly euhaline, stenohaline, and stenothermal, a member of the compound-coral biocoenosis. Only about 4 geographically separated, closely related species live today. The type species has been placed erroneously in *Lopha* by some authors; full credit for recognizing its true affinities must go to RANSON (1939-41, 1941).] *U.Cret.(Turon.)-Rec.,* worldwide.——FIG. J85,*1*. **H. hyotis* (LINNÉ), living, Nosi Bé, Madag.; *1a-c,* ext., int., and edge views of young individual with many tubular hyote spines, ×0.5 (Stenzel, n).——FIG. J85,*2*. *H. hyotis forma sinensis* (GMELIN, 1791), living, Nosi Bé, Madag.; *2a-d*, views of older specimen without tubular spines, with insertion of adductor muscle outlined by pencil in *2c*, ×0.5 (Stenzel, n). [All specimens obtained by courtesy of R. TUCKER ABBOTT, Acad. Nat. Sci. Philadelphia.] [*See* also Fig. J27.]

Neopycnodonte STENZEL, **n. genus,** herein [**Ostrea cochlear* POLI, 1795, v. 2, p. 179 (=*Peloris gracilis*+*Peloriderma cochlear* POLI, 1795, v. 2, p. 255); OD]. Medium-sized (to 9 cm. high), shell walls fragile, very thin, partly translucent, outline variable, many auriculate. LV deep, capacious;

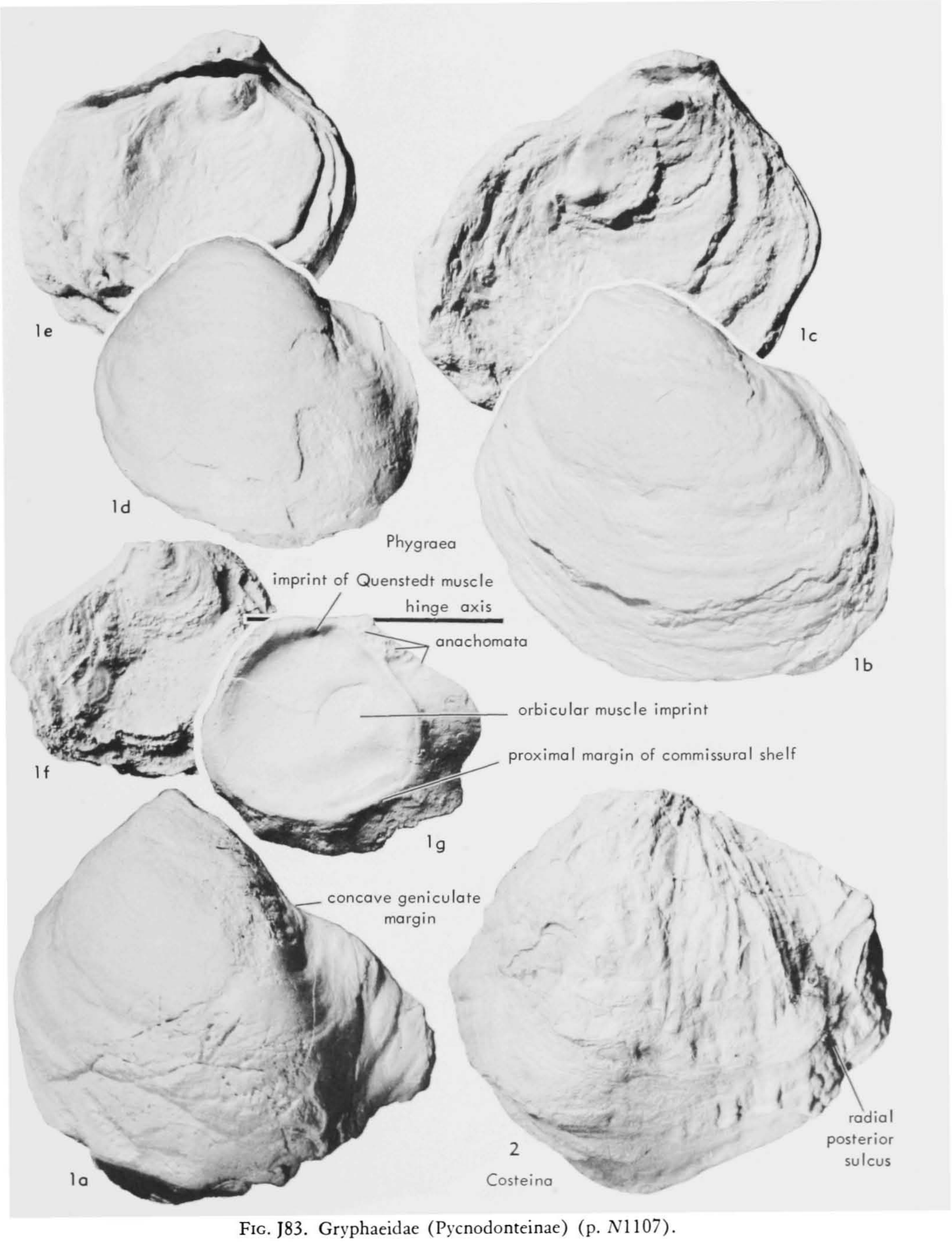

FIG. J83. Gryphaeidae (Pycnodonteinae) (p. N1107).

attachment area small to fairly large, situated commonly on region behind umbo; posterior half of LV rising vertically from substratum attachment so that hinge axis is at 45° to level of attachment; LV mostly smooth, devoid of imbrications, but older individuals have paper-thin foliaceous imbrications near valve margin, and these diverge at 30° to 45° from valve contour, imbrications of some individuals drawn out into long scalelike hyote and spoon-shaped extensions. Auricles on either side of hinge common, foliaceous, imbricate, extensive (to 2 cm.), irregular in outline. LV with 7 to 10 gentle, rounded, irregular radial plications of unequal length and cross section; fairly deep, well-rounded radial posterior groove sets off small posterior flange that

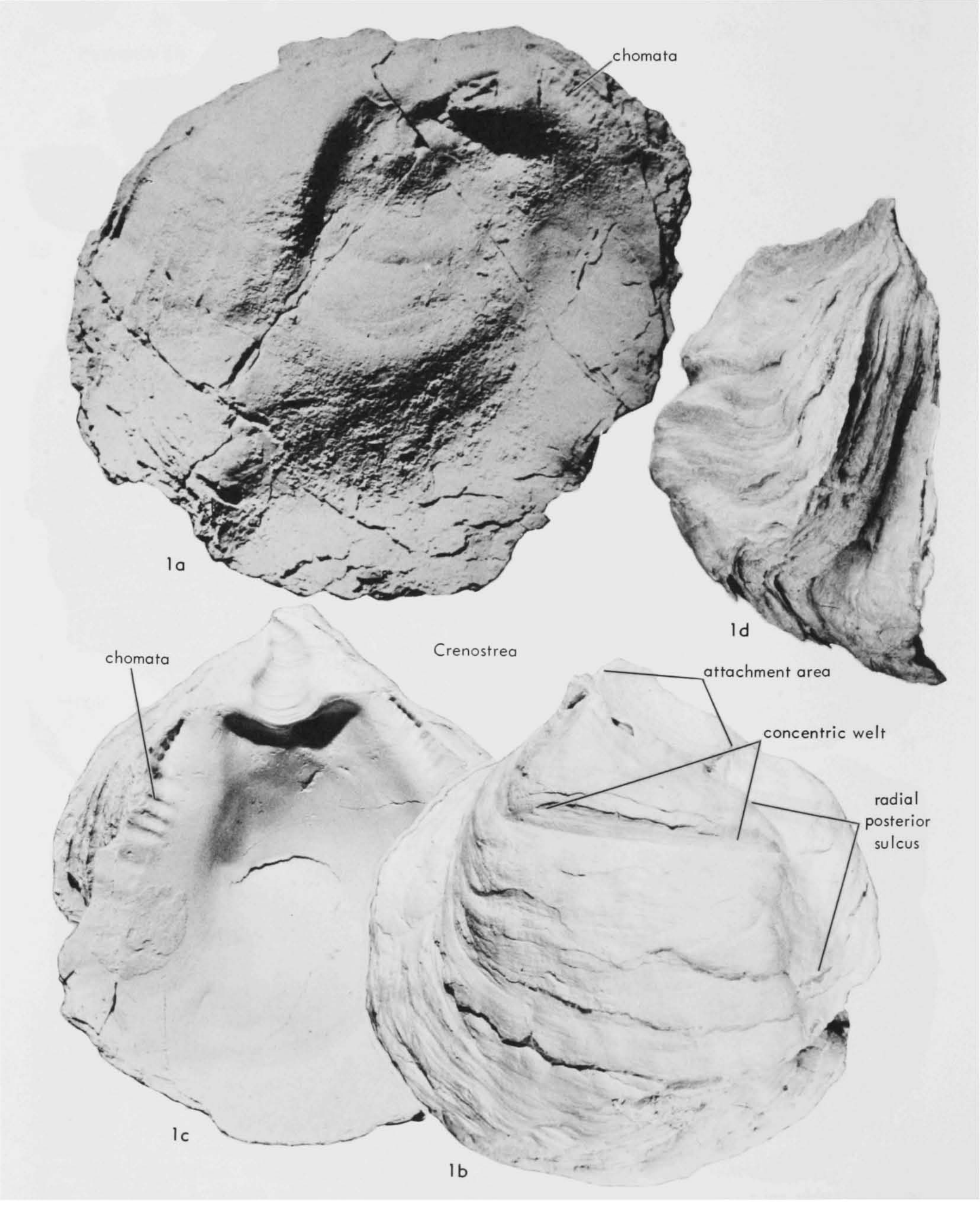

Fig. J84. Gryphaeidae (Pycnodonteinae) (p. N1107).

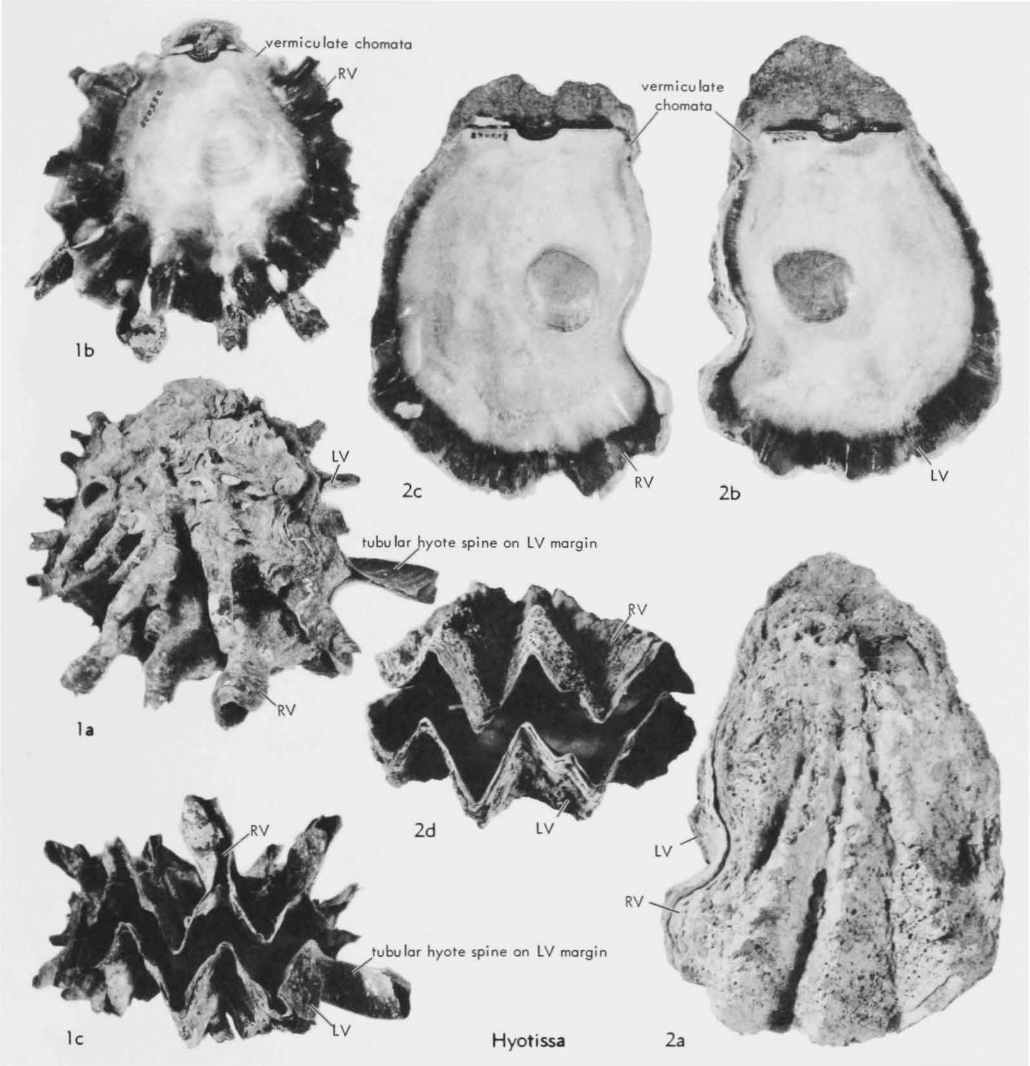

FIG. J85. Gryphaeidae (Pycnodonteinae) (p. *N*1107-*N*1109).

carries 2 plications, but is absent in some individuals and commonly rather difficult to discern. Commissural shelf of LV only in dorsal half of valve, disappearing completely on ventral half. Adductor muscle imprint large, its diameter about 0.25 of valve height. Chomata on LV up to 2 mm. long, smooth, very subdued, hardly detectable in some individuals, restricted to within 1 cm. distance from hinge. RV flat to concave, with scaly imbrications along margins parallel with contour of valve, showing fibrous prismatic structure where broken. Few sharp radial gashes as in *Pycnodonte*. Commissural shelf of RV nearly complete around periphery. [The type species, which is the only living species, has circumglobal distribution. It is strictly stenohaline and euhaline in oceanic waters at 12° to 14°C. and depths of 27 to 1,500 m. The genus descended from *Pycnodonte* and Miocene species are transitional between the two genera. Anatomy of the soft parts has been described by PELSENEER (1896, 1911), and HIRASE (1930, p. 37-41).] *Mio.-Rec.,* worldwide.——FIG. J86,*1,2*. **N. cochlear* (POLI), (="*Ostrea hiranoi* SPICER & BAKER, 1930"), dredged from 50 fathoms (91.4 m.) in Kagoshima Bay, Japan, whitened for photography except *1a; 1a-c,* LV int., int., ext.; *1d,e,* same specimen RV ext., int.; *2a-c,* another specimen, LV int., ext., both valves, all ×0.75 (Stenzel, n). [Specimens from Bernice P. Bishop Museum, Hawaii, USA.]——FIG. J86,*3*. **N. cochlear* (POLI) (="*Pycnodonta floribunda*" MONTEROSATO,

Fig. J86. Gryphaeidae (Pycnodonteinae) (p. *N*1109-*N*1111, *N*1113).

1916, holotype) from 50-60 m. depth near Palermo, Sicily; *3a,b,* cluster, both sides, ×0.75 (Monterosato, 1916).

Texigryphaea Stenzel, 1959, p. 22 [*Gryphaea roemeri Marcou, 1862, p. 95 footnote (=*G. mucronata* Hill & Vaughan, 1898, p. 63, *non* Gabb, 1869, p. 274; =*G. graysonana* Stanton, 1947, p. 28); OD] [=*Ostrea (Marcoui)* Ar-

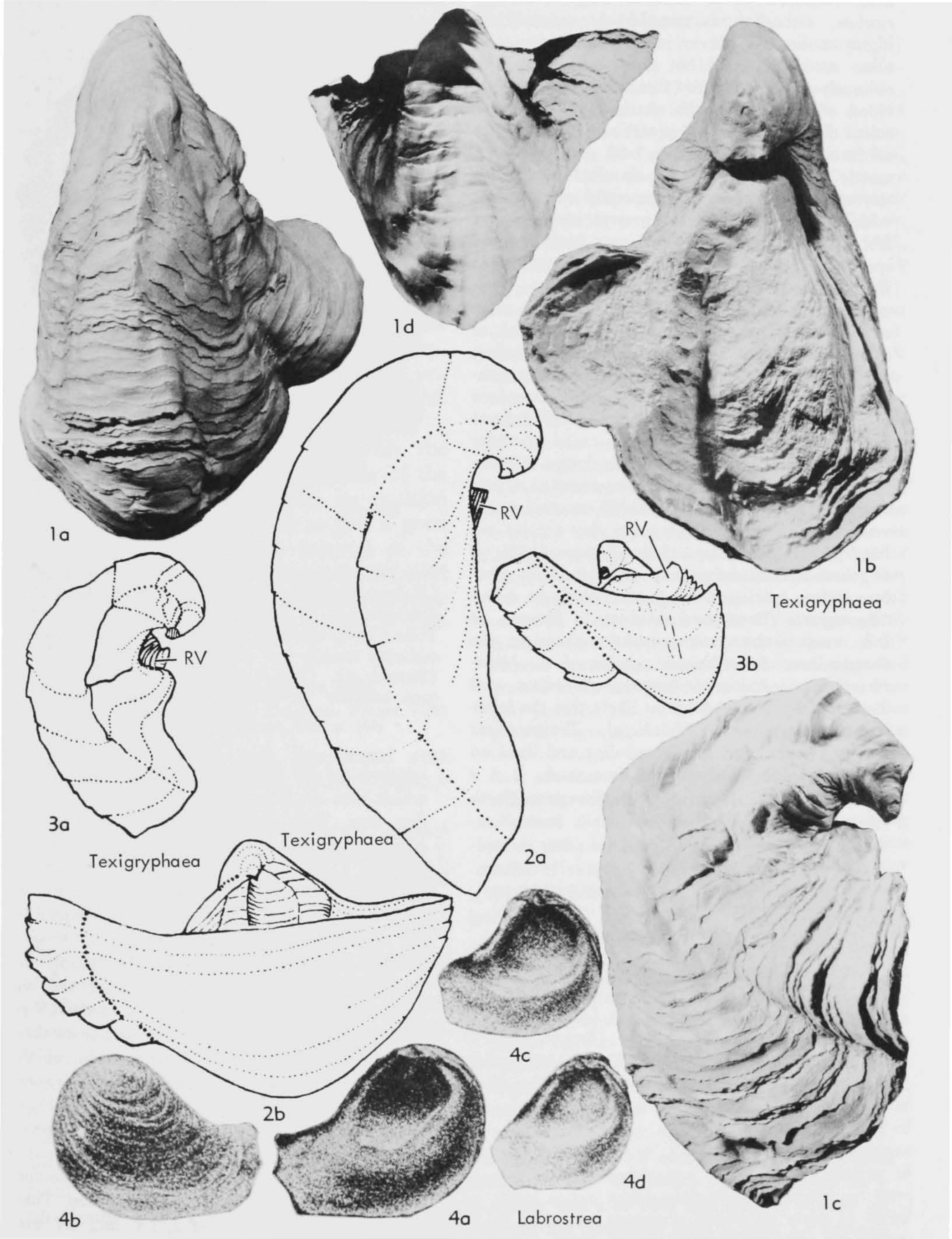

Fig. J87. Gryphaeidae (Pycnodonteinae) (p. *N*1113-*N*1114).

Kell, 1934, p. 64, *nom. nud.; O. (Corrugata)* Arkell & Moy-Thomas, 1940, p. 404, *nom. nud.*]. Small to medium-sized (to 11 cm. high), LV ranging from high and narrow or vertical-oval, bilobate-oval, or bilobate-triangular to auriculate, orthocline to considerably opisthocline, highly to broadly convex in horizontal cross section, not compressed to much compressed in obliquely anteroposterior direction, mostly provided with median radial keel; radial posterior sulcus deeply sunken and posterior flange well set off from main body of valve; beak small, pointed, mostly opisthogyral, highly inrolled and with tiny attachment area. LV generally smooth, but with some poorly appressed growth squamae and few short rounded radial ribs near keel in some species. Umbonal cavity of LV filled with solid shell deposits; no chambers. RV concave, truncated at hinge, without ribs but having some narrow radial gashes; valve margins reflexed so that it comes to lie countersunk in LV when shell is closed. Chomata straight, rarely branching, rarely vermiculate. Differs from *Gryphaea* in its vesicular shell structure, well-defined commissural shelf, chomata, deep radial posterior sulcus, and well-detached posterior flange. [When Stenzel (1959) proposed *Texigryphaea* as a new subgenus of *Gryphaea,* he failed to notice the vesicular shell structure, because the vesicles are filled in with secondary calcite. Ranson (1941, p. 64) had already recognized vesicular shell structure in one species of this genus, which he called "*Pycnodonta Tucumcarii* Marcou." Because of this structure the taxon cannot be placed in the Gryphaeinae. Late Jurassic species of *G. (Bilobissa)* are transitional between *Gryphaea* and *Texigryphaea* so that it seems likely that the latter is a descendant of *G. (Bilobissa). Texigryphaea* was stenohaline and strictly euhaline and lived on bottoms composed of clay or lime mud. It is a provincial genus restricted to southwestern North America from Kansas southward. It formed extensive shell banks composed of countless individuals.] *L.Cret.(Alb.)-U.Cret.(Cenoman.),* Mexico-SW.USA.——Fig. J87,*1.* **T. roemeri* (Marcou), Cenoman.(Grayson Marl), Texas (near Spring Valley, McLennan Co.); *1a-d,* L side, R side, post., umbonal views, ×1 (Stenzel, n).——Fig. J87,*2. T. tucumcarii* (Marcou, 1851), M.Alb.(Kiamichi F.), Texas (near Tahoka, Lynn Co.); *2a,b,* LV post. and ventral views, ×0.7 (Stenzel, 1959).——Fig. J87,*3. T. mucronata* (Gabb, 1869), mid. Alb. (Walnut F.), Texas (Tennessee Valley, Bell Co.); *3a,b,* post. and ventral views, ×0.7 (Stenzel, 1959). [*See* also Fig. J9.]

Fig. J88. *Exogyra (Exogyra) costata* Say (1820), LV from Coon Creek Tongue of Ripley Formation (Maastricht.) of Coon Creek, McNairy County, Tenn., USA, showing perfectly preserved orbicular adductor muscle pad composed of aragonite, ×0.9 (Stenzel, n). [Pad is outlined with pencil. Specimen courtesy of Geology Dept., Louisiana State Univ.]

Doubtful Genus: Labrostrea Vyalov, 1945, p. 200 [**L. labrum;* OD]. *Labrostrea* was introduced by Vyalov in 1936 and 1937 as a new section of *Liostrea s.s.* with a brief definition, but the type species had not yet been described in 1936. It was reintroduced by Vyalov (1945, p. 200-201), at which time the type species was described for the first time. Thus one might argue that *Labrostrea* remained a *nom. nud.* until 1945. However, Stenzel (1947, p. 176) argued that the definition of *Labrostrea* should be regarded as sufficient to cover its sole species and should be accepted as the description of the type species too. Vyalov (1948a, p. 26, 35) emphasized the sharply defined circumferential commissural shelf and the well set-off deep central shell cavity in the LV of this section and based his definition of it on these features. Such features are characteristic of the Pycnodonteinae and it is probable that *Labrostrea* will ultimately find its place among them. However, it is not known whether the type species has vesicular shell structure; therefore *Labrostrea* must remain of dubious taxonomic position. *Paleog.,* USSR.——Fig. J87,*4.* **L. labrum,* Tuar-Kyr, Transcaspian Reg.; *4a-d,* LV int., LV ext., LV int., LV int., ×1 (Vyalov, 1945).

Subfamily EXOGYRINAE Vyalov, 1936

[Exogyrinae Vyalov, 1936, p. 20]

Larva attached to substratum by its left anteroventral valve margin; postlarval growth either regularly spiral throughout life or regularly spiral only for early part and then straight, as in *Ostrea.* Attachment area medium-sized to large, except in few species of *Exogyra s.s.*, some species of *Rhynchostreon,* and in *Ilymatogyra,* all of which lack attachment areas. Ligamental area very short but long in anatomical height; regularly spiralled either throughout life or for early part at least; posterior bourrelet reduced in length so that it forms narrow ridge, in many shells quite sharp, along side of resilifer groove; anterior boundary of resilifer indistinct, because sloping anterior bourrelet grades imperceptibly into resilifer. Adductor muscle imprint orbicular, or nearly so (Fig. J88). *M. Jur.(Bajoc.)-Mio.*

The Exogyrinae are classed with the Gryphaeidae, because of the outline of the adductor muscle imprint and its position close to the hinge. The first to give a good description of the peculiar features of the ligamental area in the oysters now called Exogyrinae was Goldfuss and first to trace its evolution was Douvillé (1886, p. 230-232).

Tribe EXOGYRINI Vyalov, 1936

[*nom. transl.* Stenzel, herein (*ex* Exogyrinae Vyalov, 1936) ="Gruppa I." Mirkamalov, 1963, p. 152]

Postlarval growth and ligamental area regularly spiral throughout. *M.Jur.(Bajoc.)-U.Cret.(Maastricht.).*

The Tribe Exogyrini became extinct with the end of the U. Cret. (Maastricht.). However, an Eocene species was described from Fergana, Central Asia, USSR, namely *Exogyra ferganensis* Romanovskiy, 1879. This species has recently been restudied and assigned to the exogyrine genus *Amphidonta* [*recte Amphidonte*] by Gekker, Osipova, & Belskaya (1962, v. 2, p. 139). Nevertheless, this Central Asian species does not have a posterior bourrelet that is reduced in length to form a narrow ridge as in the true Exogyrini, and its adductor muscle insertion is clearly reniform as in the Ostreidae so that there is no doubt that it is an ostreine and not an exogyrine oyster. It is an *Exogyra* homeomorph and is believed to be a descendant or member species of the ostreine genus *Ferganea.* It remains an incontroverted observation that all the tribe Exogyrini became extinct with the end of the U. Cretaceous (Maastricht.).

Exogyra Say, 1820, p. 43 [**E. costata;* M] [=*Exegyra* Benett, 1831a, p. 122 *(nom. null.); Exogira* Matheron, 1843a, p. 262 *(nom. van.); Exagyra* Fischer de Waldheim, 1848, p. 464 *(nom. null.); Exogera* Desmarest in Chenu, 1859, v. 4, p. 33 *(nom. null.); Exoyra* Seguenza, 1882, p. 180 *(nom. null.)* (obj.); *Costagyra* Vyalov, 1936, p. 20 (type, *E. olisiponensis* Sharpe, 1850, p. 185; OD); *Fluctogyra* Vyalov, 1936, p. 20 (type, *Ostrea trigeri* Coquand, 1869, p. 119; OD); *Nutogyra* Vyalov, 1936, p. 20 (type, *O. fourneti* Coquand, 1862, p. 229; OD)]. Small to large, mostly medium-sized (largest diameter of largest known specimen 21 cm.). Shell very inequivalve, RV flat to concave, LV tumid, convex, much larger than RV. Attachment area variable, large in most species, very small in few; spirally curved umbonal half of LV convex and rather tumid, except in species with small attachment area, spiral keel obtuse and rounded, never prominent, evanescent in old age, hardly noticeable in most individuals. LV outline orbicular to oval, margins in most species convex throughout except for dorsalmost part of posterior margin which may be rectilinear or concave; very few species somewhat falcate in outline, with much of posterior part of the LV margin gently concave (see *Fluctogyra*). Anterior part of RV exterior with many crowded concentric upturned growth squamae parallel to anterior valve margin; posterior part of RV with flat-lying foliaceous growth squamae. LV with wide commissural shelf delimited by rounded curb in species that lack chomata or by narrower rounded curb and adjoining shallow gutter in species that have chomata. Anterior set of LV chomata consisting of 3 mm. long straight parallel radial ridgelets separated by grooves, all closely spaced; posterior set consisting of 7 mm. long, transverse, vermiculate ridgelets covering entire width of commissural shelf near hinge, this part of shelf sigmoidally curved so that it forms inward and upward projecting platform covered with vermiculate chomata in some specimens (Fig. J89, J90). RV margin reflexed to form commissural shelf which allows valve to become countersunk into LV, anterior margin reflexed at about 70°. Quenstedt muscle imprint, visible only on RV, narrow, elongate, and about 1 mm. removed from posterior end of resilifer. Sculpture of LV, and to lesser extent of RV, consisting of foliaceous growth squamae alone or in combination with various patterns of radial costae which include hyote spines or rows of successive transverse bulges on crests of radial costae. *Cret.,* N.Am.(Gulf Mexico area-Atl. Coastal Plain-Utah)-S. Eu.-N. Afr.-Angola-Nigeria-W. Asia-India.

[*Fluctogyra* VYALOV, 1936, proposed as a section of *Exogyra,* supposedly is characterized by vague radial undulations. Such costules are present also on *E. (E.) erraticostata* STEPHENSON (1914, p. 49, pl. 15, fig. 4, pl. 16, fig. 1-2), which cannot be separated from *Exogyra s.s.* However, the type species of *Fluctogyra* differs from *Exogyra s.s.* in somewhat elongate falcate outline of LV margin, which seems an unimportant distinction.——*Costagyra* VYALOV, 1936, also proposed as a section of *Exogyra,* carries chomata and has a few projecting radial ribs on RV (REESIDE, 1929) (Fig. J91). Although it is very close to *Exogyra s.s.,* it may be a valid minor subdivision.——Some apparently isolated species of *Exogyra* have LV with a very small attachment area, a not so tumid, rather slender umbonal tip end, and a greater number of spiral volutions. It is puzzling that some individuals have no chomata, whereas others have well-developed ones.]

E. (Exogyra). Sculpture of LV and to a lesser extent that of RV consisting of 1) unfrilled rough foliaceous growth squamae, 2) weak discontinuous irregular radial ribs that are rounded and separated by interspaces as wide as or wider than these ribs, 3) strong continuous dichotomous radial ribs that are round-topped and separated by interspaces as wide as or much narrower than the ribs, 4) radial series of transverse rounded bumps, or 5) hyote spines developed from crests of radial ribs. *Cret.,* N.Am.-S.Eu.-N.Afr.-Angola-Nigeria-W.Asia-India.——FIG. J89,*1*. **E. (E.) costata* (SAY), U.Cret.(Maastricht., Corsicana Marl, Navarro Gr.), Texas (San Geronimo Creek, Medina Co.); *1a,b,* shell ext. from LV and

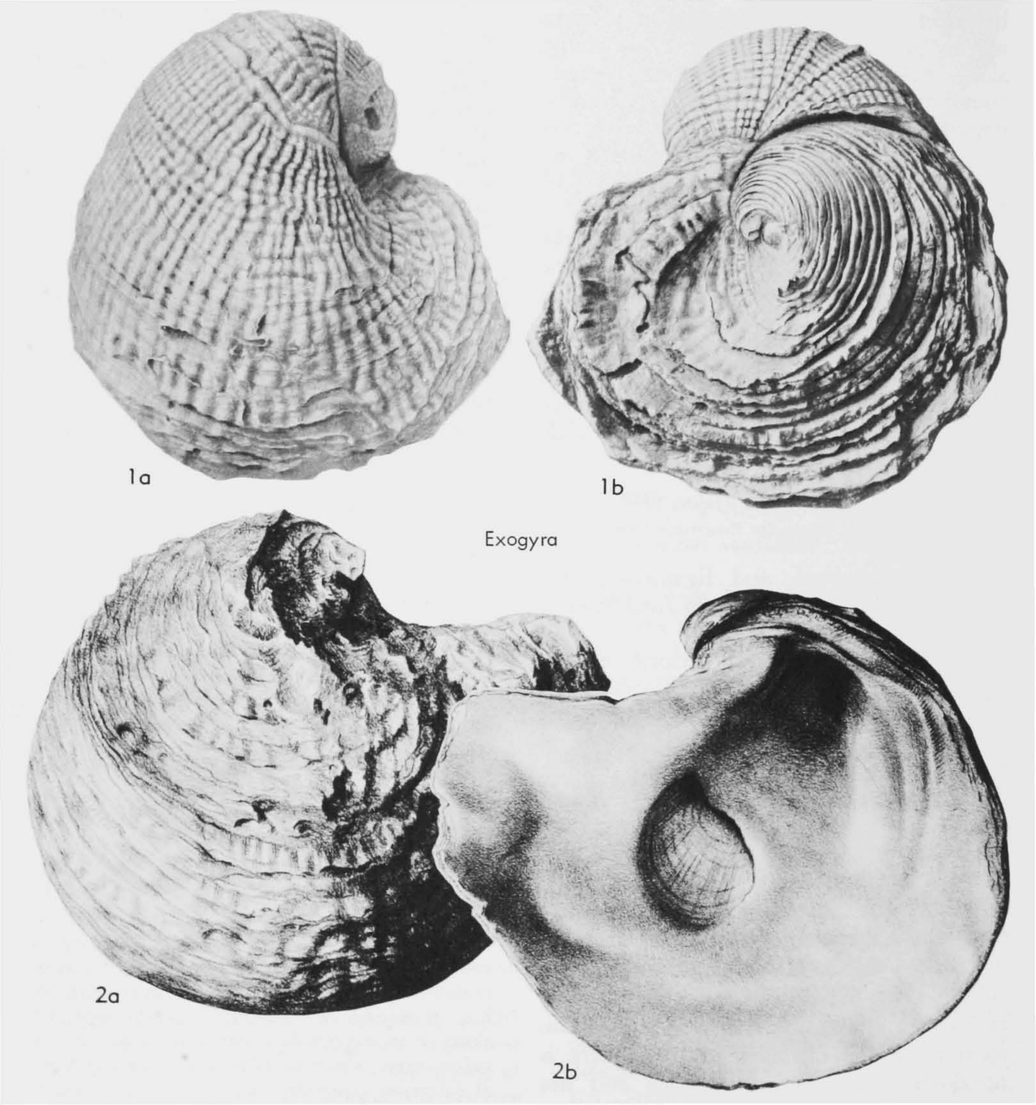

FIG. J89. Gryphaeidae (Exogyrinae) (p. *N*1115-*N*1117).

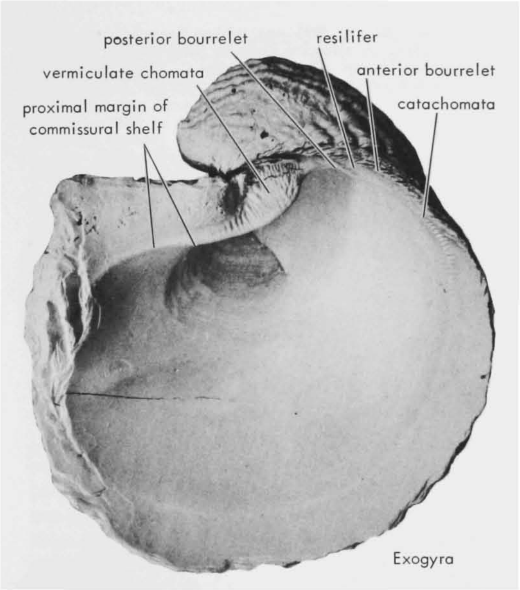

Fig. J90. Vermiculate chomata on projecting platform at posterodorsal terminus of commissural shelf in *Exogyra (Exogyra) *costata* Say, 1820, from Navesink Marl, U.Cret.(Maastricht.), New Egypt, N.J., USA; ×0.8 (Stenzel, n).

RV sides, ×0.7 (Stephenson, 1941).——Fig. J89,*2*. *E. (E.) trigeri* (Coquand, 1869) [="*Exogyra* section *Fluctogyra*" Vyalov, 1936], U.Cret. (Cenoman.), France (LeMans); *2a,b,* LV ext., LV int., ×0.7 (Bayle, 1878). [*See* also Fig. J24-J26, J88, J90.]

E. (Costagyra) Vyalov, 1936, p. 20 [**E. olisiponensis* Sharpe, 1850, p. 185; OD]. Distinguished from *Exogyra s.s.* by 7 to 12 flat-topped RV radial ribs that project beyond periphery of valve; radial ribs on LV narrow, separated by wide, concave interspaces. Rib pattern highly variable. According to Reeside (1929) some variants of type species lack radial ribs. Chomata present. *U.Cret.(Cenoman.-Turon.),* S.Am. (Colom.)-Mexico-USA(Utah)-N. Afr.-Angola-S. Eu.——Fig. J91,*1*. **E. (C.) olisiponensis* (Sharpe), U.Cret.; *1a,b,* up. Turon., Alcantara near Lisbon, Port., figured types, ×0.4 (Sharpe, 1850); *1c,* Cenoman., Tunisia; ×0.4 (Pervinquière, 1912).

Aetostreon Bayle, 1878, pl. 139 explanation [**Gryphaea latissima* Lamarck, 1819, p. 199; SD Douvillé, 1879] [=*Actostreon* Eberzin (ed.), 1960, p. 89 (*nom. null.*).] Medium-sized to large (up to 16 cm. high and 13 cm. long), inequivalve; LV deep, RV flat or even concave. LV with spiral, well-defined, although rounded keel, commonly surmounted at intervals by elongate knobs and broad, shallow well-marked groove, which runs subparallel with keel and is about 1-2 cm. from keel on posterior side of valve; groove separating gently convex posterior flange from main body of LV. Both valves lacking costae, but with many poorly appressed growth squamae; LV also with low concentric swellings parallel to growth lines. Spiral beak of LV not projecting much beyond outline of RV. No chomata. RV somewhat countersunk into LV, because its anterior margin is somewhat reflexed, although not as much as that of *Exogyra* s.s.; RV with a concavity extending from umbo to branchitellum. *L.Cret.(Valangin.-Alb.),* Eu.(Spain-France-Eng.-Switz.)-Afr. (E. Afr.-Madagascar)-Caucasus.——Fig. J92,*1*. **A. latissimum* (Lamarck), Apt., France (Wassy, Département Haute-Marne); *1a-c,* LV ext., LV ext., shell ext. from RV side, all ×0.7 (Bayle, 1878). (See also Fig. J63).

[Stenzel's (1947, p. 168) conclusion that *Aetostreon* must date from Bayle in Douvillé, 1879, is no longer correct

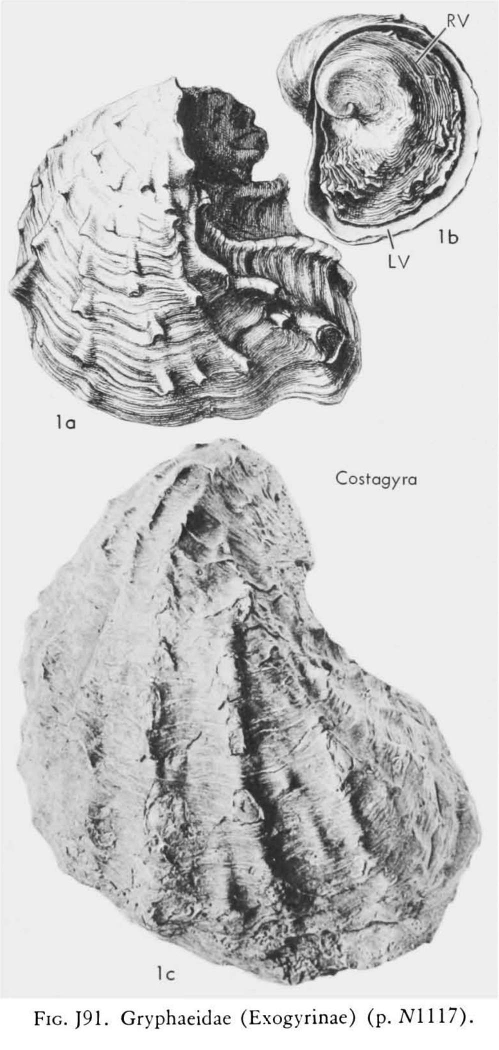

Fig. J91. Gryphaeidae (Exogyrinae) (p. *N*1117).

in view of changes made in the zoological *Code* (1964). Stenzel (1947, p. 169) also erred in concluding that the correct name of the type species is *A. aquila* (Brongniart in Cuvier & Brongniart, 1822). *Gryphaea latissima* Lamarck (1801, p. 399) was neither figured nor described but validated by reference given to illustrations "N. Bourg. Petrif. pl. 14, no. 84, 85 Esp. foss." These illustrations in Bourget clearly depict a broad exogyrine shell. Pervin-

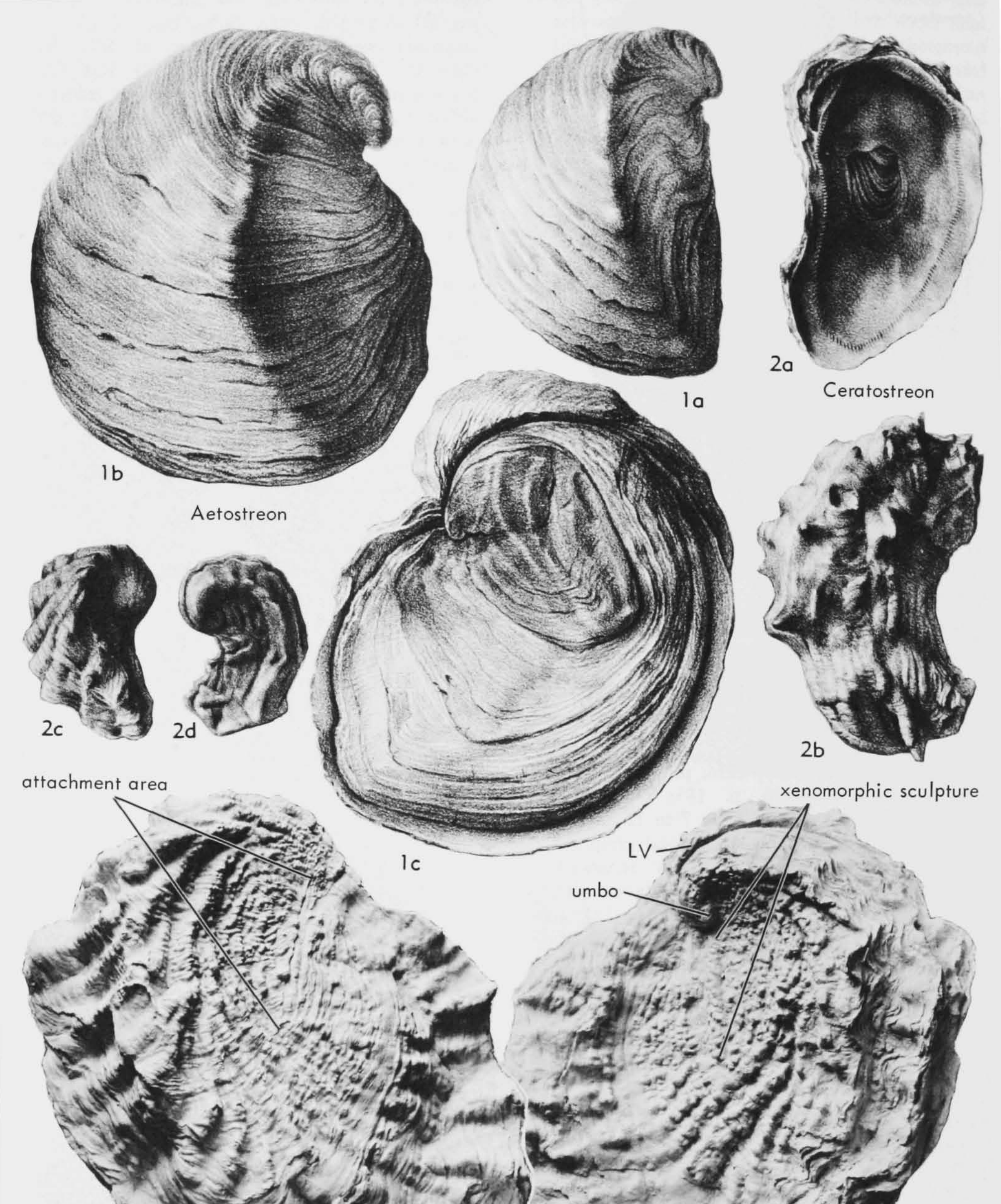

Fig. J92. Gryphaeidae (Exogyrinae) (p. *N*1117-*N*1119).

quière (1910b) figured Lamarck's two syntypes, which obviously belong to two different species, one broad and large, the other narrow and small. Only the former corresponds to the figures in Bourget. Pervinquière erred in stating that "the reference to the figure in Bourget applies as well to the small [syntype]." Relying on this statement Stenzel (1947, p. 169) was mistaken in concluding that the correct name of the type species is *Aetostreon aquila* (Brongniart). Rather, the type species is *Aetostreon latissimum* (Lamarck, 1801) and some of its synonyms or very closely related species are *Gryphaea couloni* Defrance, 1821 (=*Gryphaea sinuata* J. Sowerby, 1822; *Griphea aquila* Brongniart, 1822).]

Amphidonte Fischer de Waldheim, 1829, p. 31 [**A. humboldtii* Fischer de Waldheim, 1829, pl. 1, fig. 1-4; SD Fischer, 1886, p. 927] [=*Amphidonta* Anonymous, probably Bronn, 1831, p. 335 *(nom. van.); Amphiodonta* Agassiz, 1846, p. 18 *(nom. van.); Amphitonde* Schauroth, 1865, p. 166 *(nom. null.); Amphydonta* Vyalov, 1948c, p. 13 *(nom. null.)*]. Similar to *Aetostreon* but with many chomata, commonly along entire periphery of both valves and spiral keel that is not prominent, well rounded, and not built up as ridge above LV surface, its growth squamae less prominent and tending to be smoother. *Cret.*, USSR; *L.Cret.(up.Alb.)*, N.Am.(Texas).——Fig. J93,*1*. **A. humboldtii* (Fischer de Waldheim), U.Cret.(Cenoman.),USSR; *1a-c*, LV ext., LV int., RV int., ×0.6 (Fischer de Waldheim, 1837); *1d,e*, LV ext., RV int., ×0.6 (Mirkamalov, 1964).

Ceratostreon Bayle, 1878, pl. 133-134 explanations [**Exogira spinosa* Matheron, 1843, p. 192 (=*Ostrea matheroniana* d'Orbigny, 1848, p. 737; *Ceratostreon matheroni* Bayle, 1878, pl. 134, fig. 1-2, 10-11); SD Douvillé, 1879] [=*Ceratostrea* Haas, 1938, p. 294 *(nom. van.)*]. Medium-sized (up to 10 cm.); outline narrow, elongate and crescentically curved or comma-shaped to ovate with umbonal region forming larger end. Shell inequivalve. Attachment area generally large. Both valves keeled, but merely in sense that each has 2 different slopes which meet along spirally disposed crest that is much obscured by surface sculpture that crosses it; anterior slope narrower, descending steeply to anterior valve margin; posterior slope larger, descending more gently to posterior valve margin, flat or concave on RV, gently convex on LV. Many dichotomous, unequal, rounded costae and equally large and rounded interspaces on both valves; costae of type species short, discontinuous, and rising at their ends into prominent spines, particularly at places where costae cross keel; in other species costae are continuous and less spinous, costae in many consisting of series of contiguous transverse puckers. Chomata slender and well developed, 1-5 mm. long, situated along all periphery of the valves. *L. Cret.(Apt.-mid. Alb.)*, N. Am.(Mexico-Texas-Okla.-Kans.)-S. Am.(Colom.); *Cret.(Neocom.-Senon.)*, Eu.-N. Afr.——Fig. J92,*2*. **C. spinosum* (Matheron), U.Cret., France (Royan, Département Charente-Inférieure); *2a,b*, LV int., ext., ×0.7; *2c,d*, shell ext. from LV and RV sides, ×0.7 (Bayle, 1878).——Fig. J92,*3*. *C. texanum* (Roemer, 1852), mid.Alb.(Up. Walnut Clay), Texas (Coryell Co. near Mound); *3a,b*, shell ext. from LV and RV sides, ×1 (Stenzel, n). [*See* also Fig. J45.]

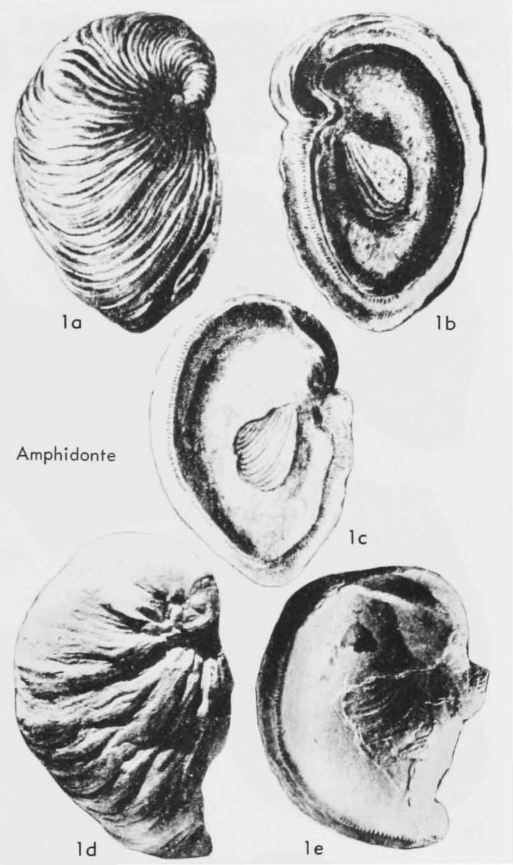

Fig. J93. Gryphaeidae (Exogyrinae) (p. *N*1119).

[d'Orbigny failed to explain why he changed the species name from *spinosa* to *matheroniana;* possibly he was aware that already an *Ostracites spinosus* von Schlotheim, 1813, p. 73, and an *Ostrea spinosa* F. A. Roemer, 1835, p. 58 were available. No proof is found to indicate that these homonyms are congeneric; therefore Matheron's name is retained in preference to the others. Stenzel's (1947, p. 171) conclusion that *Ceratostreon* must date from Douvillé, 1879, is no longer correct in view of changes in the zoological *Code* (1964).]

Ilymatogyra Stenzel, **n. genus,** herein [**Exogyra arietina* Roemer, 1852, p. 68; OD]. Small (largest diameter up to 4 cm.). Shell shape resembling elevated corkscrew spiral, highly inequivalve, LV corkscrew-shaped, RV countersunk, slightly convex, operculiform. Tip of LV umbo carrying small smooth semitranslucent pointed cap set off by deep groove, cap made by postlarval calcite infilling of prodissoconch, which, because of its original aragonitic composition, has been leached and has disappeared. No attachment area present.

Umbonal part of LV devoid of ribs for about 3 mm. from tip, covered beyond by about 35 equal wrinkled dichotomous radial costules, which disappear before size of 10 mm. is reached (Fig. J32). Rounded, but well-defined keel evanesces in later growth. Many individuals with concavity on posterior slope of LV, this concavity extending in spiral to posterior valve margin where it originates from concave part of LV margins situated close to adductor muscle. LV margin of late growth stages has several tongue-shaped protrusions separated by rounded sinuses; these show best on growth lines. RV with orbicular or indented reniform outline and reflexed valve margins, because of which it is countersunk into LV opening, its spiral nucleus carrying calcitic

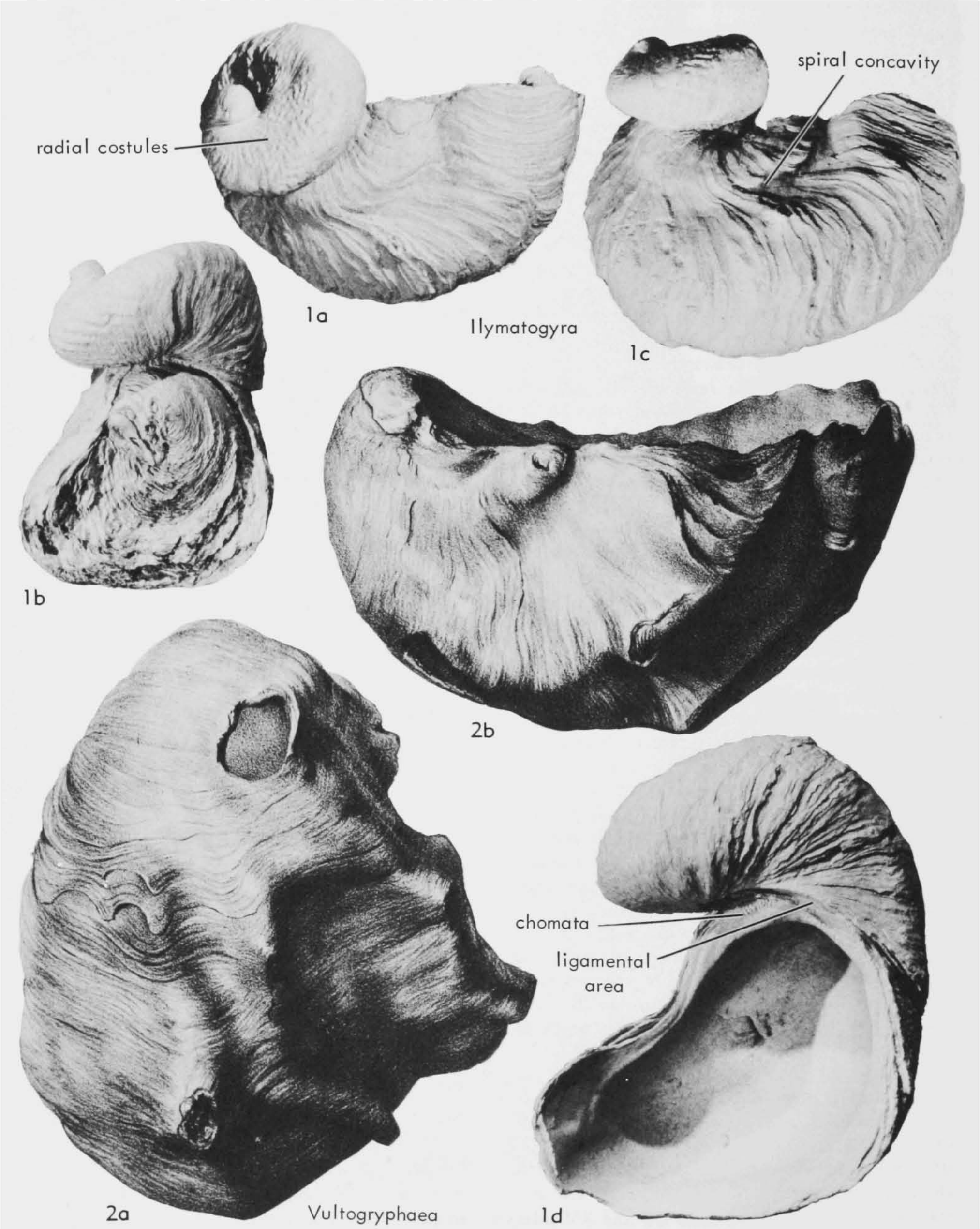

FIG. J94. Gryphaeidae (Exogyrinae) (p. *N*1119-*N*1121, *N*1124).

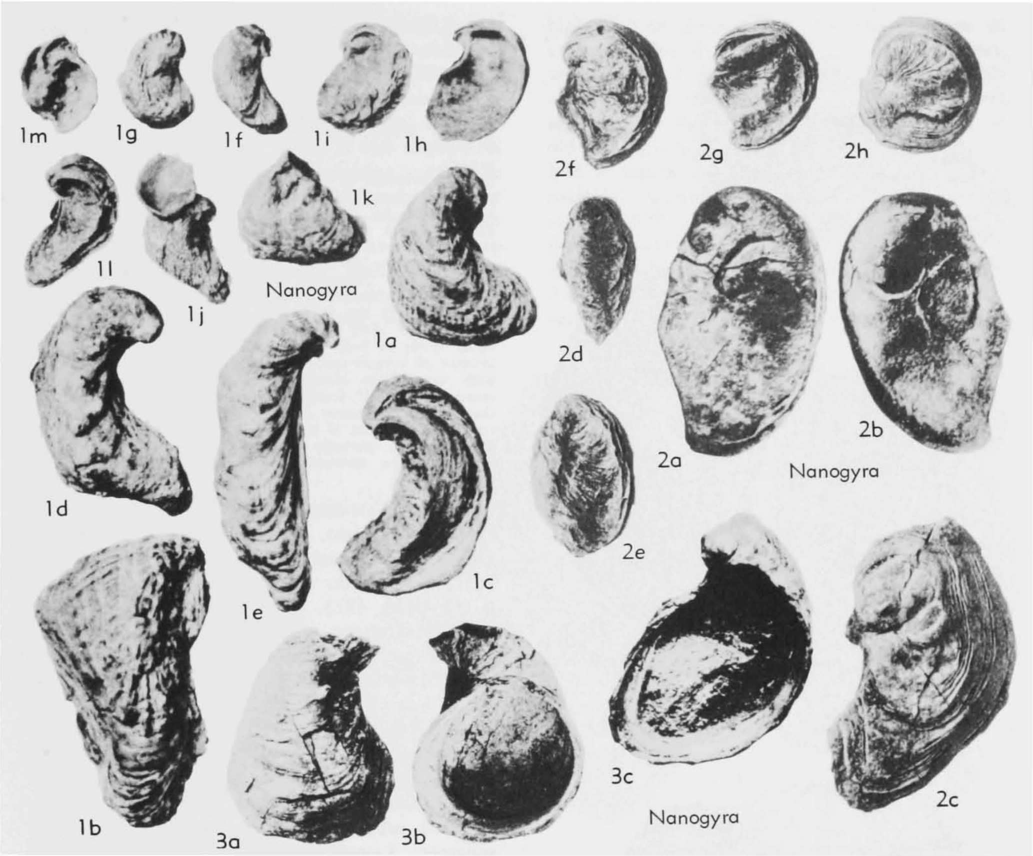

FIG. J95. Gryphaeidae (Exogyrinae) (p. *N*1121-*N*1122).

umbonal cap, similar to that of LV, and smooth early coil forming boss at indentation of reniform outline; remainder of RV covered by countless concentric upturned crestlike growth squamae. *U. Cret.(Cenoman.),* NE. Mexico-USA(Texas-Okla.).——FIG. J94,*1*. **1. arietina* (ROEMER), Grayson Marl, C.Texas; *1a-c,* bivalved specimens, various views, ×2; *1d,* LV, ×2 (Stenzel, n). [*See* also Fig. J32.]

[The genus is monotypic. Its features indicate adaptation to an ooze bottom lacking firm fragments for attachment. The sediment in which it is found is a sticky clay now (Grayson Marl or Del Rio Clay). A detailed description of the type species was given by BÖSE (1919).]

Nanogyra BEURLEN, 1958, p. 206 [**Gryphaea nana* J. SOWERBY, 1822, v. 4, p. 114; OD] [=*Palaeogyra* MIRKAMALOV, 1963, p. 152 (type, *Exogyra virgula* GOLDFUSS, 1833, p. 33, *non Ostrea virgula* DEFRANCE, 1821, p. 26, *nom. nud.,* =*Exogyra striata* (WILLIAM SMITH, 1817) *fide* ARKELL, 1933, p. 440, footnote 9)]. Shell small (greatest diameter of large individuals 3 cm.), greatly variable in shape and outline, inequivalve; LV globular to moderately convex, its outline suborbicular or subtrigonal, elliptical, ovate, to comma-shaped, all specimens spirally twisted, but shape and degree of spirality varying considerably from one to another; LV bilobate in some individuals, because spiral groove divides it into 2 unequal lobes; spiral groove ending in sinus at valve margin located dorsal of branchitellum and producing lingulate outline that is fairly common. RV flat to partly concave or gently convex, its outline varying from suborbicular to ovate, comma-shaped, or auriform to lingulate at branchitellum. LV covered with fine radial ribs or rough concentric growth squamae that have local puckers or constrictions in some places. RV with few major growth squamae except along anterior valve margin, which has many crowded upturned growth squamae. Spiral beak of LV coils tightly over ligamental area so as to obscure it largely. In contrast to *Exogyra,* ligamental area of *Nanogyra* is much more variable as to spirality, 2 bourrelets being about equal in length, and posterior one not narrower than anterior. *Jur. (Bajoc.-Portland.),* Eu. (Eng.-Scot.-France-Ger.-Pol.-Switz.)-India-Arabia (Yemen)-Afr. (Ethiopia-Somalil.-E.Afr.).——FIG. J95,*2,3*. **N. nana* (J. SOWERBY), up.Oxford.(U.Calcareous Grit), Eng.

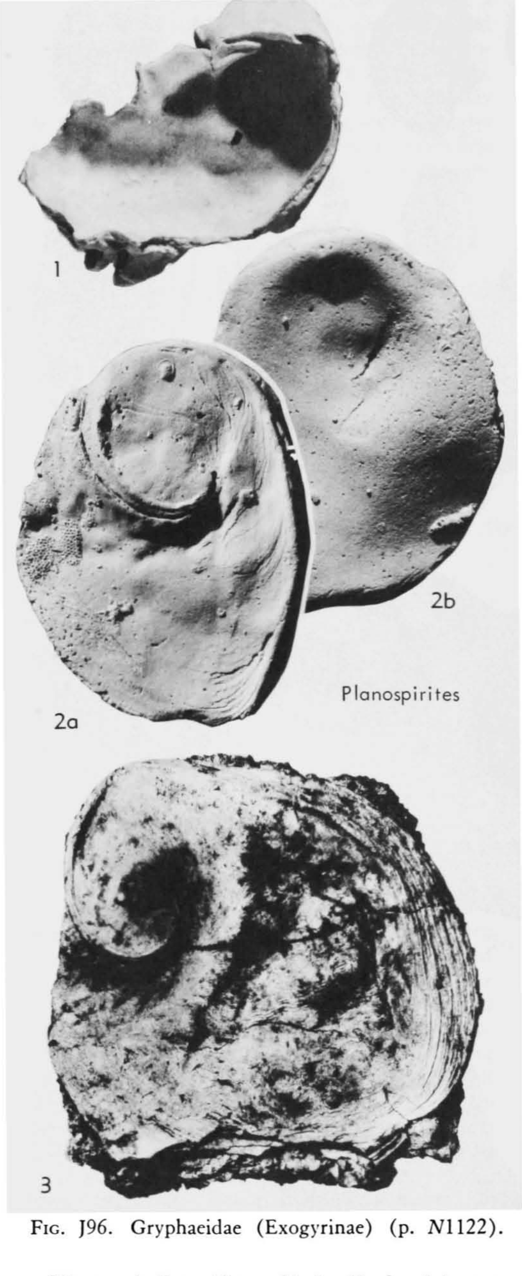

FIG. J96. Gryphaeidae (Exogyrinae) (p. *N*1122).

(Ringstead Bay, Dorsetshire) *(2a-h, 3c)*, up. Kimmeridg. [Shotover Grit Sands—Zone of *Pectinatites pectinatus* (PHILLIPS)], Shotover Hill, Oxfordshire *(3a,b)*; *2a-h*, RV ext., int., RV exteriors, ×1; *3a-c*, LV ext., int., int., ×1 (Arkell, 1932).——FIG. J95,*1*. *N. striata* (WILLIAM SMITH, 1817) (=*Exogyra virgula* GOLDFUSS, 1833, ="*Paleogyra*" MIRKAMALOV, 1963), low. Kimmeridg., France, various localities; *1a-m*, LV ext., LV ext., shell right side, LV ext., both valves left side, left side, left side, LV int., both valves right side, LV ext., LV ext., both valves right side, LV int. on cluster, ×1 (Jourdy, 1924).

[ZIEGLER (1969) regards *N. virgula* as a descendant of *N. nana* so that it is very likely that the two are congeneric.]
[Best description of the type species and excellent synonymy were given by ARKELL (1932), p. 175-180, pl. 17, fig. 2-21; pl. 18, fig. 3-11; pl. 19, fig. 4, 4a and text fig. 48). The fact that the posterior bourrelet of the ligamental area is not reduced to a narrow strip is indicative of the primitive status of the ligament, according to BEURLEN, who regarded *Nanogyra* as the link between Jurassic *Liostrea* and Cretaceous *Exogyra*. BEURLEN pointed out (1958, p. 205) the following primitive features of *Nanogyra:* small size; under-developed spirality of the left beak; spiral of beak rarely makes one complete volution; absence of inward and upward projecting platform covered with vermiculate chomata that is an extension of the commissural shelf found in *Exogyra s.s.* It is probable that the spiral groove dividing the LV of *Nanogyra* into two unequal lobes is homologous to the spiral groove of *Gryphaea*. If correctly interpreted, this condition would speak for the derivation of the Exogyrinae from the Gryphaeinae.]

Planospirites LAMARCK, 1801, p. 400 [**Planospirites ostracina* LAMARCK, 1801 (=*Exogyra planospirites* GOLDFUSS, 1863, text v., pt. 2, p. 37, *nom. van.*); M] [=*Planospirigenus* RENIER, 1807, pl. 8, rejected ICZN, Opin. 427]. Shell medium-sized to large (greatest diameter to 15 cm.), outline oval; shell very inequivalve; LV deep and basin-shaped, RV very flat; attachment area rather large, covering entire bottom of LV which has steeply upstanding to vertical anterior wall rising from attachment area and carries few irregular wavy radical costae. RV devoid of any costae, at its anterior margin with narrow spiral band composed of thin crowded subparallel upturned successive growth squamae. LAMARCK had only separate LVs and RVs of the type species, not realizing that they belonged together. He described only the RV under the name *P. ostracina*, therefore, classing it as a univalve. *U.Cret.(Maastricht.)*, W.Eu.——FIG. J96,*1-3*. **P. ostracina*, Neth.(St. Pietersberg—south of Maastricht); *1*, LV int. (type of FAUJAS-SAINT-FOND, pl. 28, fig. 5, as *Rastellum*, specimen loaned by courtesy of C. A. VAN REGTEREN ALTENA, Teyler's Museum, Haarlem, Neth., no. 5137), ×0.7; *2a,b*, RV ext., int. (topotype), ×1; *3*, RV ext. (monotype of LAMARCK, Museum Natl. d'Histoire Nat. Paris), ×0.7 (*1,2*, Stenzel, n; *3*, Jourdy, 1924).

Rhynchostreon BAYLE, 1878, pl. 138 explanation [**R. chaperi* BAYLE, 1878, pl. 138, fig. 1-5 (=*Gryphaea suborbiculata* LAMARCK, 1801, p. 398; *G. columba* LAMARCK, 1819, v. 6, pt. 1, p. 98; *R. suborbiculatum* (LAMARCK); SD DOUVILLÉ, 1879)] [=*Rhyncostreon* HILL & VAUGHAN, 1898, p. 25, 29, *nom. null.*]. Medium-sized (up to 13 cm. high), highly inequivalve; LV smooth and highly convex, especially so in anteroposterior cross section; LV beak narrow, so greatly elevated above hinge that valve height exceeds length (generally height is 108 percent of length, but may reach 143 percent), highly incoiled (up to 2 volutions), opisthogyral although it is more nearly orthogyral than LV beak of other genera in the Exogyrinae. Surface of LV very smooth, with faint and smooth growth wrinkles and closely and smoothly appressed growth squamae. Rounded keel present on LV only in its earliest growth stage, when about 1 cm. high; keel more noticeable in individuals having many fine radial costules, which are also restricted to earliest growth stage. Broad and shallow radial sulcus starting on LV in mature growth stage, easily overlooked. Attachment area absent or very small, at best 9 by 13 mm. in size. RV suborbicular to horizontal elliptical, longer than high, flat in dorsoventral direction, concave in anteroposterior direction and devoid of costules, with flat spiral umbo and smooth with smoothly appressed growth squamae, no reflexed growth squamae at anterior valve margin. Mature to old individuals have broad gentle terebratuloid fold at ventral margin. Adductor muscle imprint orbicular. Ligamental area very narrow. No chomata. [Although many authors use the species name *columba,* the earliest available name is *suborbiculatum.*] *U.Cret.(Cenoman.-Turon.),* N. Am.(Mexico-Texas-N.Mexico-Colo.-Minn.-Va. subsurface)-Eu. (Eng.-France-Ger.-Czech.-Pol.-Hung.-

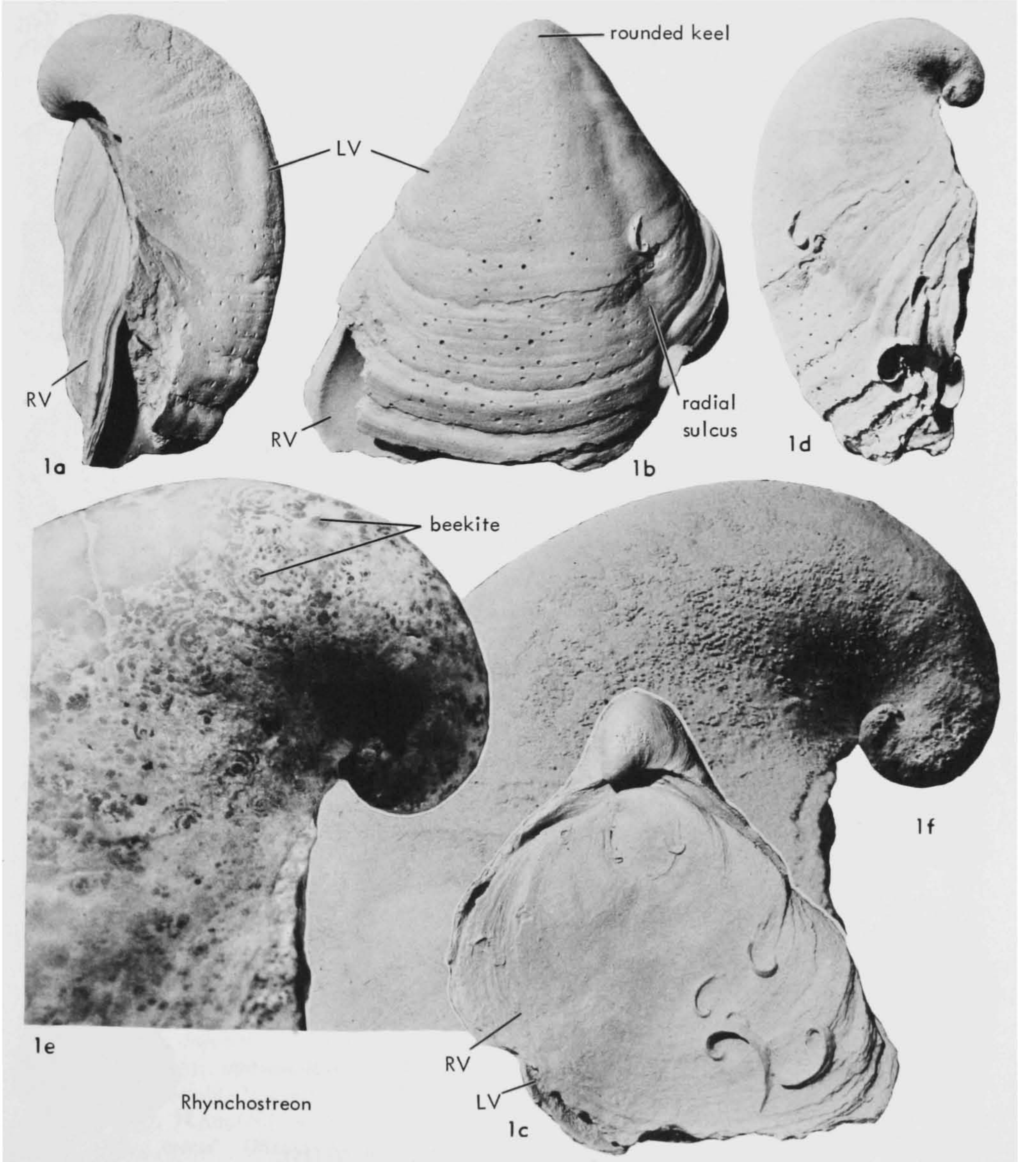

FIG. J97. Gryphaeidae (Exogyrinae) (p. *N*1122-*N*1124).

USSR-Spain-Port.-Sardinia-Switz.-Aus.) - Asia (India-Syria).——FIG. J97,*1*. **R. suborbiculatum* (LAMARCK, 1801), Turon., France (Mosne, Département Indre-et-Loire); *1a-d,* whitened for photography, various views, ×0.7; *1e,* same specimen, not whitened, post. view of umbonal region showing beekite silicification centers, ×2; *1f,* same specimen, whitened, same view, showing absence of attachment area and roughness caused by local silicification, ×2 (Stenzel, n; specimen from Naturhistorisches Mus., Basel, Switz.).

Vultogryphaea VYALOV, 1936, p. 19 [**Ostrea vultur* COQUAND, 1869, p. 118 (=*Rhynchostreon vultur* BAYLE, 1878, pl. 141, fig. 1-2); OD]. Shell medium-sized (greatest diameter about 11 cm.), shell very inequivalve. LV beak incurved, narrow, opisthogyral, with small (4 by 7 mm.) attachment area; with rounded well-developed keel, which persists from early growth stage onto about midgrowth when it broadens and becomes one of several spine-bearing radial keels. At about midgrowth 3-6 rounded radial keels arise and become more prominent with age, bearing stout hyote spines at irregular intervals, strongest of these several keels located posteroventrally and ending in tail-like projection at branchitellum. This keel is posterior neighbor of hyote-spine-bearing keel that develops out of the early juvenile keel. RV smooth, deeply concave, carrying few widely spaced shallow radial grooves. *U.Cret.,* Eu.(France).——FIG. J94,*2*. **V. vultur* (COQUAND), low. Chalk, France (Bonneuil-Matours,

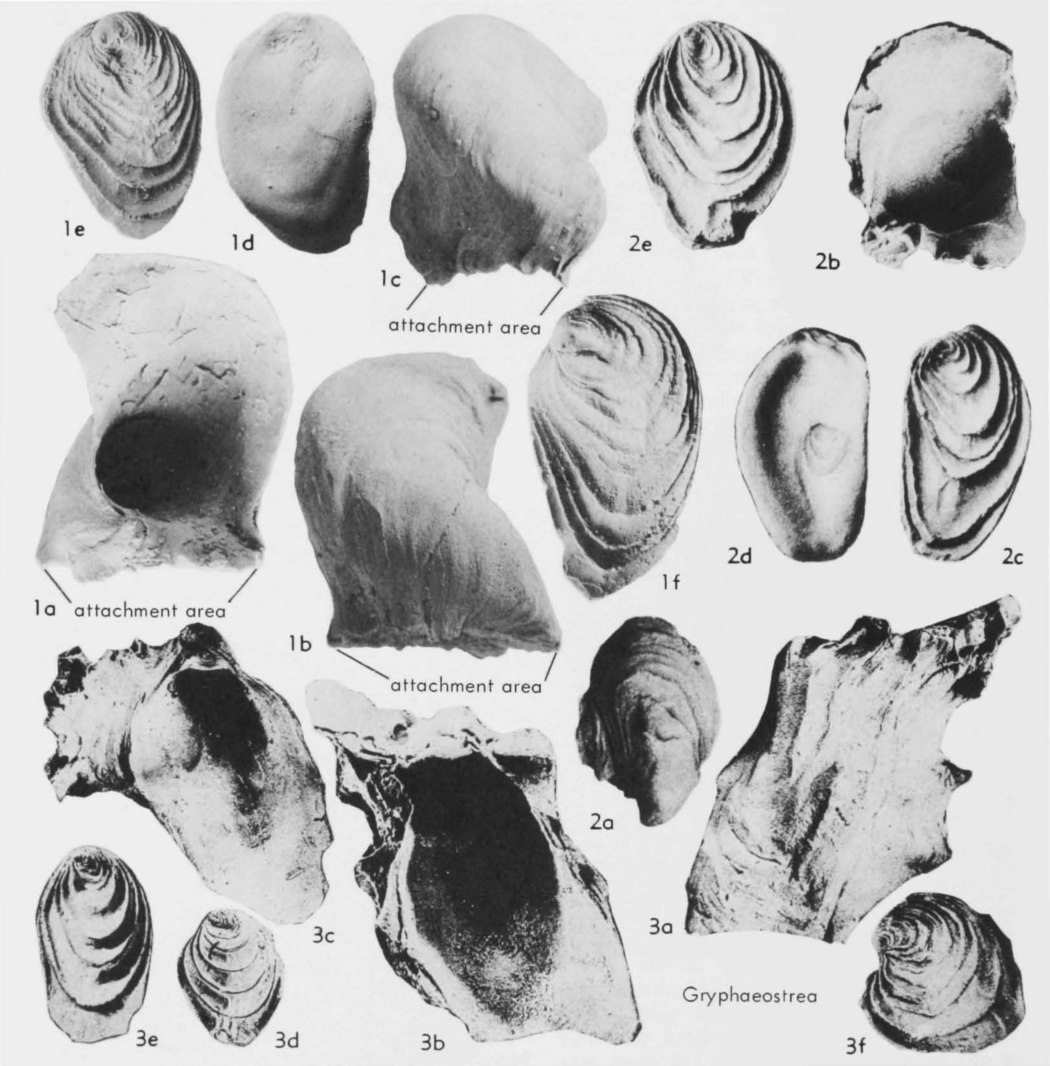

FIG. J98. Gryphaeidae (Exogyrinae) (p. *N*1125).

Département Vienne); *2a,b,* LV ext. views, ×0.7 (Bayle, 1878).

[All specimens seen were filled with hard light-colored limestone so that their interior could not be observed. The features of the ligament area of the LV were seen only obscurely in only one specimen and seemed to be as in *Exogyra*. For this reason and because of the opisthogyral turn of the beak of the LV it is believed that this is an exogyrine oyster genus. VYALOV (1936) had placed it as a new subgenus of *Fatina*, which is not closely related to it. It is a monotypic insufficiently known genus.]

Tribe GRYPHAEOSTREINI Stenzel, new tribe

[*nom. subst.* STENZEL, herein (*pro* "Gruppa II" MIRKAMALOV, 1963, p. 152)]

Postlarval shell growth and ligamental area uniformly spiral only in first part of adult life, changing by abrupt angulation to more or less rectilinear growth in later life. In later part of shell posterior bourrelet is no longer a narrow ridge but is as long and high as the anterior one. *L.Cret.(Apt.)-Mio.*

Gryphaeostrea CONRAD, 15 April 1865a, unnumbered errata page following p. 190, *nom. correct.* [**Gryphaea eversa* MELLEVILLE, 1843, p. 87; M] [=*Gryphoeostrea* CONRAD, 25 February 1865b *(nom. nud.)*; *Gryphostrea* CONRAD, 1866, p. 3 *(nom. van.)*]. Small (less than 3.5 cm.) although some species reach 3.9 by 6.5 cm. size. LV highly convex and capacious, its commissural shelf well developed but without any chomata; deep umbonal cavity overhung by hinge plate; attachment area large in many species, small in some, restricted in position to posterior or posterodorsal flank of valve and inclined at 45° to 90° roughly to anteroposterior direction. LV beak opisthogyrally spiral; anterior wall of LV spirally curved and rising up obliquely or vertically from substratum; LV smooth, lacking radial ribs or folds except in few last surviving species; smooth growth lines give way to squamae in last stages of growth; angular to spoonshaped shelly claspers grow out periodically from growth squamae of LV to provide additional attachments. RV flat; outline oval to spatulate or triangular, devoid of claspers and chomata; its umbo flat, growth squamae simple, smooth, devoid of frills, folds, ribs, or plicae, and spaced regularly apart starting close to umbo. RV considerably smaller than LV, leaving wide (up to 0.7 cm.) margin on LV uncovered in bivalved fossil specimens. On both valves ligamental area is deep narrow spiral groove which abruptly widens and straightens out near end of individual growth. *L.Cret.(up.Apt.)-Mio.(Torton.),* Eu.(Eng.-France-Neth.-Belg.-Ger.-Denm.-Sweden-Switz.-Spain-Italy- Aus.-Bulg.-USSR) - Afr. (Moroc.-Alg.-Tunisia-Libya-Egypt-Congo-Somalil.-Madag.); *L.Cret.(Alb.)-Oligo.(Rupel.),* N.Am.(N.J. to Mexico).——FIG. J98,*1*. **G. eversa* (MELLEVILLE), low.Eoc. (Thanet.), France (Paris Basin); *1a-f,* LV int., ext., another specimen LV ext., other specimens RV int., ext., RV ext., all ×2 (photographs courtesy of N. J. MORRIS, British Museum, Natural History).——FIG. J98,*2*. *G. sp.* (=*G. vomer* STEPHENSON, 1941, *non* MORTON, 1828), U.Cret. (Maastricht., Corsicana Marl), Texas(Bowie Co.); *2a-e,* LV ext., int., RV ext., int., ext., all ×1 (Stephenson, 1941).——FIG. J98,*3*. *G. plicatella* (MORTON, 1833), up.Eoc. (Jackson), Miss. (Shubuta); *3a-f,* LV ext., int., int., RV ext. (3 specimens), all ×1 (Harris, 1946).

[STENZEL (1947, p. 175) found that the type species was originally designated through monotypy. Many authors have classed the genus among the exogyras (see COSSMANN & PEYROT, 1914, p. 197; JOURDY, 1924, p. 31, 96-97, pl. 4, fig. 2; GLIBERT & VAN DE POEL, 1965, p. 56), whereas STENZEL (1959, p. 31) had argued that it must be excluded from the Exogyrinae. This opinion is no longer maintained. *Gryphaeostrea* is easily recognized as a genus, because of the configuration of the ligamental area and the regularly spaced concentric RV squamae. Only the tribe Flemingostreini has similar concentric RV squamae. *Gryphaeostrea* is the only genus of the Exogyrinae to survive the end of the Cretaceous Period. The last surviving species were *G. ricardi* (COSSMANN & PEYROT, 1914, p. 197, pl. 20, fig. 29-36) from the early Burdigal. of Saucats, Département Gironde, south of Bordeaux, France, and *G. miotaurinensis* (SACCO, 1897, p. 30, pl. 9, fig. 15-33) from the Helvetian of the Colli di Torino, northern Italy, which is reported by AZZAROLI (1958, p. 110, pl. 27, fig. 7-9) as widespread in the Miocene (Burdigal. to Torton.) of Somalia, Cirenaica, and Venetia. In North America the last species, as yet undescribed, are found in the Cooper Marl (Ludian) and Marianna limestone (Rupelian) of South Carolina and Mississippi according to F. STEARNS MACNEIL (personal communication). These last species have radial ribs on the left valve.]

Gyrostrea MIRKAMALOV, 1963, p. 152 [**Exogyra turkestanensis* BOBKOVA, 1949, p. 180; OD]. Small to medium-sized, outline quite variable, commonly oval, length to height ratio about 1:1.5, but with irregularities. LV highly convex, lacking radial keel, but surface rough with growth squamae; some species without radial ribs, few with rough rounded irregular or continuous ribs well separated from each other. RV flat, with many conspicuous growth squamae, which stand up freely on anterior half of valve. Entire shell rather rough looking. Spiral beak tending to become detached from general contour of shell by unrolling. *U.Cret.(Cenoman.-Turon.),* C.Asia (Tadzhik Basin-Gissar Mts. region-Pamir Plateau-Altai Range-Fergana-Afghanistan) - Italy - Tunisia-Palestine-Madag.-N. Am. (Mexico-Texas). [*G. cartledgei* (BÖSE, 1919) is the Mexico-Texas species.]——FIG. J99,*1*. **G. turkestanensis* (BOBKOVA), Turon., USSR(Fergana, C.Asia); *1a-c,* types of BOBKOVA, both valves, left side, right side, post. view; ×1 (Bobkova, 1961; photographs by courtesy of KH. KH. MIRKAMALOV).——FIG. J99,*2-4*. *G. akrabatensis* MIRKAMALOV, 1966, Turon., USSR(Gissar Mts., C.Asia); *2,* LV int., *3a,b,* both valves, left side, right side, *4a,b,* both valves, left side, right side, all ×1 (Stenzel, n). ——FIG. J99,*5*. *G. longa* (BOBKOVA, 1961), Turon., USSR(Tadzhik Basin, C.Asia); *5a,b,* LV ext., int., ×1 (Stenzel, n). [Specimens of Fig. J99,*2-5* were whitened for photography and were obtained by courtesy of KH. KH. MIRKAMALOV, Tashkent, USSR.]

[The genus was reproposed as new in MIRKAMALOV, 1966, p. 43-44. The type species was redescribed carefully by BOBKOVA, 1961, p. 114-117, pl. 25, figs. 1-4; pl. 26, figs. 1-5) who named it "*Exogyra turkestanensis* (BORNEMAN, 1935, *n. msc.*)." If the unexplained *n. msc.* stands for *nomen manuscriptum*, BORNEMAN's authorship lacks standing in nomenclature.]

SUPPOSED GRYPHAEIDAE HERE REJECTED FROM FAMILY

Acutostrea VYALOV, 1936, p. 18, was proposed as a new section of *Liostrea (Liostrea)*. It is here regarded as a taxon of the Ostreidae-Ostreinae and must, therefore, become independent of

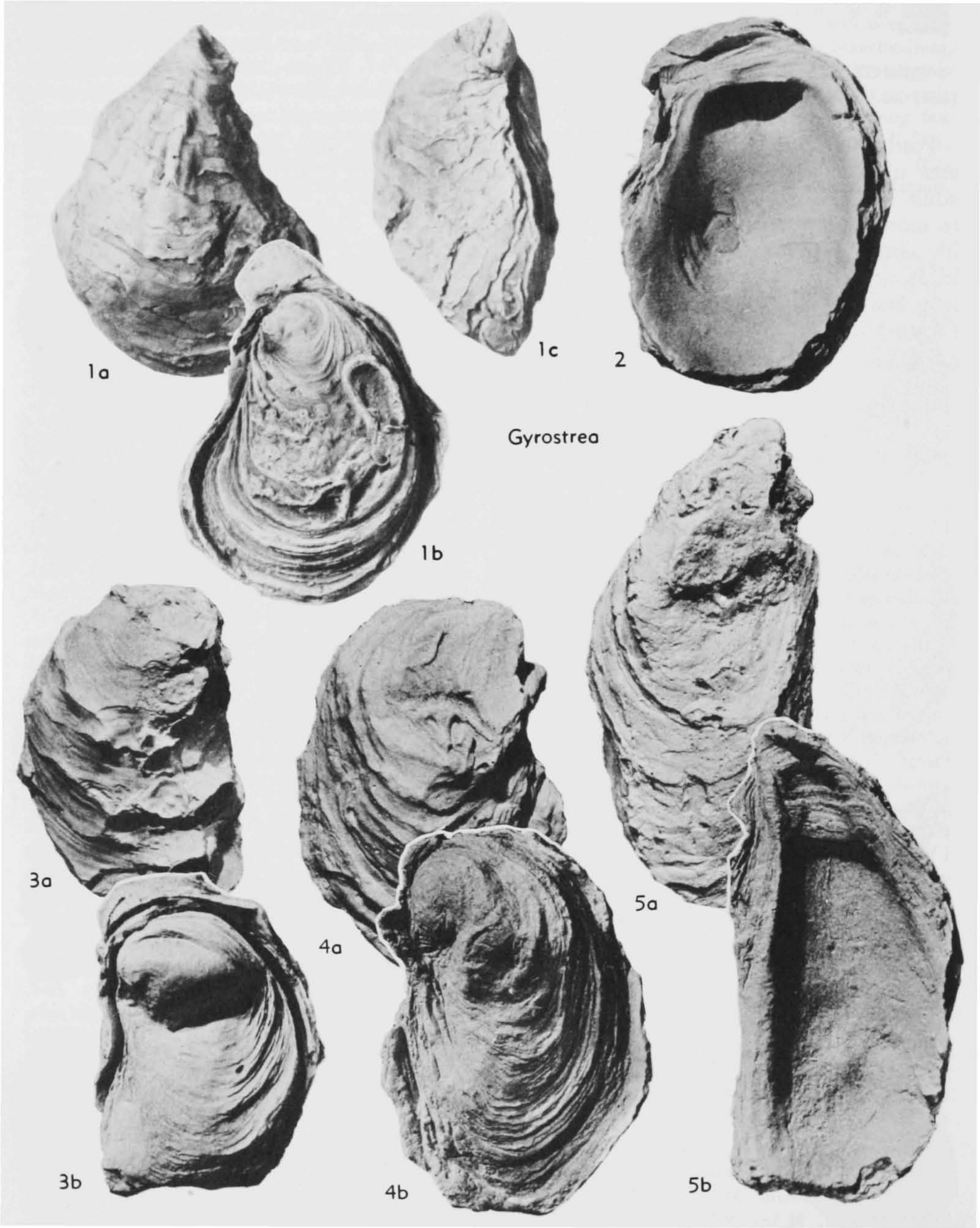

FIG. J99. Gryphaeidae (Exogyrinae) (p. N1125).

Liostrea, which is retained in the Gryphaeinae. See genus *Acutostrea* on p. *N*1128.

Anulostrea Vyalov, 1936, p. 19, was proposed as a new subgenus of *Liostrea.* It is not securely placeable in any scheme of classification, because all the known specimens of the type species have their valves closed tightly, and nothing is known of the internal features. There are indications that it may ultimately find its place among the Flemingostreini-Ostreinae-Ostreidae. See p. *N*1167.

Curvostrea Vyalov, 1936, p. 18, was proposed as a new section of *Liostrea (Liostrea).* However, it is not placeable in any scheme of classification, because all the figured specimens of the type species have their valves closed, and nothing is known of the internal features. See p. *N*1168.

Fatina Vyalov, 1936, p. 19, was proposed as a new genus of the Gryphaeinae. However, it is a junior subjective synonym of *Sokolowia* J. Böhm, 1933, p. 104-105, which takes precedence by reason of priority. The type species of *Fatina* was originally described as a variety of the type species of *Sokolowia* so close are their relationships. *Sokolowia* is a homeomorph of *Gryphaea,* but falls into the Ostreinae-Ostreidae without doubt, see p. *N*1146.

Ferganea Vyalov, 1936, p. 19, was proposed as a new genus of the Gryphaeinae. It is here regarded as a genus of the Ostreidae (Ostreinae), see p. *N*1143.

Kokanostrea Vyalov, 1936, p. 19, was proposed as a new subgenus of *Liostrea.* However, outline and position of the adductor muscle imprints show that the two taxa are not closely related and that *Kokanostrea* is one of the Ostreinae. It has been placed, with some hesitation, in the tribe Flemingostreini, see p. *N*1153.

Mimetostreon Bonarelli & Nágera, 1921, p. 21, was introduced as a subgenus of *Gryphaea,* but it must be placed near or in *Maccoyella* Etheridge, 1892, see p. *N*346.

Odontogryphaea Ihering, 1903, p. 193-227, was proposed as a new subgenus of *Gryphaea,* but must be placed in the tribe Flemingostreini-Ostreinae-Ostreidae, see p. *N*1153. It is a homeomorph of *Gryphaea.*

Quadrostrea Vyalov, 1936, p. 18, was proposed as a new section of *Liostrea (Liostrea),* but the holotype specimen of the type species has the two valves closed, and its interior is inaccessible. Its shape is reminiscent of *Flemingostrea,* but its systematic position remains unknown. see p, *N*1169.

Vultogryphaea Vyalov, 1936, p. 19, was proposed as a new subgenus of *Gryphaea,* but all the specimens seen were filled with hard limestone so that their interior could not be studied. It is here tentatively placed in the Exogyrinae, see p. *N*1124.

Family OSTREIDAE Rafinesque, 1815

[Official List, *nom. correct.* Gray, 1833, p. 777 (*pro* fam. Ostreacia Rafinesque, 1815, p. 148; see ICZN, 1955, Opin. 356, p. 105)] [=*Les ostracées* Lamarck, 1809, p. 317 (vernacular); Ostraceen Oken, 1817, p. 1167 (vernacular); Ostracés Cuvier, 1817, p. 456 (vernacular); fam. Ostreacea Schweigger, 1820, p. 712; fam. Ostracea de Blainville, 1825, p. 519 rejected ICZN Opin. 356; Ostreadae Fleming, 1828, p. 392 rejected ICZN Opin. 356; fam. Ostraceae Menke, 1828, p. 57; fam. Ostreae Eichwald, 1829, p. 287; Ostracidae d'Orbigny, 1837, p. 100; fam. Ostreinae Agassiz, 1846, p. 266; fam. Ostreana Bronn, 1862, p. 474; Ostreideae Eichwald, 1871, p. 23] [*non* suborder Ostracea Dautzenberg, 1900, p. 222]

Nonincubatory or incubatory. Prodissoconch hinge of planktonic larvae bearing on each valve four subequal tooth precursors and their corresponding sockets split by long smooth median gap into two equal groups. Promyal passage present in nonincubatory and absent in incubatory genera. Intestine passes by dorsum of pericardium and does not pierce heart. Posterior adductor muscle reniform or crescentic in cross section, placed nearly centrally or closer to opposite valve margin than to hinge; its insertion on lower valve not elevated. Valves subequal to highly unequal, with large to small attachment areas, no radial posterior groove. Umbonal cavity very deep to shallow to absent; chambers common. Prismatic shell layer present, may be conspicuous. [Several genera are euhaline, other brackish-water inhabitants; many form true reefs.] *U.Trias.-Rec.*

Subfamily OSTREINAE Rafinesque, 1815

[*nom. transl.* Vyalov, 1936, p. 20 (*ex* Ostreidae Rafinesque, 1815)]

Nonincubatory or incubatory. Promyal passage present in nonincubatory and absent in incubatory genera. Chomata present or absent; without pustules on interior surface along the valve margins, which generally are devoid of plications but rarely are irregularly plicate so that very little, if any, conformity is found among individuals. *L.Cret.-Rec.*

NONINCUBATORY GENERA

Living representatives of this informal group of oysters are nonincubatory and have a promyal passage in the exhalant chamber of the mantle cavity (Fig. J11). Their shells commonly have a more or less extensive umbonal cavity under the LV hinge plate. Extinct genera of the group are recognized

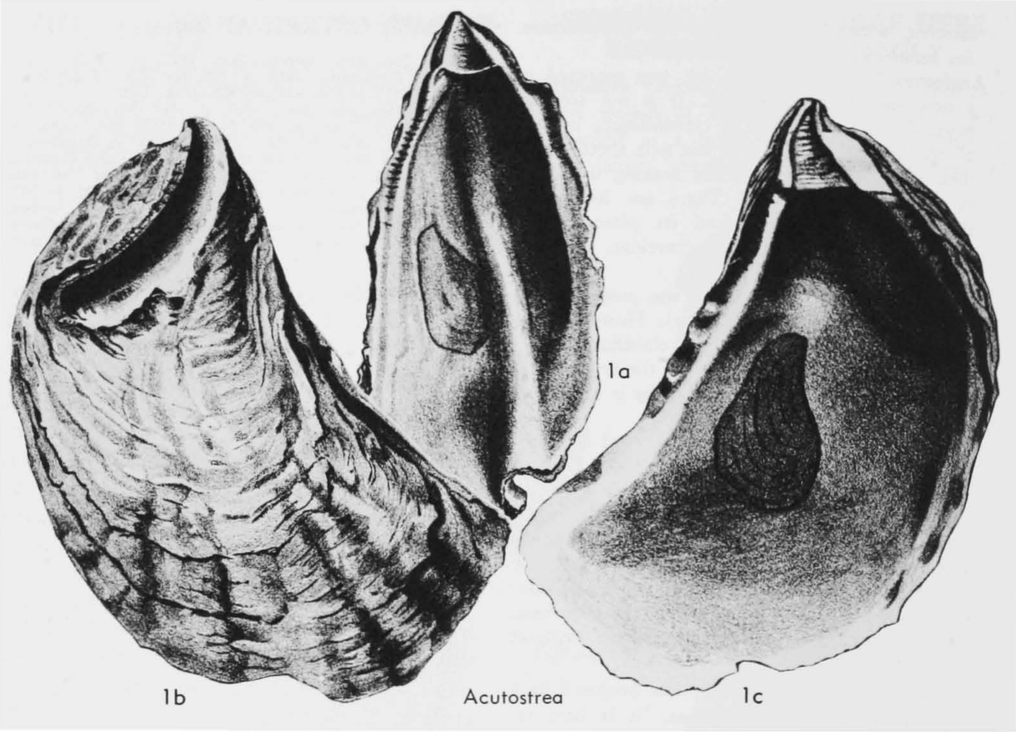

FIG. J100. Ostreidae (Ostreinae) (p. N1128).

by their LV umbonal cavity and similarity to living *Crassostrea*.

Acutostrea VYALOV, 1936, p. 18 [**Ostrea acutirostris* NILSSON, 1827, p. 31 (=*O. incurva* NILSSON, 1827, p. 30; *O. curvirostris* NILSSON, 1827, p. 30; *O. scaniensis* COQUAND, 1869, p. 44; *O. acutirustris* NILSSON in VYALOV, 1936, p. 18, *nom. null.*); OD]. Medium-sized (up to 9 cm. high); outline very variable, mostly elongate-spatulate, straight or more commonly falcate; subequivalve to inequivalve. LV beak commonly pointed, straight or variously curved, projecting beyond that of RV; LV ligamental area acuminate, high triangular; length of resilifer commonly twice that of adjoining bourrelet; deep umbonal cavity of LV overhung by hinge plate. LV commissural shelf with rounded gutter in which pits of chomata are located, both gutter and chomata well developed from hinge to region of adductor muscle, but fading out beyond. LV with many undulatory growth squamae and in some individuals few (about 6) wide low weak radial costae. RV lacking costae, but having concentric growth squamae. Except for chomata and smaller size resembles *Crassostrea*. *U.Cret.*, Eu.-N.Am. ——FIG. J100,*1*. **A. incurva* (NILSSON, 1827), *Actinocamax mamillatus* Zone, Sweden; *1a-c*, LV int., LV ext., LV int., ×1 (Hennig, 1897).

[HENNIG (1897, p. 11-14, pl. 1, fig. 15, 17, 21-23, 25-28) redescribed the type species, pointed out that NILSSON had described it under 3 species names, and selected *O. incurva* as the name to use. This decision of the first reviewer must be accepted. The genus is reminiscent of *Crassostrea* and is believed to be the ancestor of *Crassostrea*. VYALOV proposed *Acutostrea* as a section of *Liostrea* (*Liostrea*). However, *Acutostrea* has radial costae, as HENNIG pointed out, and an adductor muscle imprint that is clearly concave at its dorsal margin (see HENNIG, pl. 1, figs. 22, 28).]

Crassostrea SACCO, 1897, p. 15 [Official List, ICZN Opin. 338] [**Ostrea (C.) virginica* (GMELIN) [1791], p. 3336; OD] [=*Gryphaea* FISCHER, 1886, p. 927 (*non* LAMARCK, 1801) (type, *G. angulata* LAMARCK, 1819, p. 198; OD); *C. (Euostrea)* JAWORSKI, 1913, p. 192 (*obj.*); *Crasostrea* KOCH, 1929, p. 6 (*nom. null.*); *Dioeciostrea* ORTON, 1928, p. 320 (type, *D. americana, nom. subst. pro C. virginica* (GMELIN); OD); *Dioeciostraea* THIELE, 1934, p. 814 (*nom. null.*); *Angustostrea* VYALOV, 1936, p. 18 (type, *O. angusta* DESHAYES, 1824, p. 362; OD); *Grassostrea* VYALOV, 1948a, p. 23 (*nom. null.*); *Somalidacna* AZZAROLI, 1958, p. 115 (type, *S. lamellosa* =*C. gryphoides* (VON SCHLOTHEIM, 1813); M); *Crassotrea* MIYAKE & NODA, 1962, p. 599 (*nom. null.*)]. Small to very large (to 60 cm. high), outline very variable among individuals but very high, slender-spatulate forms with subparallel anterior and posterior margins seeming to preponderate. Surface rough, with many nonappressed, irregularly spaced growth squamae, simple or frilled along free ends; rounded, steep-sided radial ribs on some individuals, more common on LV than RV, such ribs tending to project beyond general outline of margins (Fig. J44); some shells with inconsistent variable radial undulating ribs ending at ventral margins with undulating valve commissure. Chambers common and LV with well-developed umbonal cavity (Fig. J13). No chomata. Adductor muscle imprint close to posterior valve margin and closer to ventral margin than to hinge; its outline with 2 fairly sharp corners, dorsal margin nearly straight. Slender-spatulate forms having LV ligamental area higher than long with subparallel anterior and posterior boundaries, both flanked by many growth foliations (Fig. J8), such forms possessing strongly convex resilifer and convex ligamental area on RV (Fig. J14). *L.Cret.-Rec.*, worldwide.——FIG. J101,*1*, **C. virginica* (GMELIN), living, Texas coast; *1a-d,* specimens from Port Lavaca, LV ext., LV int., RV ext., RV int.; *1e-h,* specimens from Galveston Bay, LV ext., LV int., RV ext., RV int., all specimens whitened for photography, ×0.3 (Stenzel, n).——FIG. J101,*2*. *C. angusta* (DESHAYES, 1824) (="*Angustostrea*" VYALOV, 1936), low.Eoc. (Cuis., Sables de Cuise), France (Cuise-Lamothe); *2a,b,* LV int., RV int. (holotype of DESHAYES at École des Mines, Paris), ×0.7 (Stenzel, n).——FIG. J102,*1*. *C. gryphoides* (VON

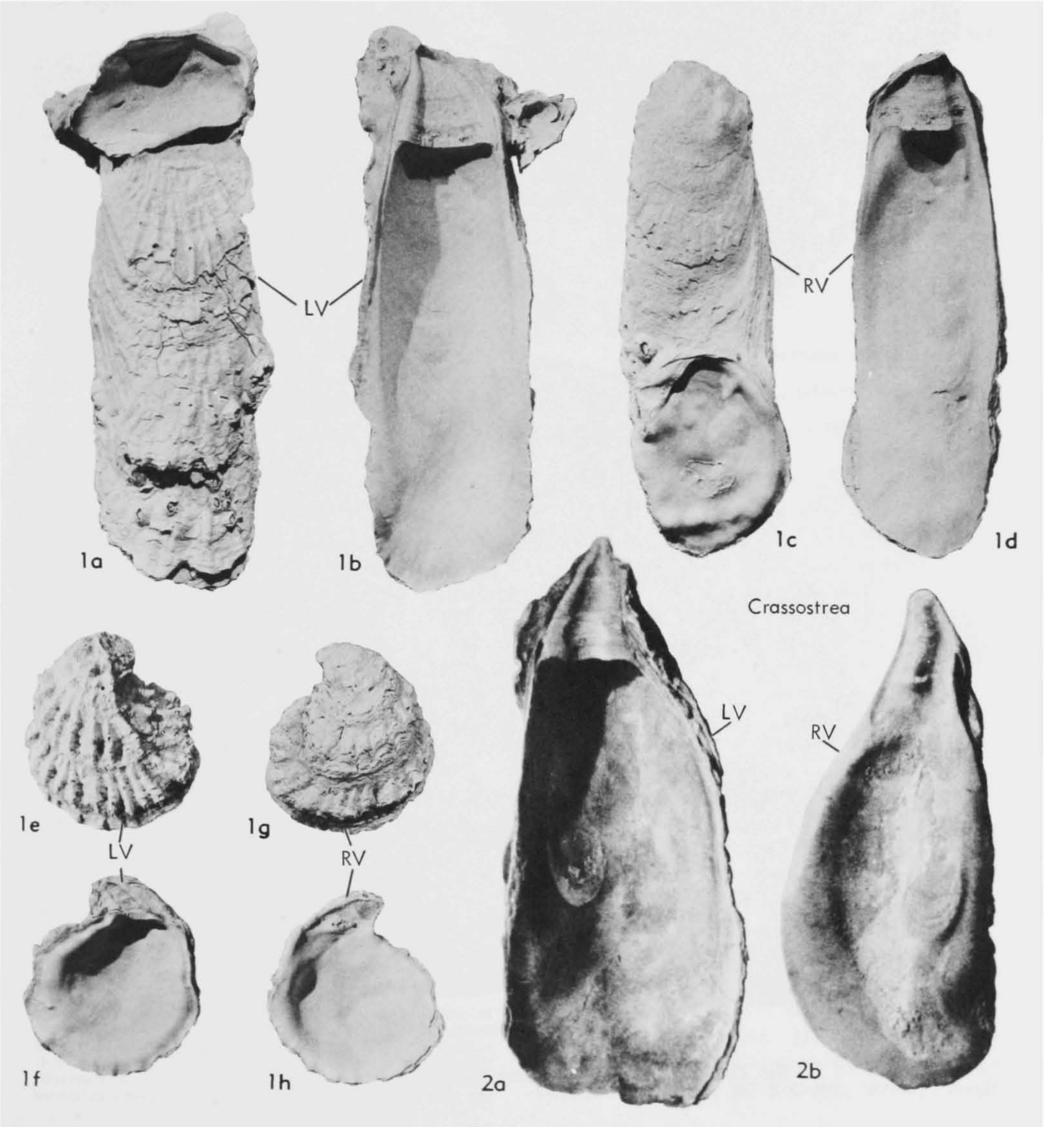

FIG. J101. Ostreidae (Ostreinae) (p. *N*1128-*N*1129, *N*1131).

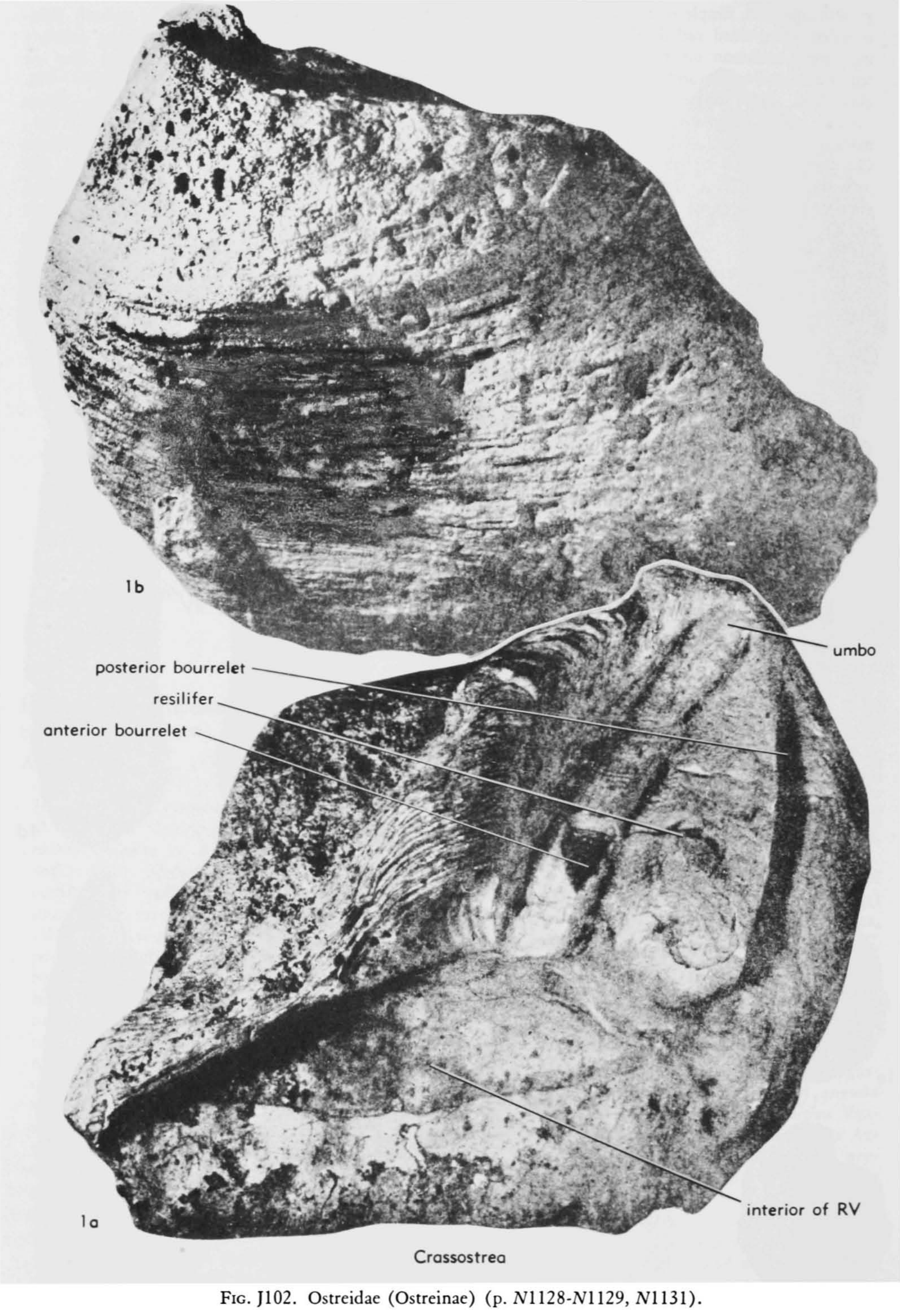

FIG. J102. Ostreidae (Ostreinae) (p. *N*1128-*N*1129, *N*1131).

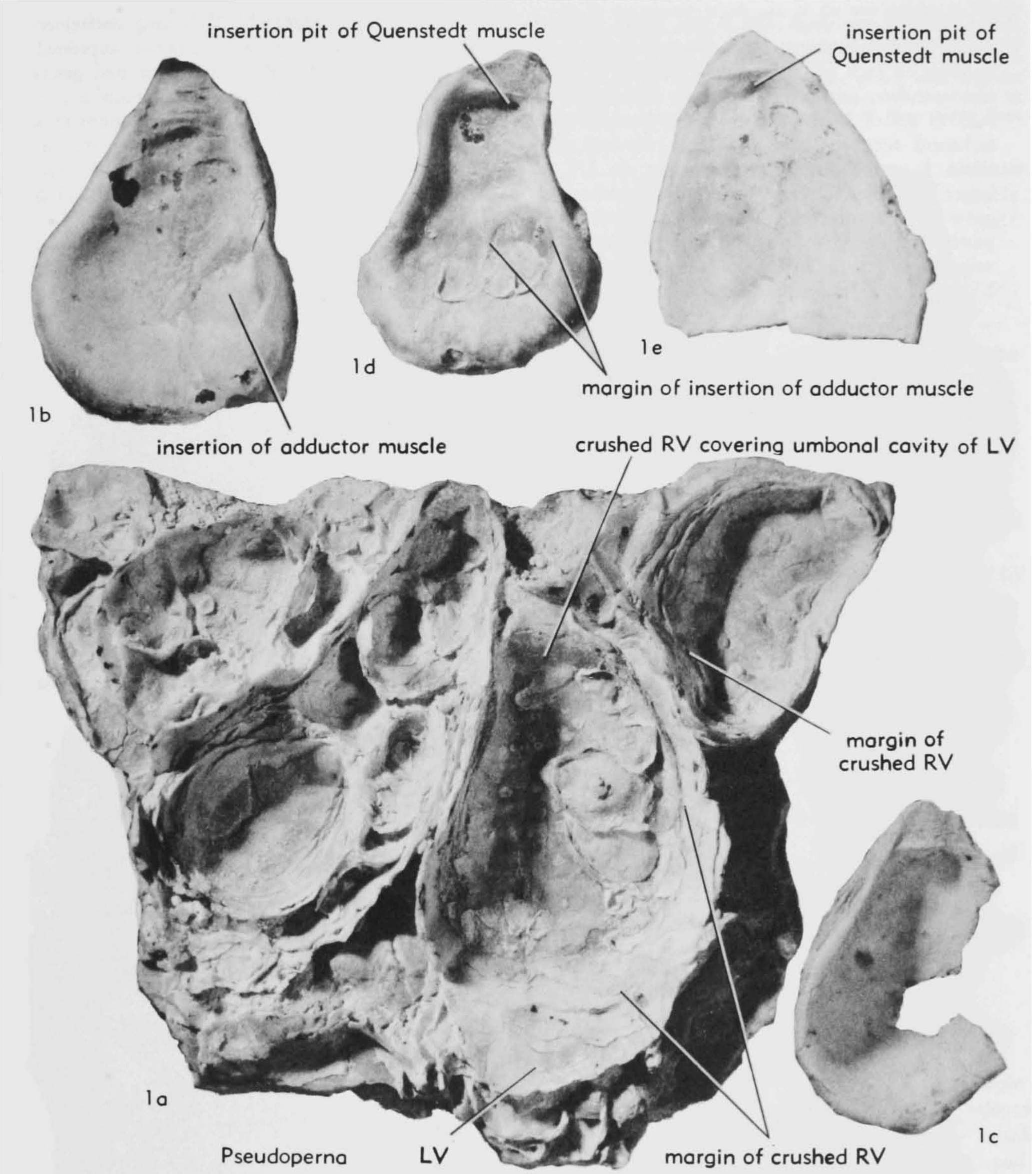

FIG. J103. Ostreidae (Ostreinae) (p. *N*1131-*N*1134).

SCHLOTHEIM, 1813) (=*"Somalidacna lamellosa"* AZZAROLI, 1958, holotype), Mio. (Serie del Guban), Somalia (hills on left bank of Wadi Merero); *1a,b,* RV hinge view, post. view, ×0.4 (Azzaroli, 1958). [*See* also Fig. J8, J14, J44, and J71.]

[Many authors have classed *Crassostrea* as a subgenus of *Ostrea*. However, species of these two genera will not at all interbreed in nature or in the laboratory, but within each genus the various species can be made to crossfertilize (GALTSOFF & SMITH, 1932; DAVIS, 1950). The northern species of *Crassostrea* are the only known oysters that can survive freezing solid for several weeks in winter. The genus is euryhaline and thrives in very low salinities (17 per mille) as well as in elevated ones (42 per mille) (BREUER, 1962).]

Pseudoperna LOGAN, 1899a, p. 95 (or 1899b, p. 215-216) [*nom. correct.* NEAVE, 1940, v. 3, p. 996 (*pro Pseudo-perna* LOGAN, 1899)] [**P. rugosa* LOGAN, 1899a (=*P. attenuata* + *P. orbicularis* + *P. torta* LOGAN, 1899a, + *P. wilsoni* LOGAN, 1899b=*Ostrea congesta* CONRAD in NICOLLET, 1843, p. 169); SD STENZEL, herein]. Small (to about 4 cm. high and 3 cm. long), outline highly irregular wherever neighboring individuals impinge on each other, otherwise tending to ovate and spatulate, with widest part of oval at about 0.25 to 0.3 of height above ventral margin. Attachment area very flat and large, leaving only about 1 cm. of freely grown edges on LV of larger individuals, these free edges tending to grow up vertically from substrate on anterior and posterior valve margins, but more obliquely at ventral margin of LV. Deep umbonal cavity in LV under thin hinge plate and very shallow resilifer groove. Free edges of LV lacking costae, erratically wavy, their growth squamae appressed. RV irregular but mostly free of costae and gently convex because of their smooth xenomorphic configuration. Chomata very small and numerous, slightly elongate at right angles to valve margin, missing in many because of abrasion. *U.Cret.*, N.Am.——Fig. J103,*1*. **P. congesta* (Conrad, 1843), Coniac.-Santon. (Smoky Hill Chalk), Kansas (Logan Co.); *1a*, fragment of flat prismatic calcite shell layer of an *Inoceramus* overgrown by individuals of *P. congesta;* large individuals are

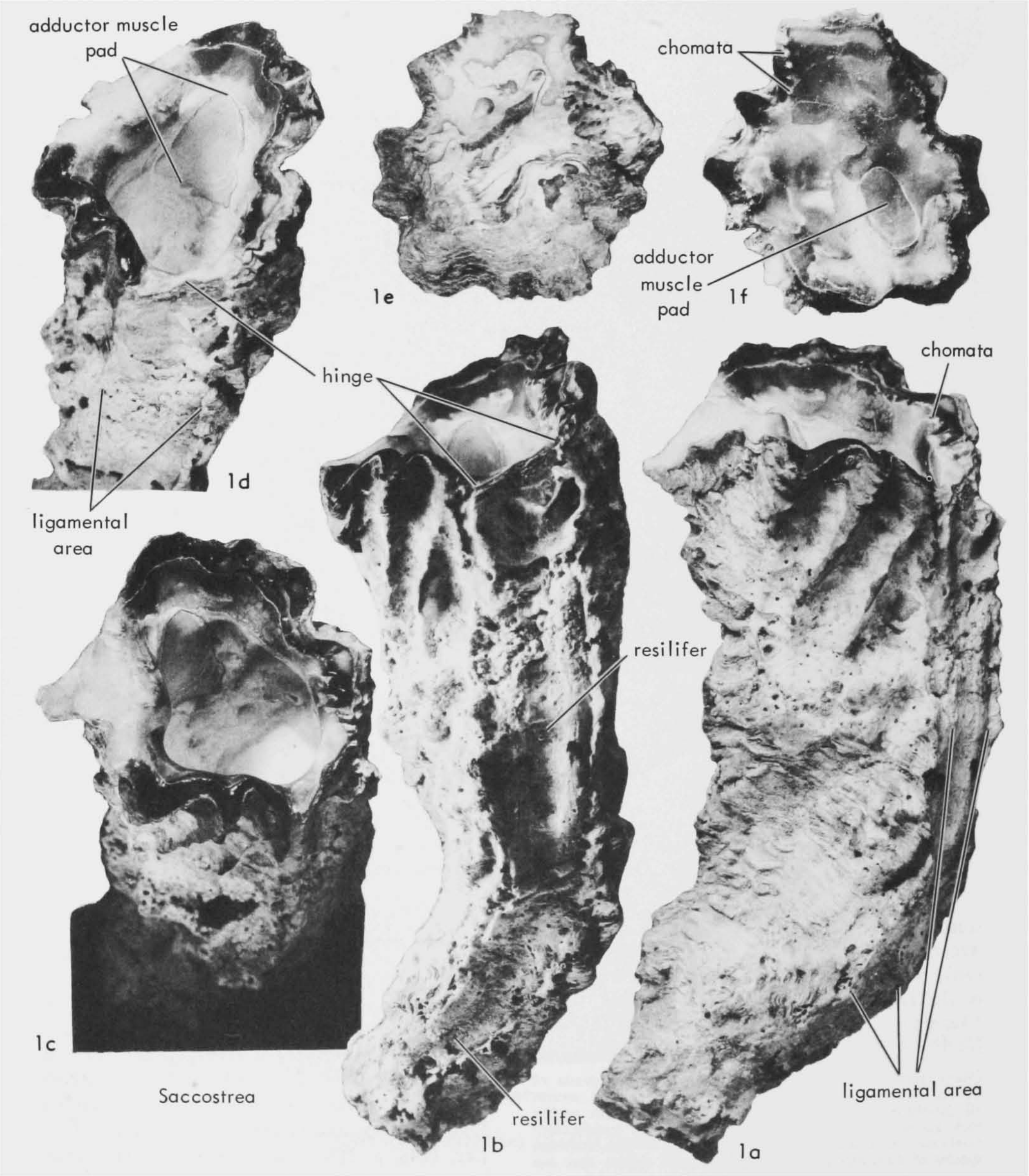

Fig. J104. Ostreidae (Ostreinae) (p. *N*1134-*N*1135).

bivalved, but their RVs have been crushed down into the hollow of the LV through compaction of the chalk; *1b-e,* four RV ints., ×2 (Stenzel, n; specimens by courtesy of D. F. Merriam, State Geol. Survey of Kansas, Lawrence, Kans.).

[It is not known which one of the two articles by Logan is the earlier one, both are dated June, 1899. However, all nominal species given by Logan under *Pseudo-perna* are junior synonyms of *Ostrea congesta* Conrad. All specimens of the type species are firmly grown onto very flat fragments of the prismatic calcite layer of ***Inoceramus*** or are free specimens that have broken off from them. Most

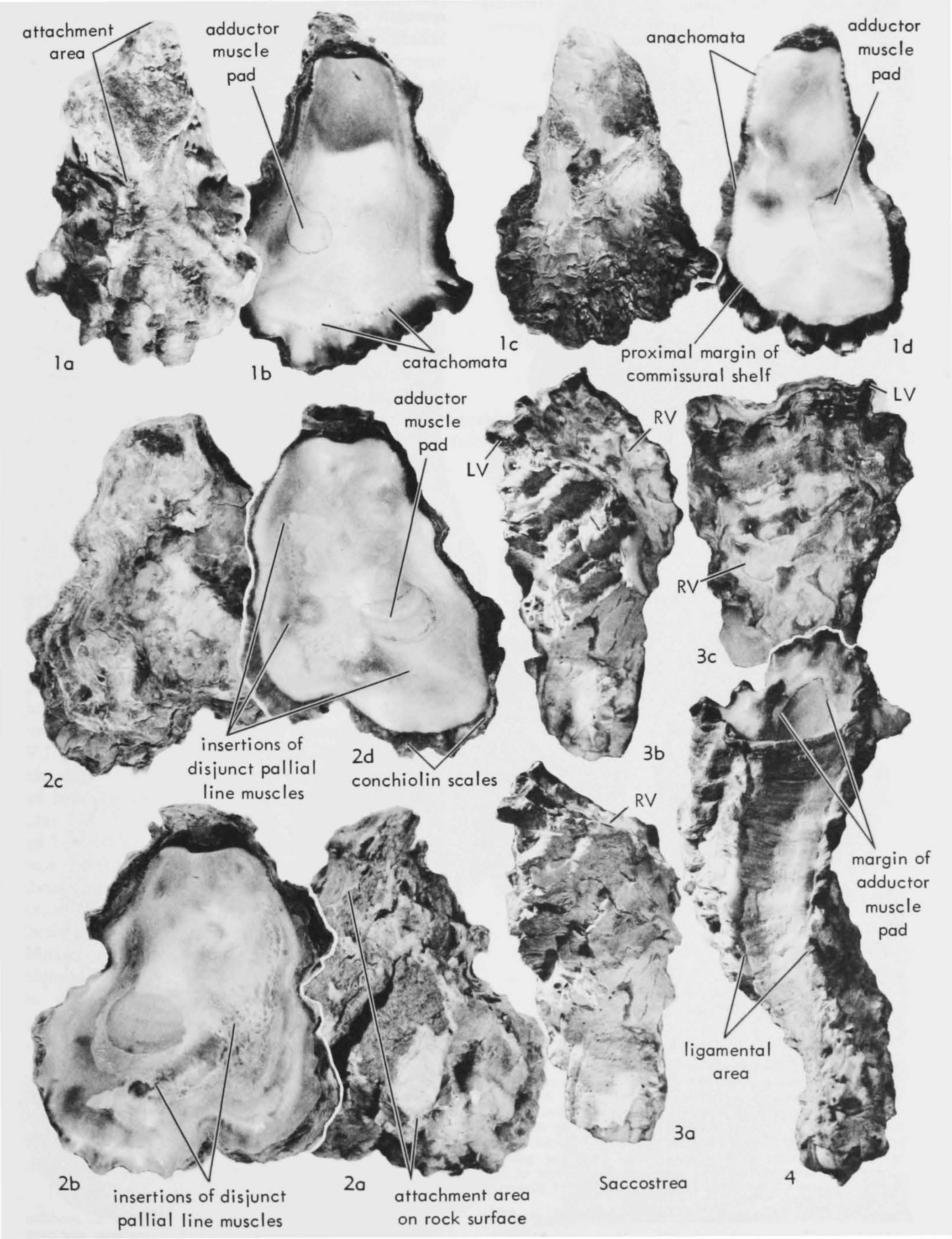

FIG. J105. Ostreidae (Ostreinae) (p. *N*1134-*N*1135).

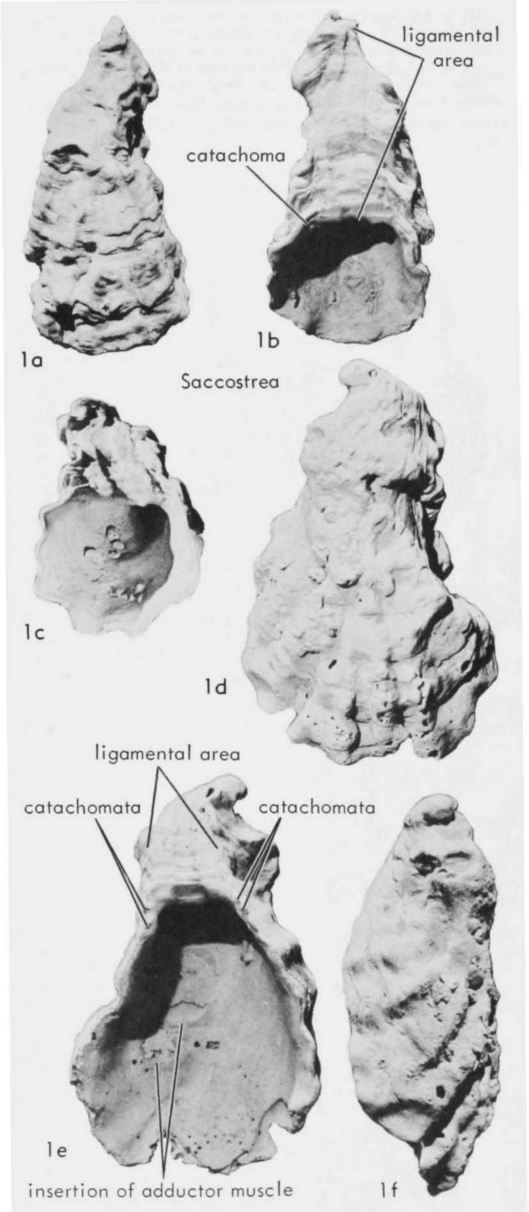

FIG. J106. Ostreidae (Ostreinae) (p. *N*1134-*N*1135).

features of the species are believed to be caused by crowding and adaptation to growth on ooze-covered sea bottoms on which the only solid substrates available were fragments of *Inoceramus* shells. The genus is similar to *Crassostrea*, but never grows large and the shells carry many chomata. It is a monotypic genus possibly descended from *Crassostrea*. Specimens of the type species from the general type area were made available through the courtesy of Dr. D. F. MERRIAM of the State Geological Survey of Kansas.]

Saccostrea DOLLFUS & DAUTZENBERG, 1920, p. 471 [**Ostrea (Saccostrea) saccellus* DUJARDIN, 1835, p. 272 (=*O. cucullata* BORN, 1778, p. 100, =*O. cucullata* BORN, 1780, p. 114); M] [=*Saxostrea* IREDALE, 1936, p. 269 (type, *S. commercialis* IREDALE & ROUGHLEY, 1933, p. 278; OD); *Sanostrea* MIYAKE & NODA, 1962, p. 599 *(nom. null.)*]. Small to medium-sized, outline variable, but divisible into normal ostreiform ecomorphs with spatulate or vertical-oval to irregular form and abnormal rudistiform ecomorphs with small, operculiform RV and large, slender conical to cornucopia-like LV carrying very high, slender ligamental area. LV has large attachment area, and grows preferentially on bare rock surfaces or mangrove, carries many rough nonappressed growth squamae and 10 to 30 rough irregular rounded dichotomous radial folds extending into small protruding lobes. Umbonal cavity in average very deep; LV umbonal region full of chambers and curved cross walls. RV flat, much corroded through bacterial decay, free of folds but carrying many scaly growth squamae of conchiolin. Both valves with strong chomata, which commonly encircle entire valve. Nonincubatory. A distinct pallial line of separate small muscle insertions connects Quenstedt muscle with posterior adductor muscle imprints. Differs from *Crassostrea* in its deeper umbonal cavity, strong chomata, and tendency to conical rudistiform or cornucopia-like shapes. *Mio.-Rec.*, circumglobal in tropical climates.——FIG. J104,*1;* J105,*1-4;* J106,*1.* **S. cuccullata* (BORN, 1778); J104,*1,* rudistiform ecomorph living on rocks at Keppel Bay, Queensland, Australia (=*"Ostrea cornucopiaeformis"* SAVILLE-KENT, 1893); *1a,b,* LV ext., two views; *1c,d,* LV, two views into umbonal cavity; *1e,* RV ext., showing corroded surface; *1f,* RV int., all ×1 (Stenzel, n) [possible types of SAVILLE-KENT loaned by courtesy of D. F. MCMICHAEL, Australian Museum, Sydney]; J105,*1,2,* ostreiform ecomorph, living, Australia (=*"Saxostrea commercialis"* IREDALE & ROUGHLEY, 1933); *1a,b,* LV ext., int.; *1c,d,* RV ext., int. (outline of adductor muscle pad and some catachomata are outlined by pencil line); *2a,b,* LV ext., int.; *2c,d,* RV ext., int., all ×0.7 (Stenzel, n) [specimens donated by D. F. MCMICHAEL]; J105,*3,4,* rudistiform ecomorph living on rocks at Keppel Bay, Queensland, Australia (=*"Ostrea cornucopiaeformis"* SAVILLE-KENT, 1893); *3a-c,* post. view, oblique post. view, right side; *4,* LV ext., showing spirally twisted ligamental area, all ×1 (Stenzel, n) [possible types of SAVILLE-KENT loaned by courtesy of D. F. MCMICHAEL, Australian Museum, Sydney]; J106,*1,* Mio., C.France (Pontlevoy, Département Loir-et-Cher) (=*"Ostrea saccellus"* DUJARDIN, 1835); *1a-f,* LV ext., int., umbonal cavity, LV ext., int., ant. views, ×1 (Stenzel, n) [specimens donated by GEORGES LECOINTRE, La Chapelle Blanche, Département Indre-et-Loire, France; both whitened for photography]. [*See* also Fig. J7.]

[LECOINTRE (personal communication) regards *S. saccellus* (Mio., S. France) as equivalent to *S. cuccullata;* not even deserving subspecific distinction. This conclusion is supported here. The spelling *cuccullata* is orthographically erroneous but must be retained, because it is older by two years than the emended *cucullata*. The rudistiform ecomorphic growth pattern has evoked comment (FISCHER, 1880-87, fig. 684; KLINGHARDT, 1922, 1929) without developing explanation of its causes. The best account of living ecomorphs of the type species and their ecology has been given by MACNAE & KALK (1958). The ostreiform ecomorphs grow on sea cliffs exposed to wave action. The rudistiform ecomorphs grow in crowded situations not exposed to strong wave action. Some authors (THOMSON, 1954, p. 150) have regarded *Saccostrea* or *Saxostrea* as a junior synonym of *Crassostrea*. This is believed to be erroneous, because the two can be distinguished consistently by shell features and because eggs of *S. cucculiata* have no effect in stimulating ejaculation of sperm from ripe males of *Crassostrea virginica* and species of these two genera cannot be made to crossfertilize each other (GALTSOFF & SMITH, 1932).]

Striostrea VYALOV, 1936, p. 17 [**Ostrea (S.) procellosa*, "VALENCIENNES" in LAMY, 1929, p. 71

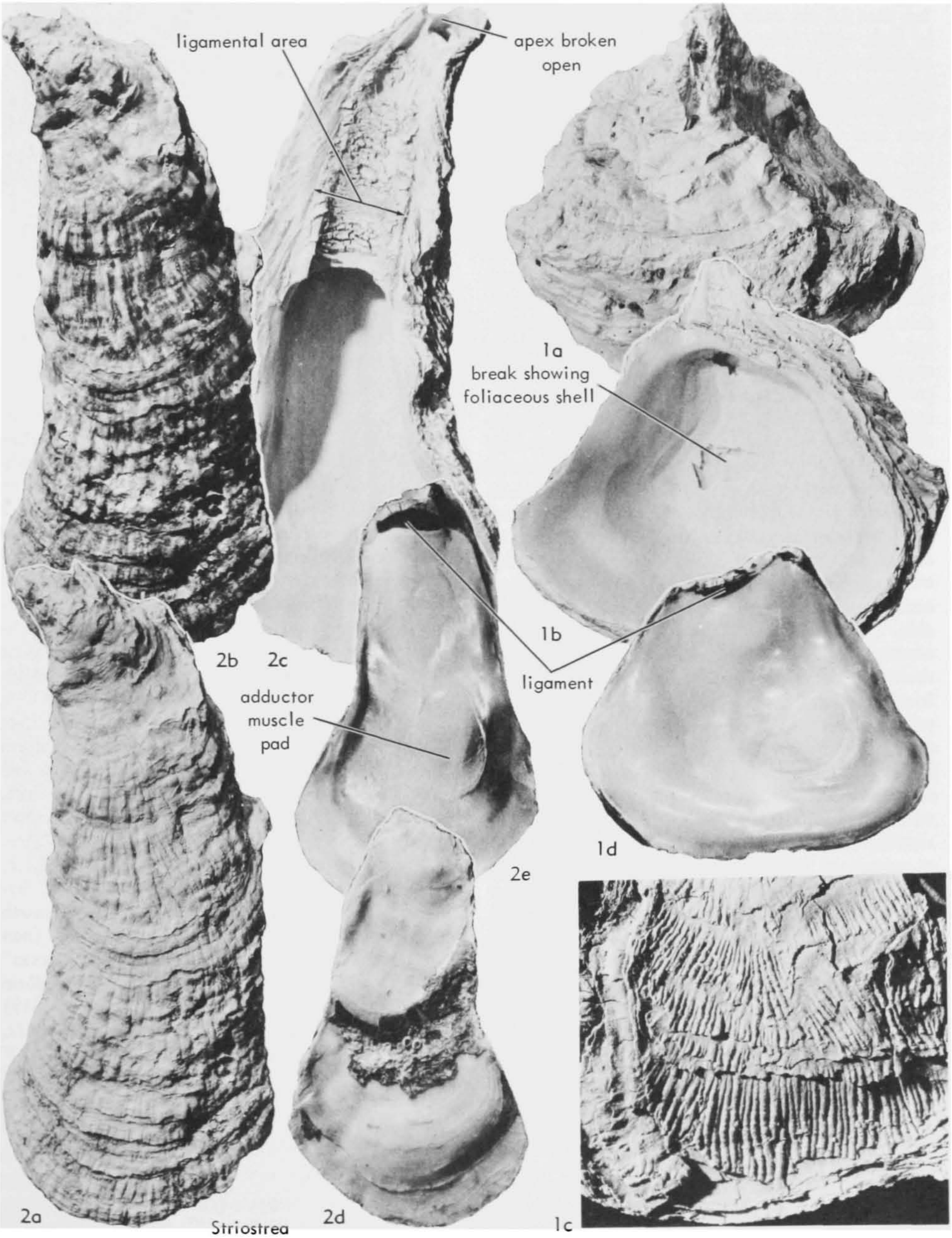

FIG. J107. Ostreidae (Ostreinae) (p. *N*1135-*N*1137).

(*nom. subst. pro O. multistriata* HANLEY, 1845, p. 106, *non* DESHAYES, 1830, p. 294) (=*O. margaritacea* LAMARCK, 1819, p. 208); OD]. Small to large (to 20 cm. high), with successive growth forms consisting of young ostreiform individuals represented by type specimens of *O. procellosa,* and older, larger, rudistiform individuals corresponding to lectoholotype of *O. margaritacea.* 1) *O. procellosa* form irregular, commonly flattish, generally less than 3.5 cm. wide, up to 11 cm. long and equally high, with rather variable outline approaching suborbicular and rounded-triangular. RV covered by many thin, readily dehiscent, conchiolin-rich imbricating layers that have prismatic shell structure and carry on their tops many narrow (1.3 mm. or less wide) dichotomous flat-topped radial riblets separated by narrower interspaces, riblets converging and diverging irregularly from place to place, producing shaggy appearing surface, becoming less abundant and less prominent in later growth stages. Wherever imbricating layers have peeled off, surface is smooth and carries paper-thin iridescent appressed or nonappressed growth squamae. LV irregular, with large attachment area; where grown free from substrate having crowded delicate paper-thin noniridescent nonappressed somewhat undulant growth squamae that produce very foliaceous surface. Internal face of both valves nacreous and iridescent. Adductor muscle imprint reniform, well rounded, twice as long as high, with dorsal boundary concave and fully rounded at ends; outline similar to that of *Ostrea s.s.* Position of imprint central, as in *Ostrea s.s.,* but in individuals with deep umbonal cavity tending to be more ventral. Chomata variable, absent in some, medium-sized in others, coarse and thick in many. Umbonal cavity mostly shallow, generally clearly defined. Conchiolinous fringe at margin of RV extensive (up to 2 cm. wide). 2) *O. margaritacea* growth form large (up to 20 cm. high), generally slender, rudistiform, highly inequivalve, twisted spirally, sigmoidally, or otherwise. LV tall, slender, twisted conical, with very high ligamental area; RV flattish, irregular, concave or slightly convex from dorsum to venter; its ligamental area mostly lost through corrosion. Exterior of LV, where not destroyed by erosion, crowded with delicate paper-thin noniridescent nonappressed somewhat undulating growth squamae that produce very rough foliaceous surface. Outer face of RV generally devoid of any remnants of conchiolinous prismatic shell layers, but riblets less crowded where preserved and less prominent than in *O. procellosa* form. Otherwise, RV covered with many appressed or nonappressed growth squamae without riblets. Internal faces of both valves nacreous and iridescent. Adductor muscle imprint of LV variable, from reniform and similar to that of *O. procellosa* form to nearly twice as high as long, commonly with concave dorsal margin and small well-rounded horns; its position on LV close to posterior valve margin; on RV farther from ventral margin than on LV. Chomata variable, absent in some individuals, as few as 3 in others, better developed on RV than LV. Umbonal cavity excellent (up to 2 cm. deep), with many paper-thin cross walls that produce chambers. Ligamental area of LV long (to 3.7 cm.) and very high (to 13 cm.), divided into much larger, sunken-in, flat-bottomed resilifer and 2 subequal flat-topped bourrelets. Well-defined groove (2 mm. wide) delimiting anterior and posterior margins of ligamental area. Nonincubatory; promyal passage extensive. Riblet-bearing layers usually lost owing to their delicate nature. Differs from *Crassostrea* in its reniform adductor muscle imprints, chomata, nacreous and iridescent interior, very foliaceous shell structure, and rudistiform growth pattern. *Mid.Eoc.(Gosport Sand),* N.Am.(Ala.); *Rec.,* SE.Afr.-Madag.-C.Am. (W. coast-Baja Calif.-Panama).——FIG. J107,*1,2;* J108,*1.* **S. margaritacea* (LAMARCK, 1819), living, S.Afr.(Knysna Lagoon); *procellosa* growth form (=*Ostrea multistriata* HANLEY, 1845 (*non* DESHAYES, 1830) =*O. procellosa* "VALENCIENNES" in LAMY, 1929) (J107,*1,* and J108), rudistiform growth form (=*O. margaritacea* LAMARCK, 1819) (J107,*2*); J107,*1a,b,* LV ext., int., ×1; J107,*1c,* RV ext. showing radial riblets, ×2; J107,*1d,* RV int. showing nacreous luster, ×1; J107,*2a-e,* LV ext., LV ext., LV int., RV ext., RV int. showing nacreous luster, ×0.6 (Stenzel, n); J108,*1,* very young (5 mo.) specimen showing numerous radial riblets, ×3.3 (Ranson, 1951).

FIG. J108. Ostreidae (Ostreinae) (p. *N*1135-*N*1137).

[Until 1949, *O. procellosa* and *O. margaritacea* had been regarded as separate species (LAMY, 1929, p. 71,272). RANSON (1949d, p. 251) first recognized that both names are applicable to a single species which he chose to call *Gryphaea margaritacea.* Later (RANSON, 1959) he described it and figured both growth forms. My study of specimens, including the types of both, deposited in Paris collections (Mus. Natl. d'Hist. Nat.), showed that these can be arranged in a continuous growth series leading from one growth form to the other, thus proving that they belong to a single species. On describing *O. multistriata* Hanley (1845) incidentally indicated that his material, which came from Africa, consisted of young oysters only. Korringa (1956) described and figured both growth forms as *Crassostrea* (*Gryphaea*) *margaritacea* without mentioning the name *O. procellosa* and its identity problem. His work has yielded the best description of the biology of the type species. Vyalov (1936) cannot have been aware of the rudistiform terminal growth form when he proposed *Striostrea* as a subgenus of *Ostrea*. Because *Striostrea* is nonincubatory, has an extensive promyal passage, and has quite

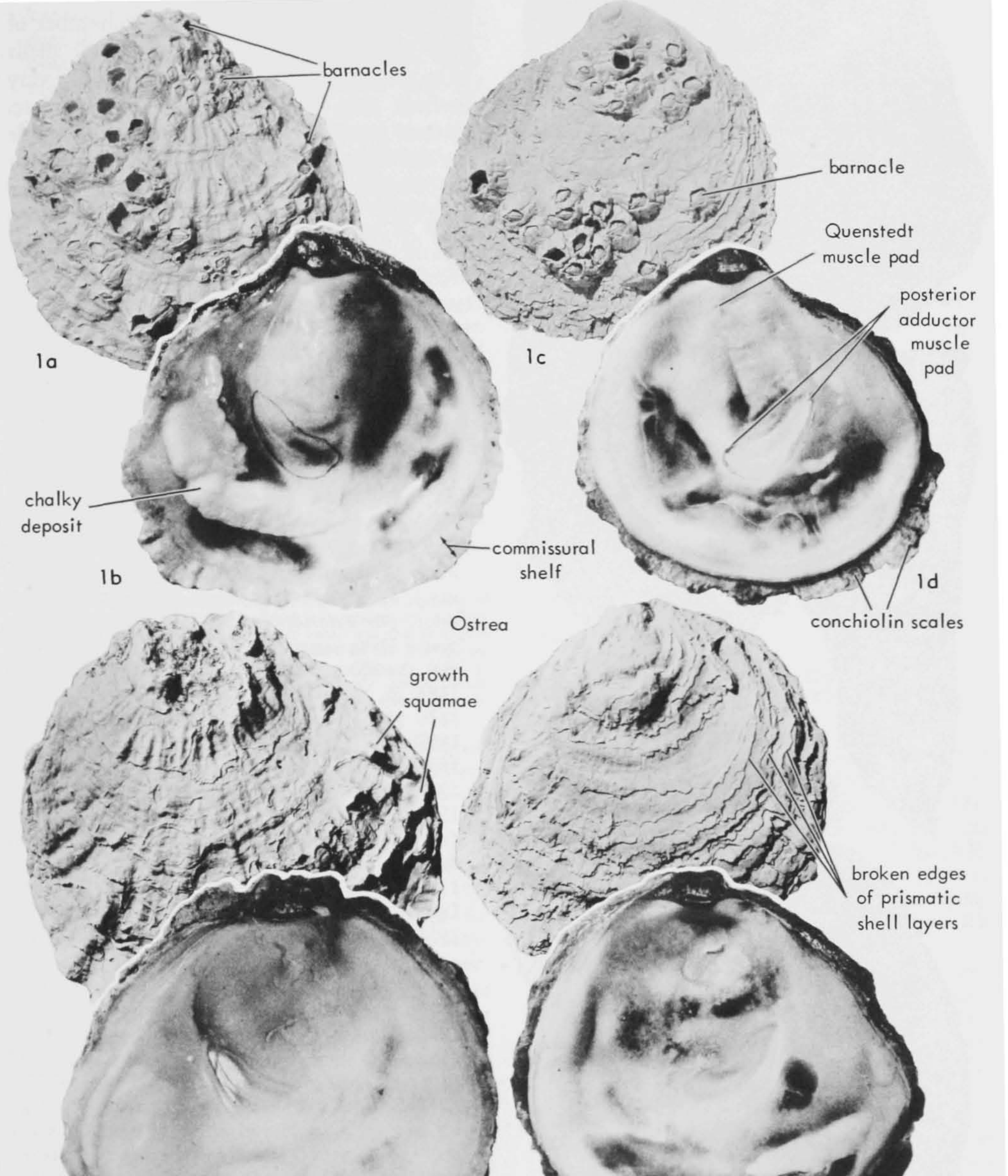

Fig. J109. Ostreidae (Ostreinae) (p. *N*1138-*N*1139).

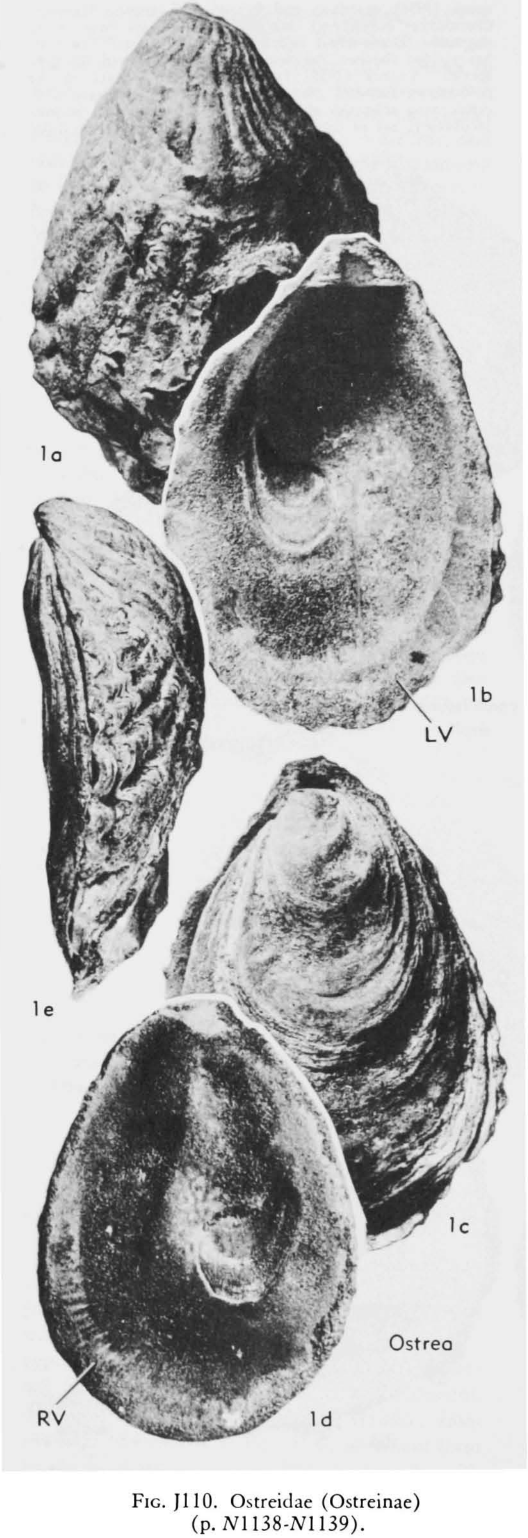

FIG. J110. Ostreidae (Ostreinae) (p. N1138-N1139).

different conchological features than the incubatory *Ostrea*, the two genera cannot be close relatives.]

INCUBATORY GENERA

Living representatives of this informal group of oysters are incubatory and lack a promyal passage in the exhalant chamber of their mantle cavity. Commonly, their shells have no umbonal cavity, or only a very shallow one beneath the LV hinge plate. Extinct genera of the group are recognizable by the less capacious LV and absence or shallowness of an umbonal cavity in it. The sculpture pattern is commonly similar to that of *Ostrea,* in which the LV has radial ribs and the RV lacks them.

Ostrea Linné, 1758, p. 696 [Official List, ICZN Opin. 94 and 356] [**O. edulis;* SD ICZN, Opin. 94] [=*Ostracites* Gesner, 1758, p. 39 (*nonbinom.*); *Ostreum* Da Costa, 1776, p. 249 *(nom. van.)* (obj.); *Peloris* Poli, 1791, p. 33 (type, *O. edulis* Linné; SD Gray, 1847, p. 201) (obj.); *Ostracites* Gmelin, 1793, p. 404 (rejected ICZN, Opin. 296); *Peloriderma* Poli, 1795, p. 255 (*nom. subst. pro Peloris* Poli, 1791) (obj.); *Ostracarius* Duméril, 1806, p. 168 *(nom. van.); Ostreigenus* Renier, [1807] (rejected ICZN, Opin. 427); *Ostraea* G. B. Sowerby, Jr., 1839, p. 75 *(nom. van.); Peloridoderma* Agassiz, 1846, p. 277 *(nom. subst. pro Peloriderma* Poli, 1795) (obj.); *Ostreites* Herrmannsen, 1847, p. 177 (*nom. subst. pro Ostracites* Auctt.); *Ostreola* Monterosato, 1884, p. 4 (type, *Ostrea stentina* Payraudeau, 1826 [1827], p. 81; OD); *Cymbulostrea* Sacco, 1897b, p. 12 (type, *Ostrea cymbula* Lamarck, 1806, p. 165; OD); *Ostrea (Eostrea)* Ihering, 1907, p. 42 (type, *Ostrea puelchana* d'Orbigny, 1841, p. 672; SD Iredale, 1939, p. 394); *Ostrea* (section *Anodontostrea*) Suter, 1917, p. 86 (type, *Ostrea angassi* G. B. Sowerby, Jr., 1871, v. 18, pl. 13; SD Finlay, 1928, p. 264); *Ostrea (Euostrea)* Douvillé, 1920, p. 65 (*non* Jaworski, 1913, p. 192) (type, *Ostrea edulis* Linné; OD); *Monoeciostrea* Orton, 1928, p. 320 *(nom. van.)* (obj.); *Ostroea* Tolmer, 1928, p. 91 *(nom. null.); Osrea* Tzankov, 1932, p. 78 *(nom. null.); Monoeciostraea* Thiele, 1934, p. 814 *(nom. van.); Ostrea (Ostrea)* section *Bellostrea* Vyalov, 1936, p. 17 (type, *Ostrea bellovacina* Lamarck, 1806, p. 159; OD)]. Medium-sized to large (to 18 cm. high and 20 cm. long), variable outline, but average shells tending to be roughly orbicular with hardly prominent umbones obtusely pointed and flanked by small to very large auricles or lacking them, posterior auricle, if present, much larger than anterior one. Width about 0.25 of height, resulting in rather flat shell. RV flat to gently convex, covered by many fragile flattish conchiolinous growth squamae, peripheral conchiolin fringe extensive (up to 1.5 cm. wide), so that calcareous part of

RV is much smaller than that of corresponding LV, as conspicuous as in some fossil bivalved specimens. Concentric undulations absent or present, never conspicuous on RV. LV slightly convex, hardly ever deeply cupped, covered by many long unequal rounded radial ribs interrupted by free-standing frilled delicate growth squamae less abundant than those on RV; some concentric undulations present. Although radial rib patterns differ much from species to species, no hyote spines are developed on them. Ligamental areas commonly longer than high, forming triangles of long base lines. Chomata always present, but differing in prominence from species to species, few (4 or 5) in some, inconspicuous and tuberculiform (see Fig. J113), abundant and conspicuous in others, forming elongate ridgelets (see Fig. J31) arranged all around periphery. Adductor-muscle imprint reniform; both ends well rounded, with length about 4 times height; more centrally located than in other genera. LV mostly without umbonal cavity. Typical species tend to have large round flat shells with flat commissures, whereas others have small vertically elongate shells with twisted or irregularly plicate commissure. [Genus is incubatory. Diagnostic features are outline and position of adductor muscle, chomata, flattish shape of shell, absence of umbonal cavity, and different ornamentation of opposing valves.] *Cret.-Rec.*, worldwide except in polar regions.

[There is some confusion concerning the type species of *Anodontostrea* Suter, 1917. Suter was under the impression that the New Zealand oyster's name was *Ostrea angasi* Sowerby (*recte angassi*), which he listed as the first species under *Anodontostrea*. It now appears (Hollis, 1963, p. 2-8) that name rather refers to the closely similar South Australian oyster, whereas the New Zealand oyster is to be called *O. lutraria* Hutton, 1873.]

O. (Ostrea). No plications along valve margins; chomata few and inconspicuous. *Cret.-Rec.*, cosmop.——Fig. J109,*1,2*. **O. (O.) edulis* Linné, living, Eng.; *1a-d*, LV ext., int., RV ext., int., ×0.7; *2a-d*, LV ext., int., RV ext., int., ×0.7 (Stenzel, n) [specimens donated by E. J. Denton, the Laboratory, Citadel Hill, Plymouth, Eng.; *1a,1c,2a*, and *2c* whitened for photography]. ——Fig. J110,*1*. *O. (O.) bellovacina* Lamarck, 1806 (="*Ostrea (Ostrea)* section *Bellostrea*" Vyalov, 1936), Eoc. (Thanet.; Sables de Bracheux), France (Butte de la Justice at Bracheux near Beauvais); monotype of Lamarck at Museum de Genève, Switz.; *1a-e*, LV ext., int., RV ext., int., ant. view, ×1 (Clerc & Favre, 1910-18).——Fig. J111,*1*. *O. (O.) cymbula* Lamarck, 1806 (="*Cymbulostrea*" Sacco, 1897), Eoc. (Lutet.), France (Grignon, Département Seine-et-Oise, near Paris); *1a-c*, RV ext., LV int., LV ext., ×1 (Cossmann & Pissarro, 1904-13).——Fig. J112,*1,2*. *O. (O.) stentina* Payraudeau, 1826 (1827) (="*Ostreola*" Monterosato, 1884), living, Egypt (Port Said, Medit. Sea); *1a-b*, LV ext., int., *1c-e*, RV ext., ext., int., ×1; *2a,b*, LV ext., int., *2c-e*, RV ext., ext., int., ×1 (Stenzel, n) [*1a,b,d,e*, and *2a-e* whitened for photography].——Fig. J113,*1*. *O. (O.) puelchana* d'Orbigny, 1841 (="*Ostrea (Eostrea)*" Ihering, 1907), living, Brazil (Rio Grande do Sul); *1a-d*, LV ext., int., RV ext., int., ×0.7 (Stenzel, n).——Fig. J113,*2*. O. *(O.) lutraria* Hutton, 1873 (=*Ostrea (Ostrea)* "section *Anodontostrea*" Suter, 1917), living, N.Z.(Foveaux Strait), *2a-d*, LV ext., int., RV ext., int., ×0.7 (Stenzel, n).

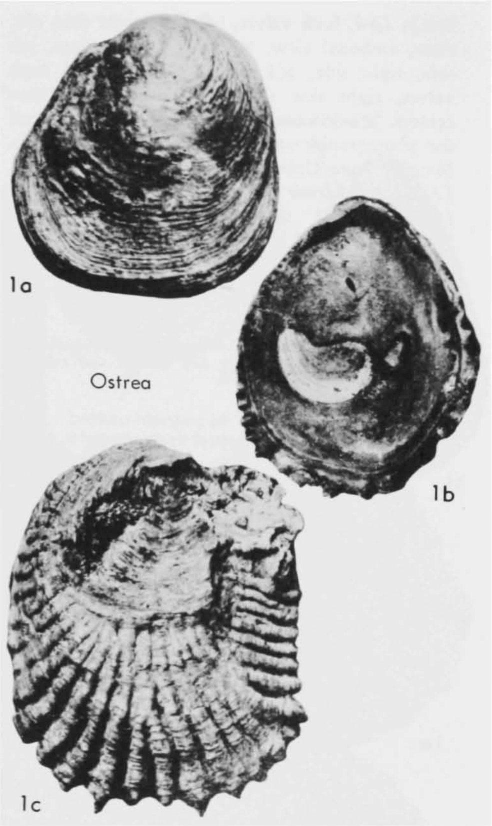

Fig. J111. Ostreidae (Ostreinae) (p. *N*1138-*N*1139).

O. (Turkostrea) Vyalov, 1936, p. 18 [**O. turkestanensis* Romanovsky, 1878, p. 112 (=*O. strictiplicata* Raulin & Delbos, 1855, p. 1158); OD] [=? *Goridzella* Haas, 1938, p. 294, *err. pro Gorizdrella* Vyalov, 1936, p. 17 (type, *Ostrea gorizdroae* Vyalov, 1937b, p. 16-18; OD); *Gorizdrella* Vyalov, 1936, p. 17 *(nom. nud.)*; *Gorizdrella* Vyalov, 1948a, p. 34; *Turcostrea* Vyalov, 1948b, p. 60 *(nom. null.)*]. Differs from *O. (Ostrea)* in having strong chomata and many strong continuous, fairly narrow radial ribs on LV and tendency of ligamental area to turn in opisthogyral spiral fashion. *Low.Eoc.(Ypres.)-Mid. Eoc.(Alaisk.)*, Mesogean region (N.Afr.-C.Asia). ——Fig. J114,*1-4*. **O. (T.) strictiplicata* Raulin & Delbos, 1855 (=*O. turkestanensis* Romanovskiy, 1878), mid.Eoc.(Alaisk.), C.Asia(USSR,Uzbek.); *1a-d,* both valves, left side, right side, ant. view, umbonal view, ×1; *2a,b,* both valves, left side, right side, ×1; *3,* LV ext., ×1; *4,* both valves, right side showing beekite silicification centers, ×1 (Stenzel, n) [all specimens whitened for photography and donated by D. P. Naidin, Moscow State Univ., USSR].——Fig. J115,*1*. *O.* (*?T.*) *gorizdroae* Vyalov, 1937 (="*Ostrea* (*Cymbulostrea*) section *Gorizdrella*" Vyalov, 1936, *nom. nud.*), Paleog., USSR (Fergana); *1a-e,* LV ext., LV ext., RV ext., LV ext., int., ×0.9 (Vyalov, 1937). [*See* also Fig. J30 and J31.]

[Valves are commonly thick-walled. This thickening is attributed to the prevailingly hot climate and calcium-rich environment. Astre (1922) gave an account of the variants of the type species in the western Mesogean region. Yang Kieh (1930) reviewed the evolution of O. (*Turkostrea*) into *Sokolowia*. His claim that *O. strictiplicata* is an earlier name for *O. turkestanensis* is accepted here, notwithstanding the fact that Russian authors do not (Vyalov, 1936, etc.; Gekker, Osipova, & Belskaya, 1962). *Gorizdrella* Vyalov, 1936, was proposed as a section of *Ostrea* (*Cymbulostrea*) and accompanied by a brief definition and the citation of a type species. However, at the time the type species was a *nomen nudum*. It was later described in Vyalov, 1937b. Haas listed *Goridzella,* evidently an error *pro Gorizdrella;* he defined it and gave a type species indirectly by reference to Vyalov, 1936. Haas, 1938, is thus the first nomenclaturally acceptable introduction of this taxon. To judge by the figures given in Vyalov, 1937b, *O. gorizdroae,* the type species, is based on young and small oyster specimens (Fig. J115,*1*) which cannot be classified without recourse to additional, more full-grown specimens. They might be the young of an *Ostrea* (*Turkostrea*).]

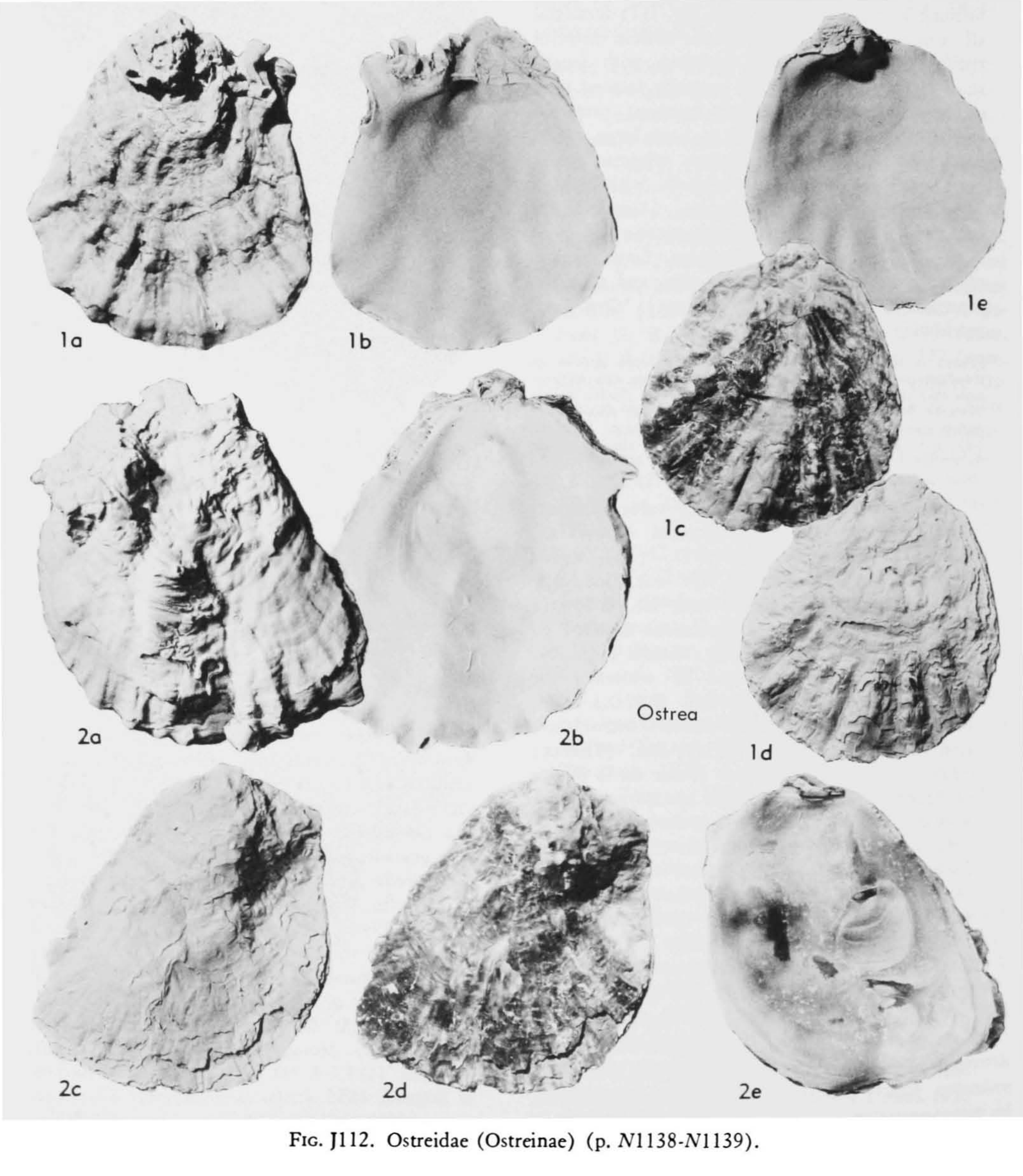

Fig. J112. Ostreidae (Ostreinae) (p. *N*1138-*N*1139).

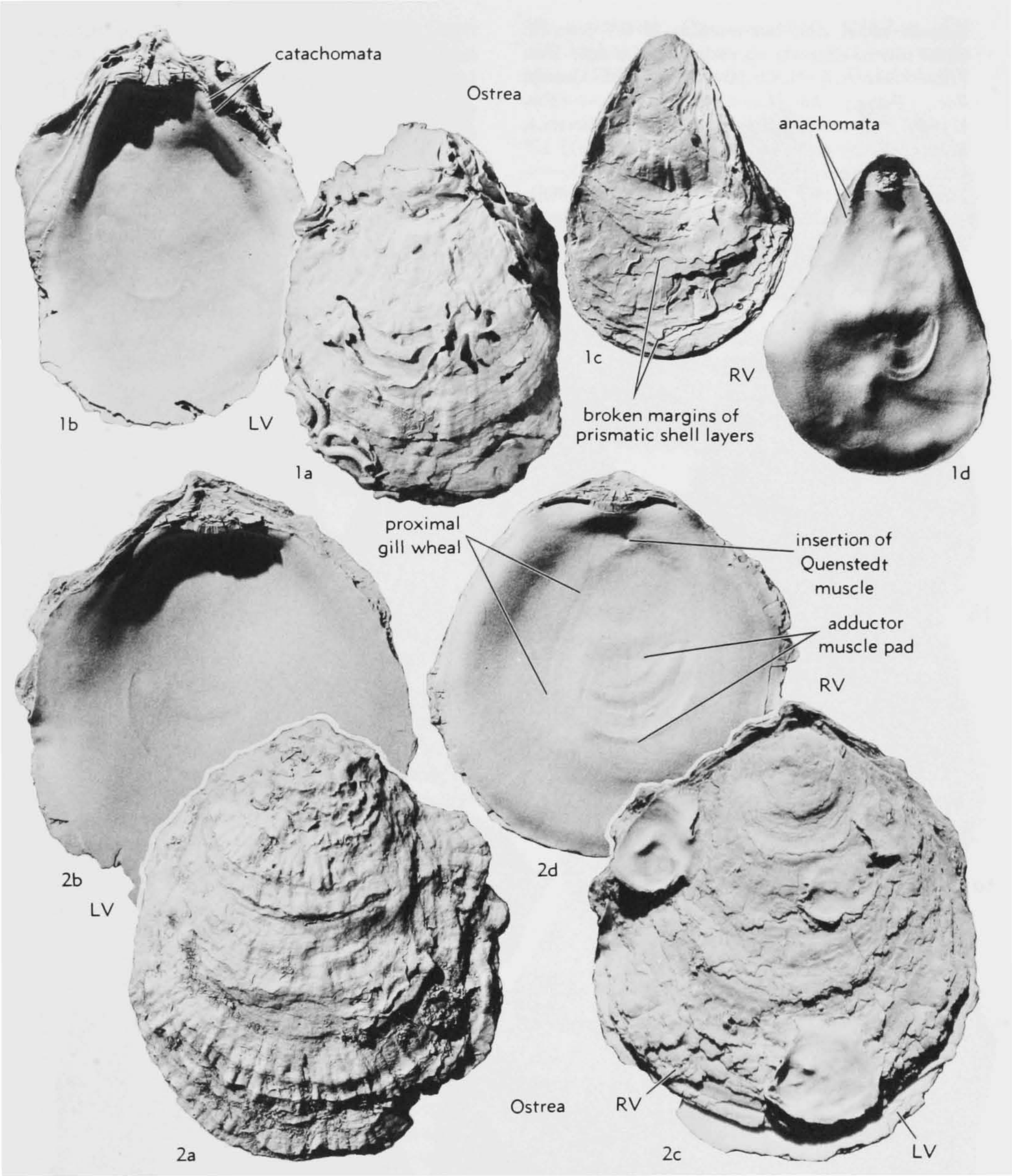

FIG. J113. Ostreidae (Ostreinae) (p. N1138-N1139).

Cubitostrea SACCO, 1897a, p. 99 [**Ostrea cubitus* DESHAYES, 1832, p. 365; OD]. Small to medium-sized (largest dimension of LV up to 8 cm.), outline curved, crescentic to crescentic-triangular. Crescentic species generally thin-walled, with flat to slightly convex RV, those tending to triangular shapes thick-walled, with RV strongly convex on outside but almost flat on inside. LV obscurely keeled; keel crescentic, located nearer to concave posterior than to anterior valve margin, which is broadly rounded in crescentic species, angulate in triangular ones, angulation indicating position of inhalant pseudosiphon and widest part of gills during life. Branchitellum much produced and narrowly rounded. Posterior auricle present on LV of some species. Adductor muscle imprint comma-shaped to reniform, located approximately halfway between hinge and branchitellum. LV with concentric growth squamae and high, narrowly rounded, dichotomous or intercalating, long radial ribs separated by deep, sharply rounded interspaces narrower than ribs. RV without ribs, having only appressed concentric growth squamae. Margins of LV strongly crenated by concavities beneath radial ribs, but margins of RV smooth. Short row of chomata on each side of hinge. *Eoc.(Lutet.-Auvers.)*, N.Am.(Gulf Coast-Atl. Coast); *Eoc.*, Patag.; *Eoc.(Lutet.)-Oligo.*, Eu.——FIG. J116,*1*. **C. cubitus* (DESHAYES), Eoc.(Auvers.), France (Crépy-en-Valois, Département Oise); LV ext., ×1 (Stenzel, Krause, & Twining, 1957).——FIG. J116,*2;* J117,*1*. *C. perplicata* (DALL, 1898), mid.Eoc. (U.Tallahatta F.), USA (Ala., Catons Bluff on Conecuh R., Covington Co.); J116,*2a-d*, RVs ext., ×1; J116,*2e-h*, RVs int., ×1 (all topotypes) (Stenzel, n); J117,*1a*, both valves, right side, ×2; J117,*1c-g*, LVs ext., ×1; J117,*1b,h,i*, LVs int., ×1 (all topotypes) (Stenzel, n). [*See* also Fig. J17, J43,*1*, and J70.]

[Close relationship between this genus and *Ostrea* is proved by the rib patterns of the valves and the chomata. For this reason it is believed that the genus was incubatory. The two opposing valves differ much in size, LV extending a good distance beyond the periphery of the RV (see Fig. J17 and p. N977), indicating that the latter had extensive marginal conchiolin fringes while the animal was alive. A special provincial stock of this genus evolved on the east and south shores of North America into the weird *C. sellae-*

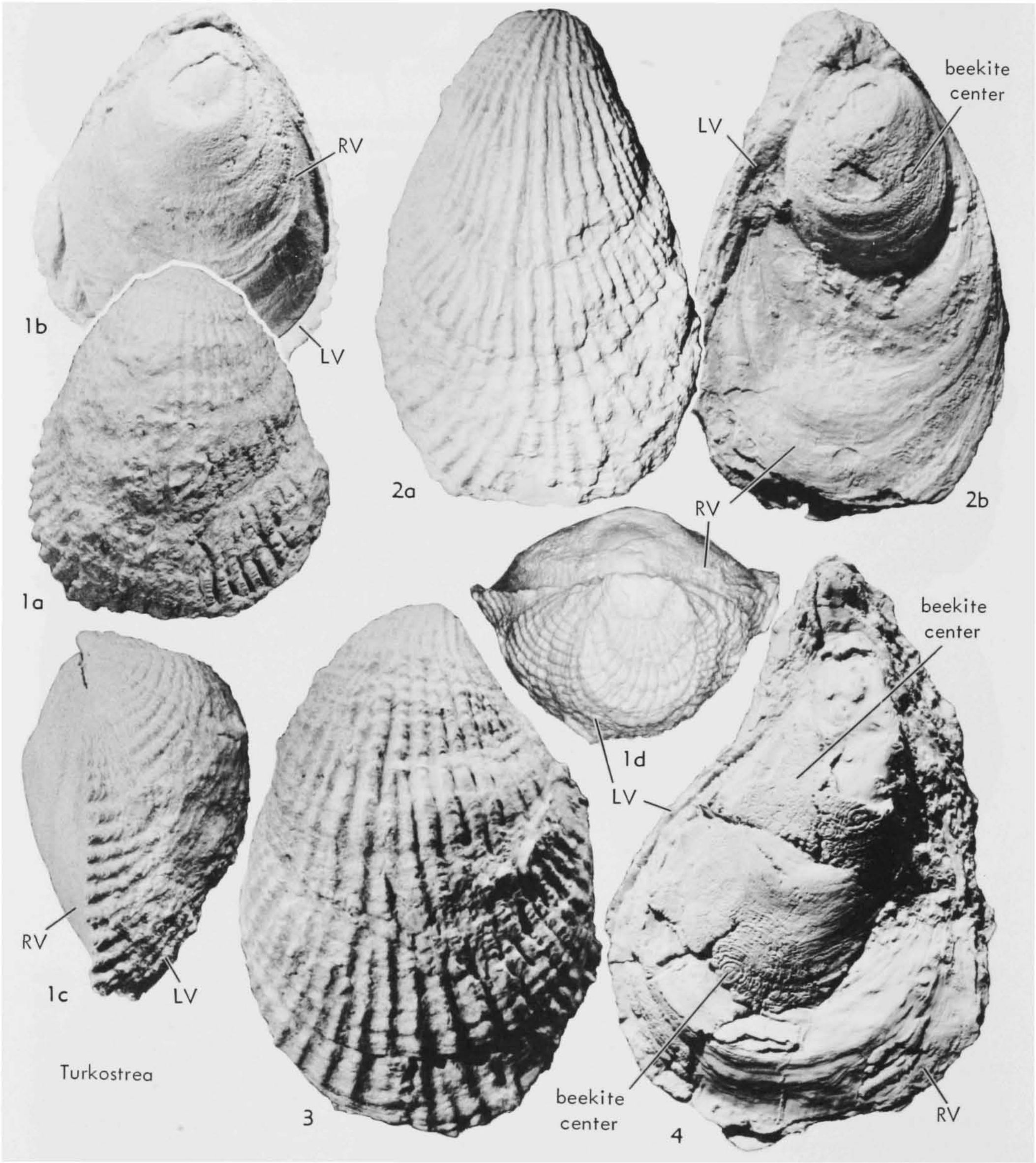

FIG. J114. Ostreidae (Ostreinae) (p. N1139-N1140).

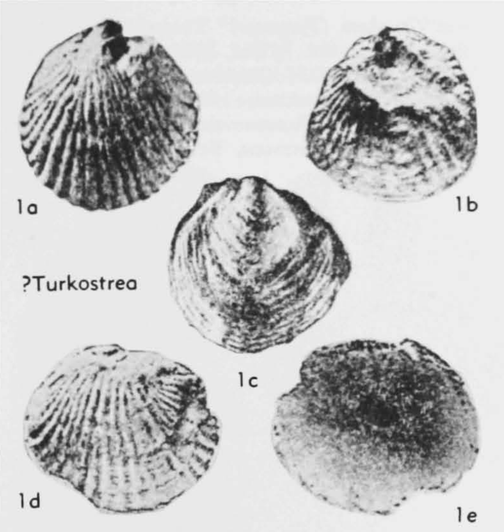

FIG. J115. Ostreidae (Ostreinae) (p. *N*1139-*N*1140).

formis (CONRAD, 1832), which had a large, heavy, twisted, saddle-shaped, and auriculate shell (Fig. J70). Evolution of this provincially isolated stock has been elucidated by STENZEL (1949), compare p. *N*1079.]

Ferganea VYALOV, 1936, p. 19 [**Gryphaea sewerzowii* ROMANOVSKIY, 1883, p. 251, *nom. nud.*= *G. sewerzowii* ROMANOVSKIY, 1884, p. 54-55, pl. 12, figs. 1-3; OD]. Small to medium-sized (to 12 cm. high), mostly roughly squamate. LV high and narrow (*H* is about 120 to 200 percent of *L*), highly convex in horizontal cross section, convex in dorsoventral direction, compressed in arteroposterior direction but devoid of a radial keel or radial sulcus; beak large, pointed, prosogyral to nearly orthogyral, somewhat inrolled and with small attachment area; umbonal region of LV thickly filled with shell material so that there is no umbonal cavity. RV flat to lightly convex, exterior covered with many projecting growth squamae; outline ovate, higher than long (*H* is 123 to 132 percent of *L*). Chomata small, present only in well-preserved specimens. Some species developed a loosely spiraled orthogyral ligamental area, more rarely the spiral twist was stronger in the older, umbonal part of the shell. [These forms were described as *Exogyra ferganensis* ROMANOVSKIY, 1879, p. 153-154, text fig. 2, which was later assigned to *Amphidonta* [*recte Amphidonte*] because of its chomata (GEKKER, OSIPOVA, & BELSKAYA, 1962, v. 2, pl. 15). However, their ligamental area does not have a narrow, crest-shaped posterior bourrelet, and the adductor muscle insertion is clearly reniform so that there is no doubt that *Ferganea ferganensis* (ROMANOVSKIY, 1879) is not an exogyrine oyster but an ostreine *Exogyra* homeomorph.] *Oligo.(Sumsarskiy Yarus),* C.Asia-USSR.——FIG. J118,*1-6*; J119,*2-4*.

**F. sewerzowii* (ROMANOVSKIY); J118,*1a-c,* LV with broken ventral margin, ext., int., post. views, ×1; J118,*2a,b,* RV ext., int., ×1; J118,*3a,b,* RV

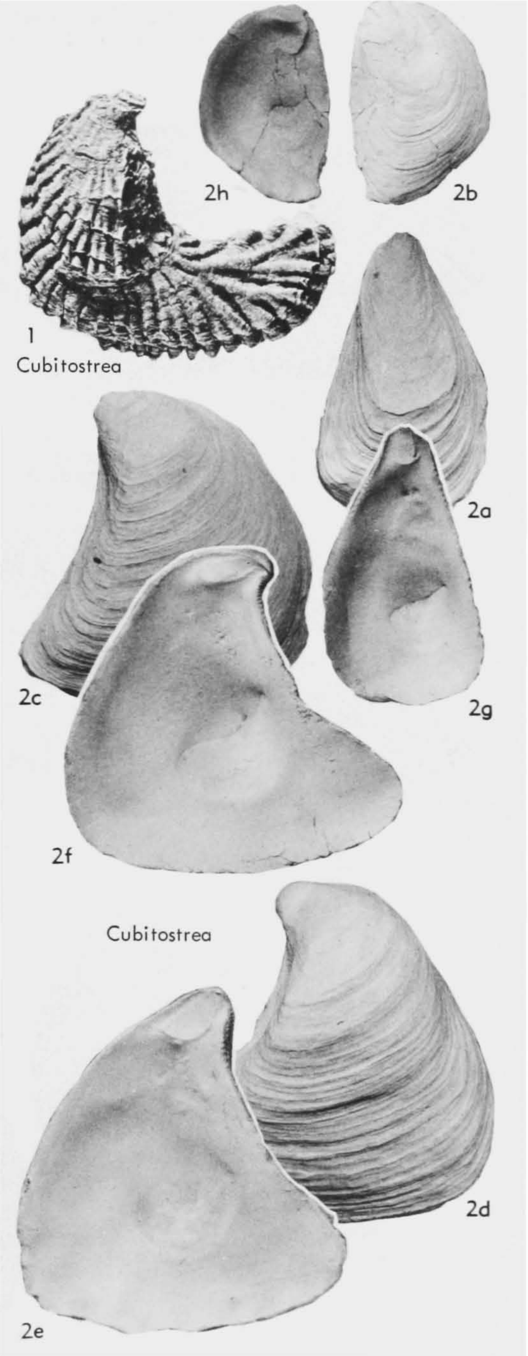

FIG. J116. Ostreidae (Ostreinae) (p. *N*1141-*N*1143).

ext., int., ×1; J118,*4,* LV oblique view onto insertion of post. adductor muscle, ×1; J118,*5a,b,* RV ext., int., ×1; J118,*6a,b,* broken LV int., post., ×1 (Stenzel, n) (all specimens whitened for photography; specimens from Paleont. Inst. Akad. Nauk SSSR, collected by R. F. Gekker); J119,*2-4* (="*Gryphaea (Ferganea)*" Vyalov, 1936); J119,*2a,b,* LV int., ant., J119,*3,* LV int.; J119,*4a,b,* RV ext., int., all ×0.75 (Romanovskiy, 1884).

Platygena Romanovskiy, 1882, p. 46-47, 58-60 [**Ostrea asiatica* Romanovskiy, 1879, p. 150; M] [=*Platigena* Borneman, Burachek, & Vyalov,

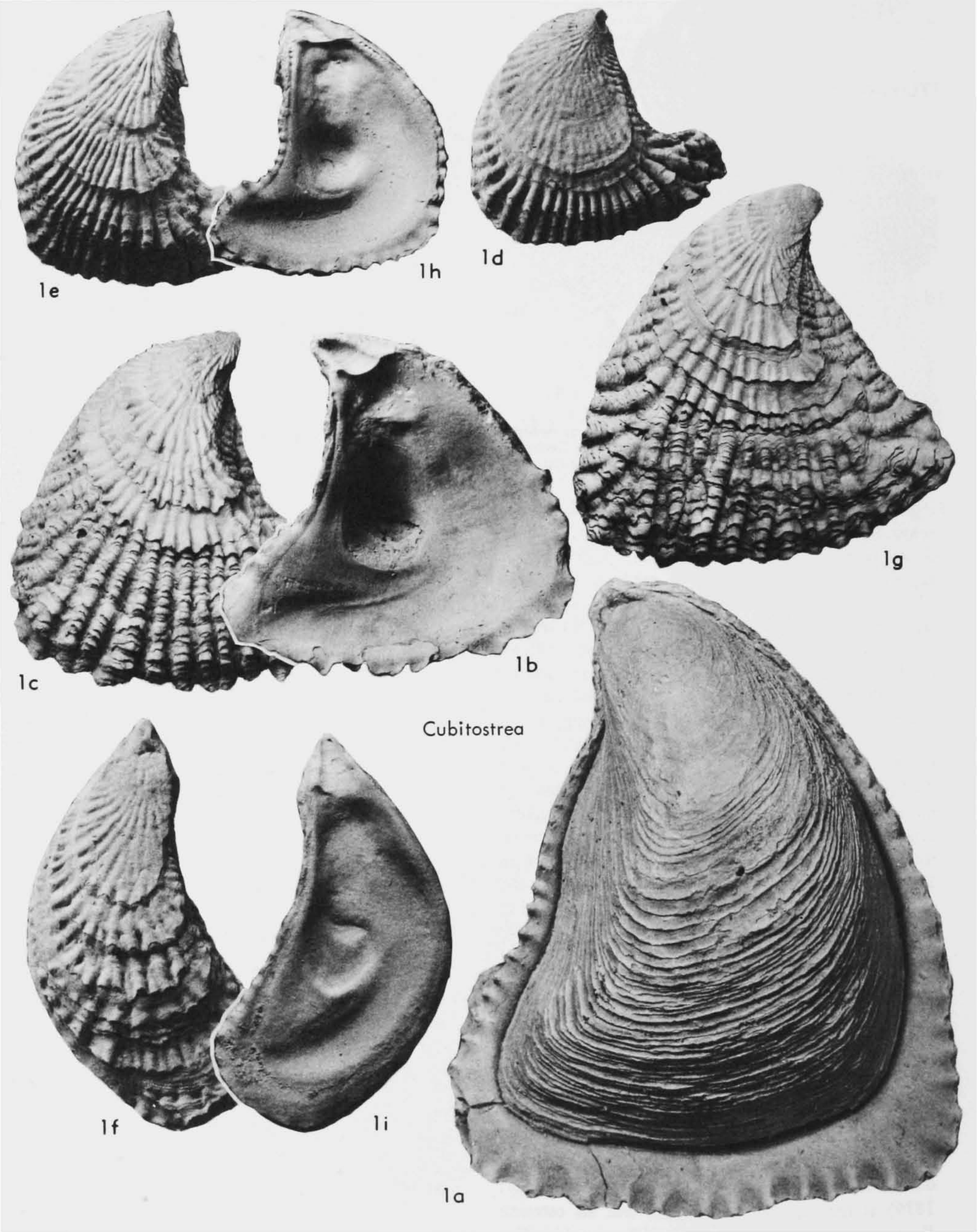

Fig. J117. Ostreidae (Ostreinae) (p. *N*1141-*N*1143).

1934, p. 260 *(nom. null.)*]. Medium-sized to large and flattish, width about 0.16 to 0.25 of height; outline roughly orbicular; old shells higher than long. LV gently convex, RV even less convex. Outline of valve cavity in LV banjo-shaped (resembling guitar-shaped valve cavity of *Sokolowia*), with slender subparallel-sided dorsal neck and suborbicular ventral banjo body. Space on

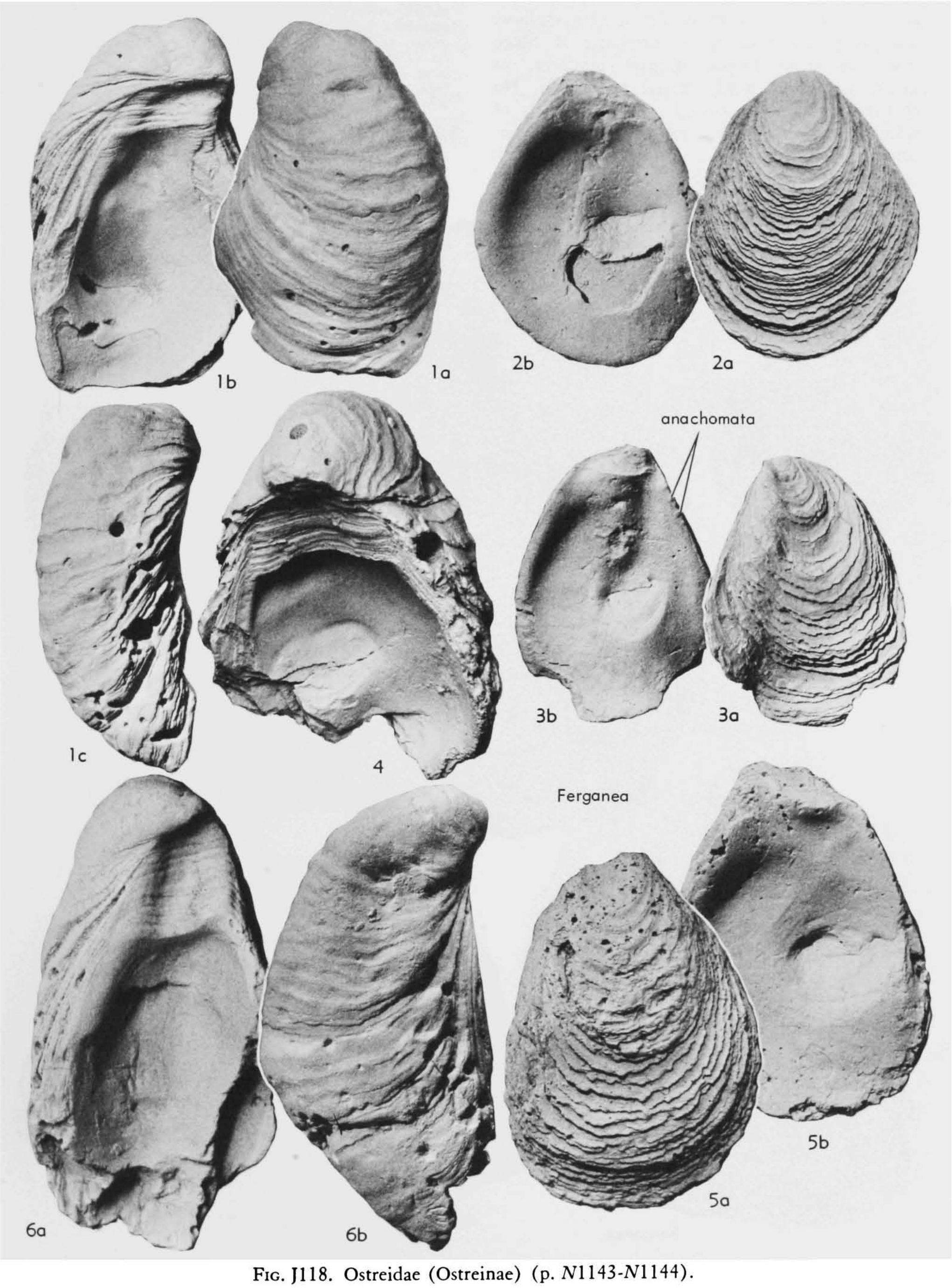

FIG. J118. Ostreidae (Ostreinae) (p. *N*1143-*N*1144).

either side of banjo neck filled out with former temporary anterodorsal and posterodorsal valve margins left behind during growth of shell. Later growth restricted to continued gradual shift of shell cavity in ventral direction without increase in size of cavity, which in LV is very shallow, without umbonal cavity or overhang at hinge plate. Adductor muscle imprint reniform, its longer axis tilted, nearly central in location. No chomata. Numerous growth squamae, many of which are frilled in harmony with nearly continuous small radial ribs. *Up.Eoc.(Rishtan.),* C. Asia-USSR-Afr.(Sudan-Libya).——Fig. J120,*1*. **P. asiatica* (Romanovskiy), USSR; *1a-e,* LV ext., int., RV int., part of ext., both valves post. view, ×0.48 (Romanovskiy, 1882).

[*Platygena* is similar to *Deltoideum*, from which it differs in central location of the reniform muscle imprint. The genera evidently are only superficially similar. *Platygena* resembles *Sokolowia*, but differs in its flatness, lack of shell twists, and in being not at all a *Gryphaea* homeomorph. Its very shallow shell cavity proves that it never had a large gonad lodged within it. Therefore, it must have been an incubatory oyster that produced few eggs. Closeness to *Ostrea* is proved by its reniform muscle imprint.]

Sokolowia J. Böhm, 1933, p. 104 [**Gryphaea buhsii* Grewingk, 1853, p. 114 (=*Gryphaea esterházyi* Pávay, 1871, p. 375, pl. 8-9); OD]

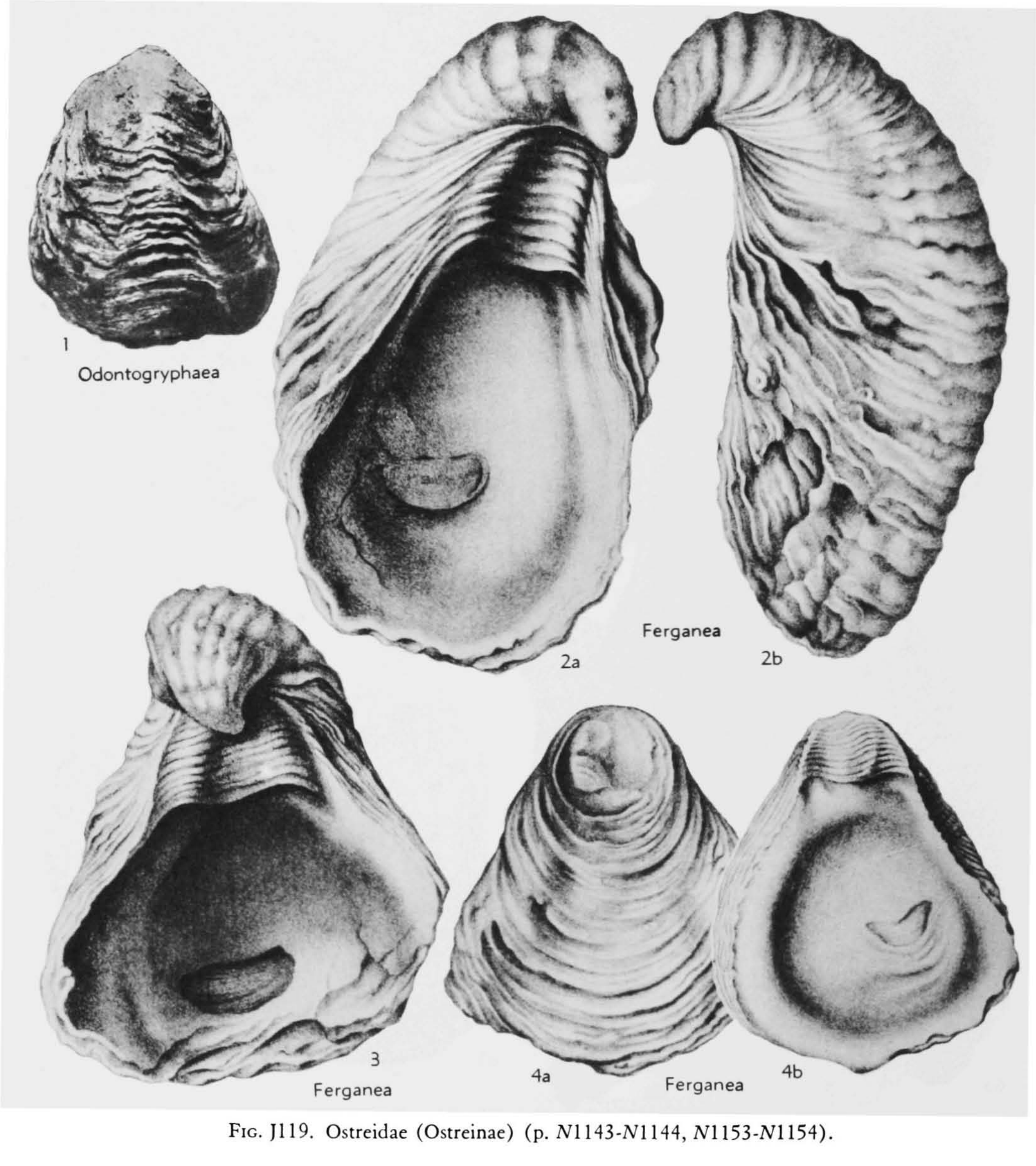

Fig. J119. Ostreidae (Ostreinae) (p. *N*1143-*N*1144, *N*1153-*N*1154).

[=*Sokolovia* BORNEMAN, BURACHEK, & VYALOV, 1934, p. 260 *(nom. van.)* (obj.); *Fatina* VYALOV, 1936, p. 19 (type, *Gryphaea esterhazyi* PÁVAY, *var. beldersaiensis* GORIZDRO, 1915, p. 22; OD); *Kafirnigania* GEKKER, OSIPOVA, & BELSKAYA, 1962, v. 2, p. 115 (type, *K. orientalis;* OD)]. Small to large (to 15 cm. long and 21 cm. high), highly inequivalve, homeomorphous with *Gryphaea;* LV umbonal region extending beyond RV; outline triangular. Chomata well developed. Adductor muscle imprint reniform, centrally placed. LV with ventral margin convex, evenly curved, and marked at each end by prominent corner, anterior and posterior margins straight to concave. In all young to mature individuals length about same as height or larger (*H* 75 to 100 percent of *L*). With advancing age LV tends to quit growing in length but continues growing in ventral direction so that valve becomes much higher (*H* up to 172 percent of *L*), losing triangular outline and prominent corners. LV convex from umbo to venter and even more so from anterior to posterior; beak small, pointed, incurved, reaching over to right side. Attachment area mostly small. Surface cov-

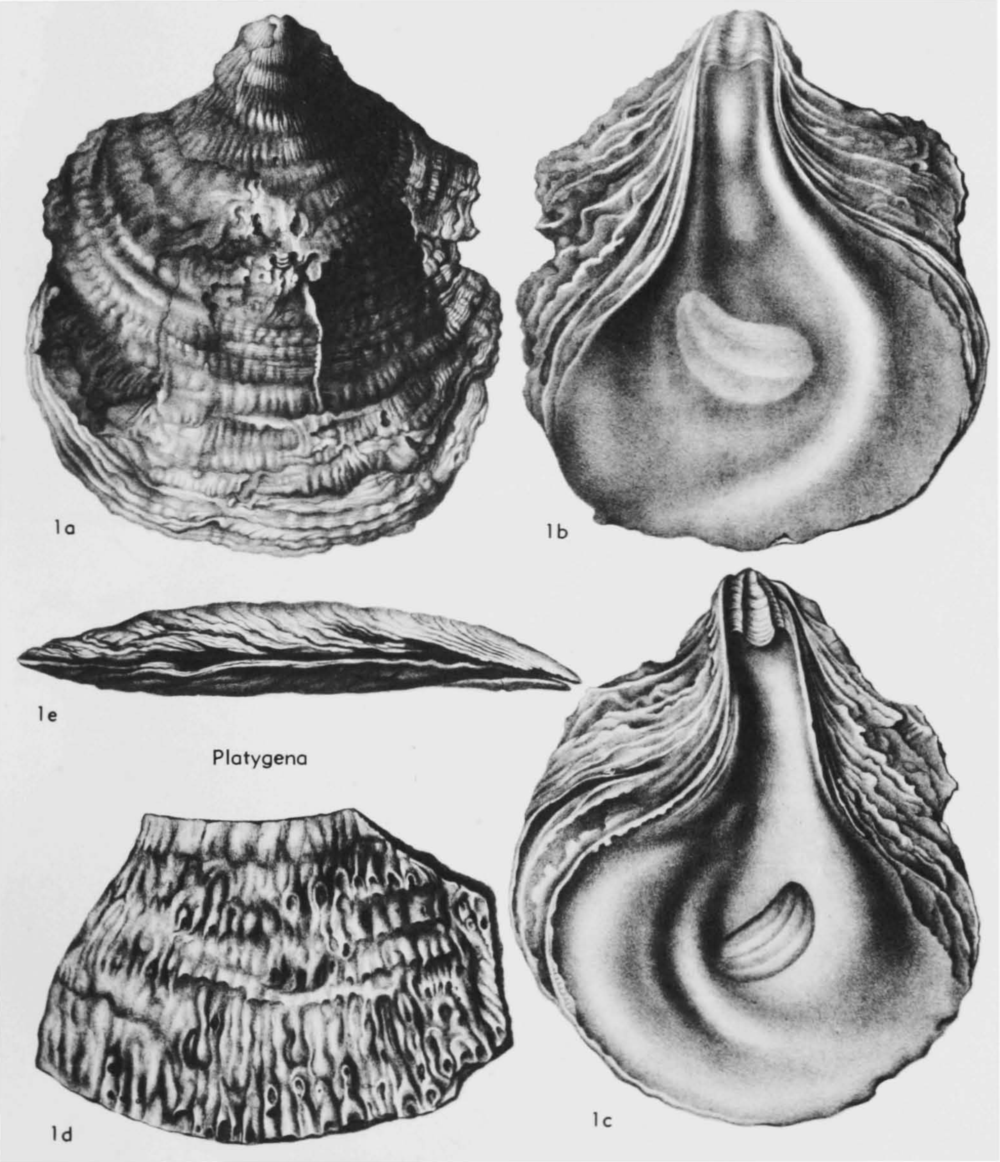

FIG. J120. Ostreidae (Ostreinae) (p. *N*1144-*N*1146).

ered partly or entirely by many subequal, parallel, even-crested, strong to obsolescent radial ribs; no free-standing growth squamae on umbonal half of valve. Valve cavity guitar-shaped in outline even in very high, old shells, because anterior and posterior valve margins are pinched in. Umbonal cavity filled in with shell deposits. RV flat to concave, with triangular outline like that of LV but truncated at umbo by ligamental area, which stands vertical to commissural plane; devoid of

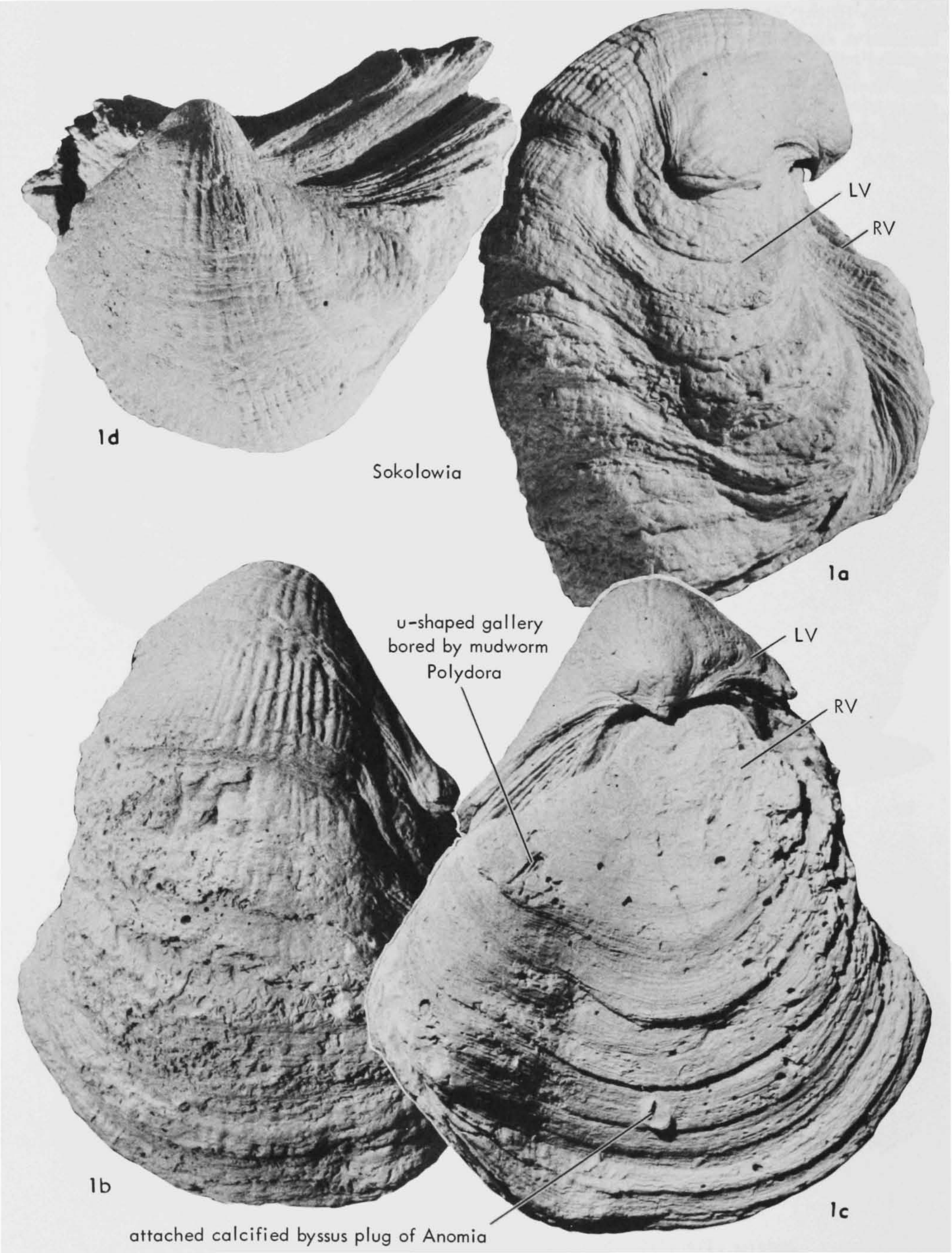

FIG. J121. Ostreidae (Ostreinae) (p. N1146-N1150).

ribs, but with prominent growth squamae and may have auricles. *Eoc.(Turkestan.)(=up.Lutet. +Auvers.),* Rumania(Transylv.)-C.Asia.——FIG. J121,*1*. **S. buhsii* (GREWINGK), USSR (Fergana); *1a-d,* both valves, post. view, left side, right side, umbonal view, ×0.7 (Stenzel, n). [Specimen whitened for photography; from Paleont. Inst. Akad. Nauk SSSR, collected by R. F. GEKKER.] ——FIG. J122,*1*. *S. beldersaiensis* (GORIZDRO, 1915) (="*Fatina*"), USSR (Fergana); *1a-d,* both valves post. view, left side, right side, umbonal view, ×1 (Stenzel, n). [Specimen whitened for photography; from Paleont. Inst. Akad. Nauk SSSR, collected by R. F. GEKKER.]——FIG. J123,*1*. *S. orientalis* (GEKKER, OSIPOVA, & BELSKAYA, 1962) (="*Kafirnigania*"), USSR (Baba-Tag); *1a,b,* LV ext., both valves from right side, ×1 (Gekker, Osipova, & Belskaya, 1962).

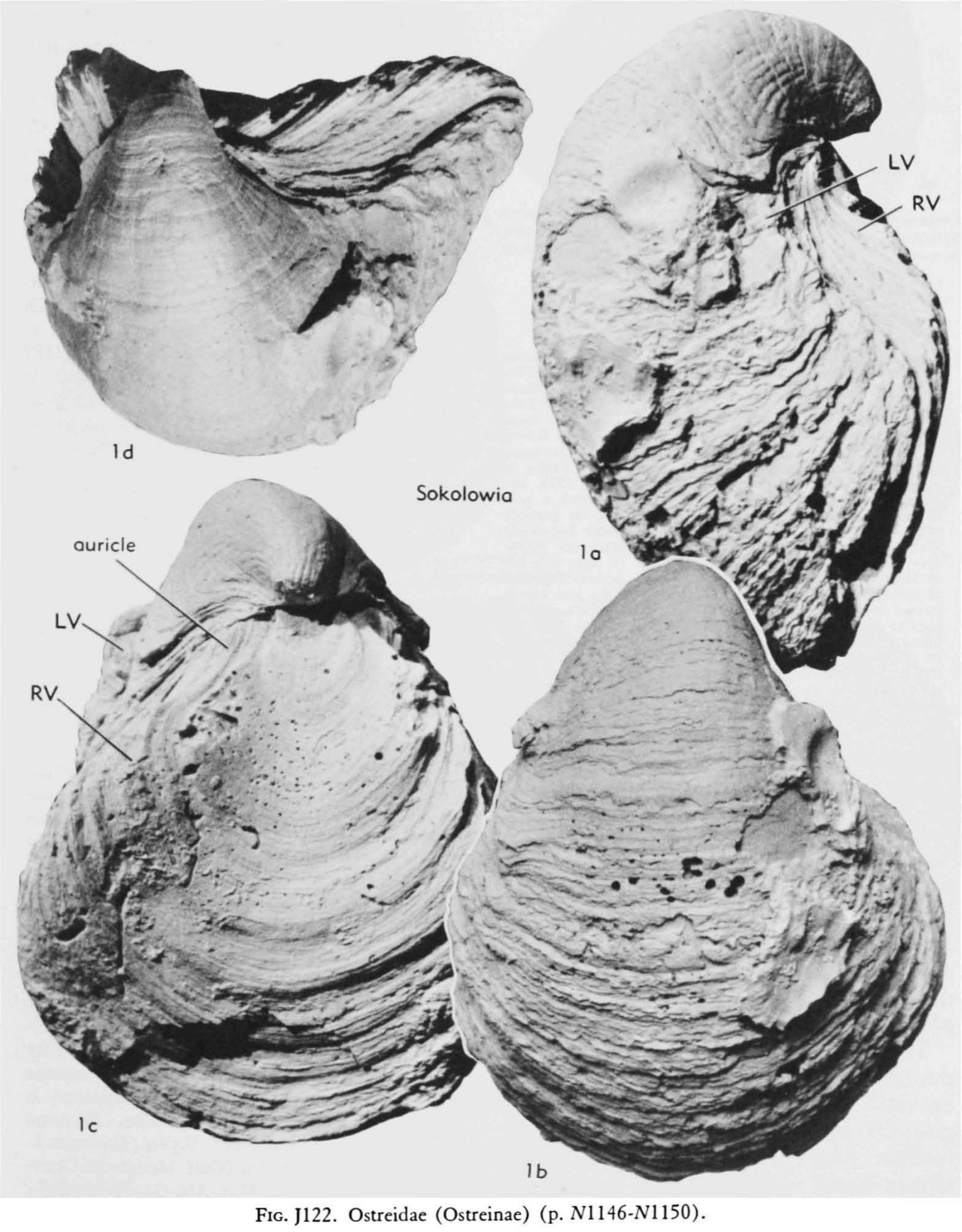

FIG. J122. Ostreidae (Ostreinae) (p. *N*1146-*N*1150).

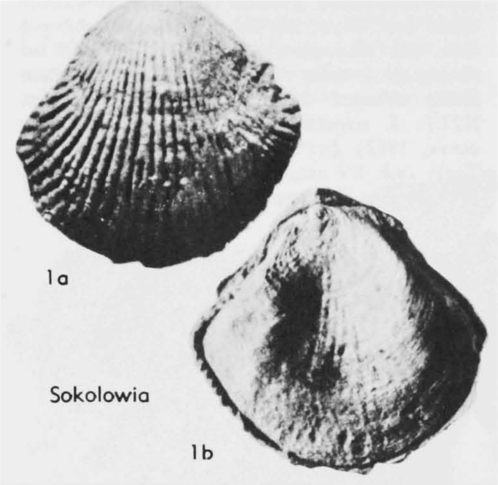

FIG. J123. Ostreidae (Ostreinae) (p. N1146-N1150).

[*Sokolowia* is interpreted to be a descendant of *Ostrea* (*Turkostrea*), which in turn descended from *Ostrea* (*Ostrea*). Evolution was quite rapid and produced a *Gryphaea* homeomorph (YANG KIEH, 1930; GEKKER, OSIPOVA & BELSKAYA, 1962). The stock was a provincial offshoot from *Ostrea, s.s.* and retained some generic characters of *Ostrea s.s.*, namely, reniform muscle imprints and discrepant sculpture of the valves. When VYALOV proposed *Fatina* as a new genus in 1936 he placed *Sokolowia* BÖHM, 1933, under it as a mere section of *Fatina* (*Fatina*). Such a procedure is not sanctioned by the *Code*, which on grounds of priority requires that *Fatina* be placed under *Sokolowia* (*Sokolowia*). VYALOV was correct in estimating the difference between the two forms to be slight. In fact, they are so little that the type species of *Fatina* is best regarded as merely another species of *Sokolowia* and the two names treated as subjective synonyms. The same conclusion applies to *Kafirnigania*. It seems unlikely that more than one genus could evolve from *Ostrea s.s.* in the same province, in the same extensive sea basin, and in the same sedimentary environments, without separating geographic barriers. It has been generally overlooked that *Sokolowia esterhazyi* (PAVAY) was first described and figured as *Gryphaea buhsii* GREWINGK, 1853, from the vicinity of Nemekeh and Surt, in the eastern part of the Elburz Mountains in northern Iran. The species is readily identifiable from this earlier description, which is nomenclaturally available. Therefore, the prior valid synonym is the name given by GREWINGK.]

Tribe FLEMINGOSTREINI Stenzel, new tribe

Consists of the genera *Flemingostrea, Odontogryphaea, Ostreonella,* and possibly *Kokanostrea*. *Anulostrea* and *Quadrostrea* ultimately may find place in this tribe, but now are insufficiently known. *Odontogryphaea* is a *Gryphaea* homeomorph.

The following are common features of this tribe: 1) U-shaped or terebratuloid fold on valve commissure at ventral valve margins; LV arched up toward left side to form rooflike fold; RV with semicircular or tongue-shaped ventral extension that reaches over to left side fitting into corresponding sinus of LV. 2) Adductor muscle imprints longer than high, with straight to concave dorsal margins and imprints located rather close to ventral and posterior valve margins. 3) Shell walls exceptionally thick (up to 3.5 cm.) in umbonal half of valves. 4) Resilifer one to three times as long as each flanking bourrelet of ligamental area. 5) Ligamental area commonly rather long but low, its ends producing shoulders on shell. 6) Attachment area never large, very small to absent in *Odontogryphaea;* no tendency of one individual to grow upon another. Terebratuloid fold makes its appearance at fairly advanced stage of growth, commonly when shell reaches a height of about 2 cm. At that place growth changes its direction, and a prominent smooth hump in shell profile is the result. *U.Cret.(Cenoman.)-Mio.*

Flemingostrea VREDENBURG, 1916 [**Ostrea (Flemingostrea) flemingi* D'ARCHIAC & HAIME, 1853, p. 275; OD] [?=*Solidostrea* VYALOV, 1948a, p. 24 (type, *Ostrea hemiglobosa* ROMANOVSKIY, 1884 (in 1878-90), p. 26; OD)]. Medium-sized to large; overall shape flattish; valves subequal, neither highly convex nor compressed in anteroposterior direction. LV umbo not prominent or hook-shaped, terebratuloid fold broad and gentle, arising gradually at later growth stage than rooflike fold does in *Odontogryphaea;* no radial sulcus delimiting fold on its posterior flank which has gradual slope. Calcite prisms long and well developed in prismatic shell layers (see Fig. J20). Many species with regularly spaced concentric imbrications on RV recalling *Gryphaeostrea;* imbrications composed of prismatic shell layers and separated from each other by smooth concentric bands with sigmoidal profiles. Chomata present or absent. Ligament growing rapidly in length, but not in height in early years resulting in somewhat shouldered appearance of RV with shoulders at ends of ligamental area approaching rectangular shape. [*Flemingostrea* has several features that distinguish it from other genera of the tribe: 1) LV umbo not prominent and not beaked, 2) shell not as highly convex as in *Odontogryphaea* and not compressed anteroposteriorly at any stage, 3) shell shape less globose, tending to be flattish, 4) valves more nearly equal in size, 5) terebratuloid fold appearing later and very gradually, 6) flanks of terebratuloid fold remaining poorly delimited. These features are more primitive than corresponding ones in other genera of the tribe, because they more nearly approach those of the normal, average ostreine prototype. Therefore, *Flemingostrea* is regarded as the ancestor of the tribe. Its acme was in Late Cretaceous time]. *U.Cret.(Cenoman.)-Mio.*, S.Am.(Peru)-N.Am.(Gulf Mexico-Atl.Coast-NE.Mexico-Texas-Ark.-Miss.-Ala.-Ga.-N.Car.-N.J.-Utah)-Eu.(Belg.)-Afr.(Alg.-Egypt-Sudan-Senegal-

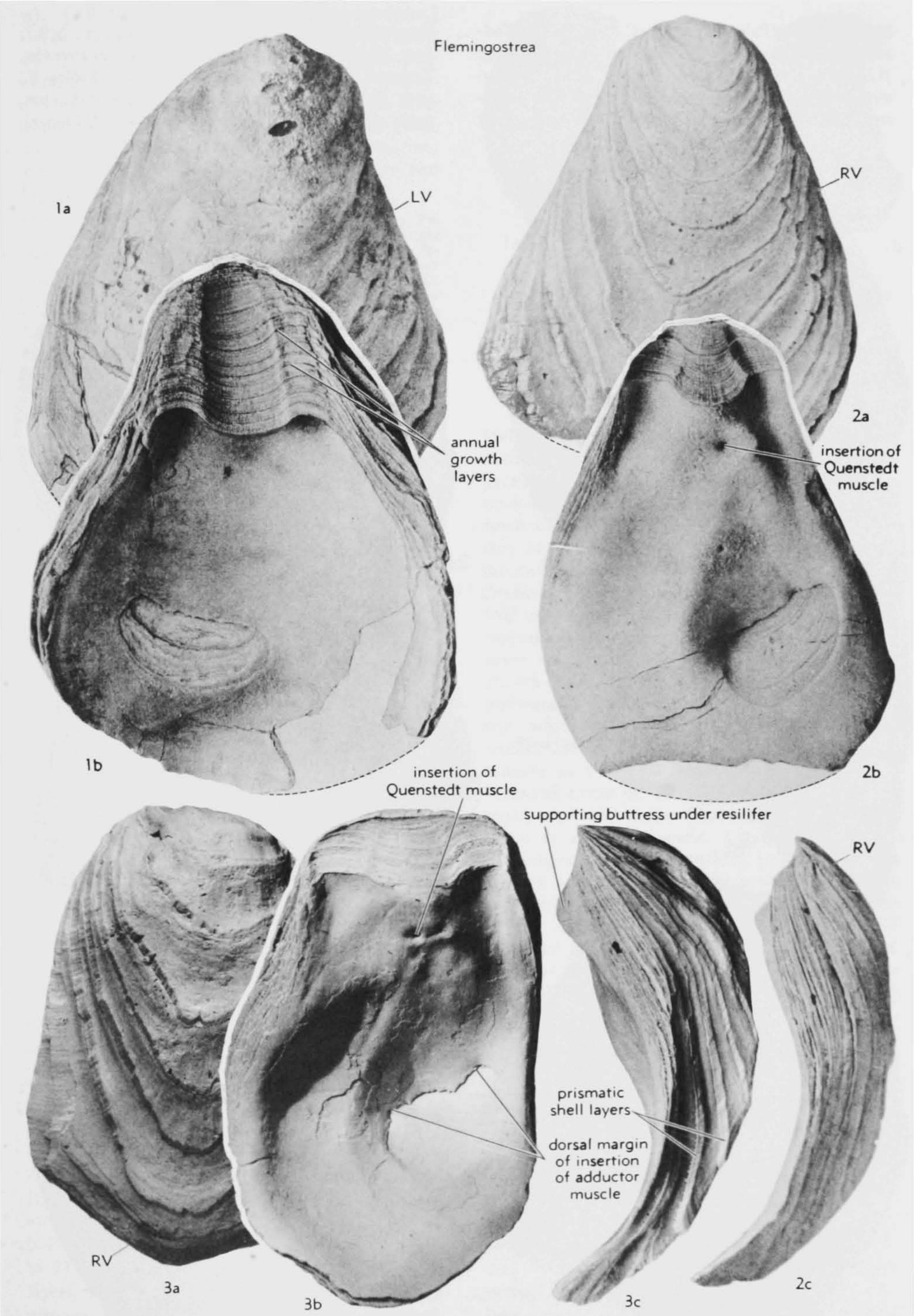

FIG. J124. Ostreidae (Ostreinae) (p. *N*1150, *N*1152-*N*1153).

Madag.) - Asia (Pak. - Afghan.) - C.Asia - USSR (Tadzik Basin-Gissar Mts.-Transalaii Mts.). — Fig. J124,*1-3*. *F. subspatulata* (Forbes, 1845) (=*Ostrea owenana* Shumard, 1861), U.Cret.(Maastricht.); *1a,b,* Nacatoch Sand, Navarro Gr., near Greenville, Hunt Co., Texas, LV ext., int., ×0.7; *2a-c,* Nacatoch Sand, near Corsicana, Navarro Co., Texas, RV ext., int., post., ×0.7; *3a-c,* Ripley F., near Braggs, Lowndes Co., Ala., RV ext., int., post., all × 0.7 (*1,2,* Stephenson, 1941;*3,* Stenzel,

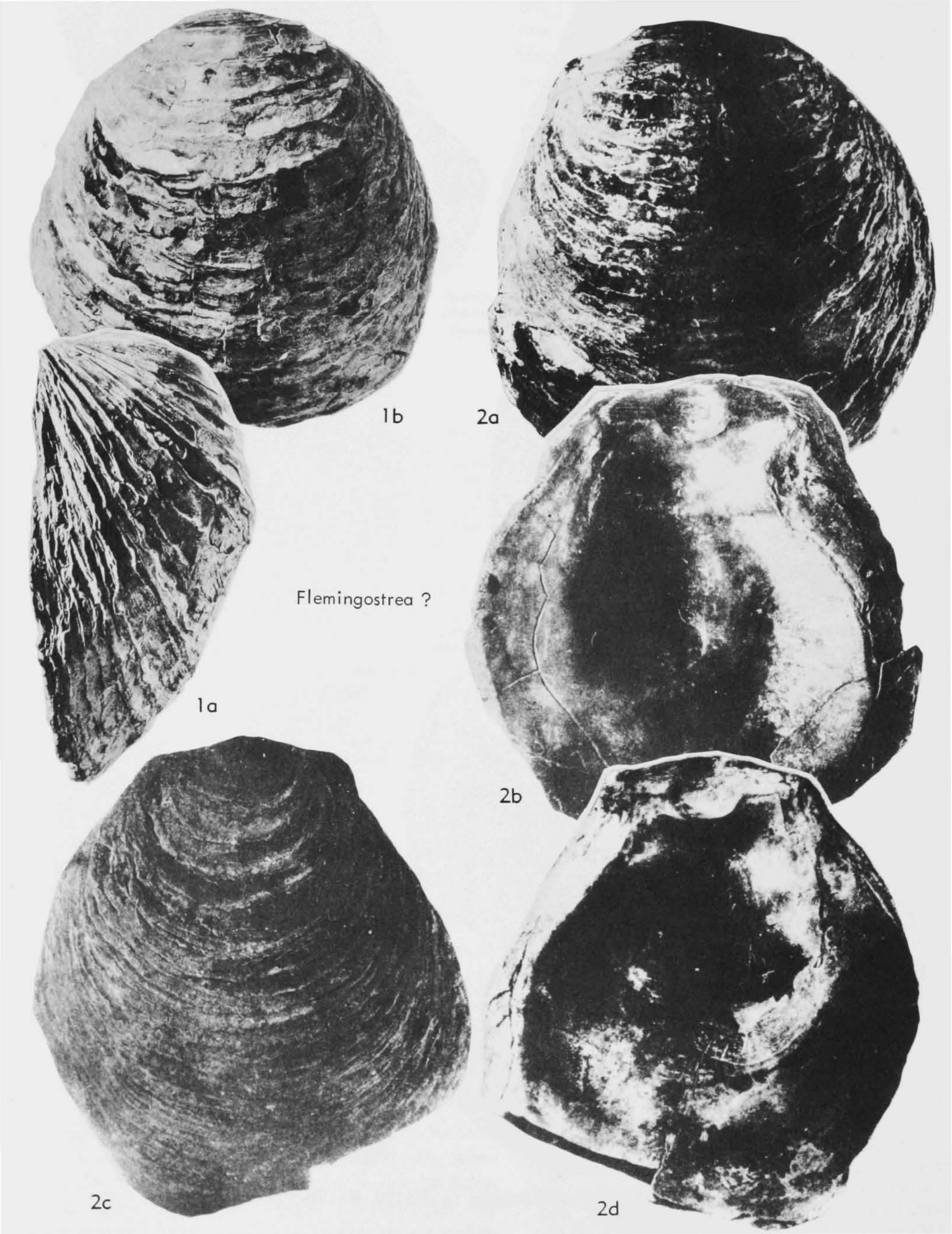

Fig. J125. Ostreidae (Ostreinae) (p. *N*1150, *N*1152-*N*1153).

n). [All specimens whitened for photography.] —Fig. J125,*1,2*. *F.? hemiglobosa* (Romanovskiy, 1884) (=*Ostrea gigantica* Cox, 1938 (*non* Solander, 1766), =*Ostrea* (*Solidostrea*) (Vyalov, 1948c), Eoc. (Suzakian Stage); *1a,b,* Tash Kurghan, N. Afghan., LV ant., ext., ×0.5 (Cox, 1938); *2a-d,* Tadzik Basin, USSR, LV ext., int., RV ext., int., ×0.5 (Vyalov, 1948c). [*See* also Fig. J20.]

[*Solidostrea* was described as new a second time, by Vyalov, 1948b, p. 13-19, pl. 3-7. The type species has some superficial resemblance to "*Gigantostrea*" *gigantica* Solander in Brander, 1766 (*recte Pycndonte* (*Pycnodonte*) *gigantica*) and Cox in Cizancourt & Cox (1938, p. 39-42, pl. 5, fig. 5a,b) described specimens of *Flemingostrea? hemiglobosa* from Afghanistan under the former name in spite of his observations that they lacked vesicular shell structure and had a reniform adductor-muscle imprint. The two differ greatly, because *Pycnodonte* and its junior synonym *Gigantostrea* have orbicular muscle imprints and vesicular shell structure. *Solidostrea* is presumably a junior synonym of *Flemingostrea,* because the type species of both have the characteristic well-spaced concentric undulations of sigmoidal cross section, each one ending in a growth squama, a very thick shell wall of the LV, and a humped profile of the LV, noted and well-figured by Cox.]

Kokanostrea Vyalov, 1936, p. 19 [**Ostrea kokanensis* Sokolov, 1910, p. 73; OD]. Small (up to 3.5 cm. high), highly inequivalve; outline oval with umbones at small end. LV highly convex, profile hook-shaped, with prominent hump about 15 mm. from umbo which is acute or bluntly cut off, not prominent and not *Gryphaea*-like, but prosogyral; tendency to form wing at anterior valve margin. RV operculiform, flat to concave. Chomata present. Adductor muscle imprint semicircular, longer than high, located closer to posterior and ventral valve margins. Both valves devoid of radial ribs, both with uniformly spaced smooth concentric growth squamae. *Eoc.(Turkestan.) (up.Lutet. + Auvers.),* C.Asia. —— Fig. J126,*1*. **K. kokanensis* (Sokolov); *1a-c,* both valves, oblique post. view, LV int., RV int., ×1 (Sokolov, 1910).

[Information on this genus is scanty and its taxonomic position is open to question. Vyalov (1936, p. 19) gave the following definition for it: Beak well developed, gryphoidally inrolled; ligamental area inclined toward anterior; posterior slope of shell steeper than the anterior one. He placed it as a subgenus of *Liostrea,* as did Gekker, Osipova, & Belskaya (1962). However, because of differences in outline and position of the adductor muscle imprints, the two taxa evidently are not closely related. *Kokanostrea* is possibly a member of the Flemingostreini; indications for this placement are the humped and hooked profile of the LV, recalling *Odontogryphaea,* and the outline and position of the adductor muscle imprint.]

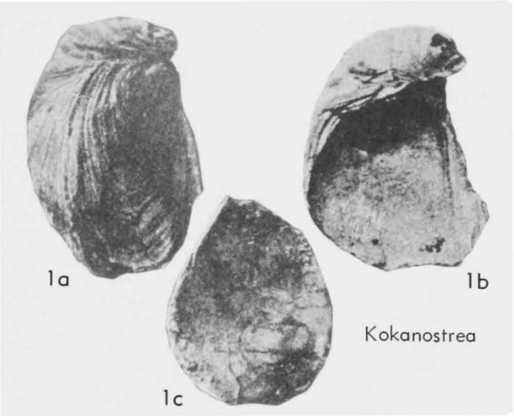

Fig. J126. Ostreidae (Ostreinae) (p. *N*1153).

Odontogryphaea Ihering, 1903, p. 194 [**Gryphaea consors* var. *rostrigera* Ihering, 1902, p. 113 (= *G. (Odontogryphaea) rostrigera* Ihering, 1903, p. 212; OD] [=*Sinustrea* Vyalov, 1936, p. 18 (type, *Ostrea (Flemingostrea) morgani* Vredenburg, 1916, p. 197; OD); *Sinostrea* Haas, 1938, p. 294 *(nom. van.)*]. Small to medium-sized (up to 13 cm.), composed of lamellar and prismatic layers; vesicular and chalky layers absent. Outline orbicular or oval to triangular, umbo at small end. No auricles near hinge. Shell subequivalve to inequivalve, but in most species not highly inequivalve. Valve commissure twisted, with terebratuloid fold at venter. LV convex and capacious, with prominent beak mostly somewhat opisthogyral, rarely prosogyral, incurved unevenly in hook-shape. In nearly all species beak does not reach through plane of valve commissure to right side of shell. LV compressed in anteroposterior direction in most species in early growth stage; developing rather abruptly rounded rooflike radial fold at beginning of later growth stage; fold delimited on its posterior flank by radial sulcus. RV never really operculiform, simply convex in early growth stage, convex along line from umbo to mid-ventral margin except at tonguelike ventral end, which may be slightly concave and fits into rooflike fold of LV. RV slightly convex to deeply concave in transverse (anteroposterior) direction. Umbonal cavity of LV filled with solid shell material, and LV quite thick-walled from tip of umbo to adductor muscle. Ligamental area usually longer than high; resilifer is 1.5 to 2 times as long as either flanking bourrelet. Chomata to both sides of ligament, very extensive in type species, placed so close to valve margins of RV that their growth tracks are visible on the outside. Posterior adductor muscle imprint never orbicular; placed close to venter. Imprint outline different in each valve, one on left side longer and more reniform to ribbon-shaped. Surface features of both valves similar, consisting of foliaceous growth squamae irregularly spaced, but farther apart in early growth stage. Radial costae, either absent or small, developed only on rooflike fold of LV as discontinuous fine frills of crowded foliaceous growth squamae. *U.Cret.(Maastricht.)-Eoc.,* France (Paris Basin, *Thanet.;* Corbières, *Sparnac.-Lutet.*)-S. Asia(Baluch.)-S. Am.(Patag.)-N. Gulf Mexico(Ga.-Ala.-La.-NE.Mexico). —— Fig. J127,*1-3*. **O. rostrigera* (Ihering), Eoc., Arg. (Patagonia, Chubut Terr.); *1,* LV int.; *2,* RV int.; *3a-c,* both valves, oblique left ventral view, oblique right ant. view, ant. view, all ×0.75 (Ihering, 1903).——Fig. J119,*1*. *O. morgani* (Vredenburg, 1916) (=*"Liostrea (Liostrea)* section *Sinustrea"*

Vyalov, 1936), U.Cret.(Maastricht.), NW.Pak. (Des Valley, Baluch.); both valves, left side, ×0.75 (Vredenburg, 1916). [*See* also Fig. J9, J34, J64.]

[Vredenburg was unaware of *Odontogryphaea* and did not separate this genus from *Flemingostrea* which he regarded as a subgenus of *Ostrea,* showing thereby that he was not impressed by the homeomorphous similarities with *Gryphaea.* Vyalov (1936, 1948a) was unaware of *Odontogryphaea.* Therefore, he proposed a new taxon, *Sinustrea,* as a section of *Liostrea* (*Liostrea*) where he also placed *Ostreonella* as a section. Thus both were somewhat removed from *Flemingostrea,* which he left standing as a subgenus of *Ostrea,* following Vredenburg. All three were placed in the Ostreinae in spite of the *Gryphaea*-like beaks in some of the species. His apparent reason, not expressed in print, for not placing *Sinustrea* in the Gryphaeinae was that the Gryphaeinae, according to him, must have a flat or concave upper valve, an astute observation in this case. Indeed, *Odontogryphaea* has a RV that is convex in its early adult growth stage, presumably because it is descended from *Flemingostrea,* which has a similarly convex RV. Both are clearly members of the Ostreinae, although *Odontogryphaea* is a homeomorph of *Gryphaea.*——Some species, notably *Odontogryphaea thirsae* (Gabb, 1861, p. 329) from the Nanafalia Formation (Thanet.) of the Wilcox Group in Alabama, lack imprints of former attachment at their left umbones. They must have grown from larval to adult stage without becoming attached to a firm substrate. The feature is probably the result of their adaptation to a substrate lacking places of firm attachment. (See Fig. J34 and J64.)]

Ostreonella Romanovskiy, 1890, p. 101[**O. prima;* OD] [=*Ostronella* Nikitin, 1894, p. 171 *(nom. null.)*]. Small (to 5 cm. high), overall shell shape biconvex lenticular when young to globose when old. Valves almost equal, highly inflated, highly convex, somewhat compressed anteroposteriorly so that they may become wider than long (length is 75 percent, width 95 percent of height). LV umbo not prominent, not hook-shaped, with small attachment area. Terebratuloid fold obscure in young; poorly delimited at its flanks, rising rather slowly, gradually, and fairly late during growth; ending in U-shaped semicircular hollow at valve commissure. Concentric growth squamae on both valves evenly and regularly

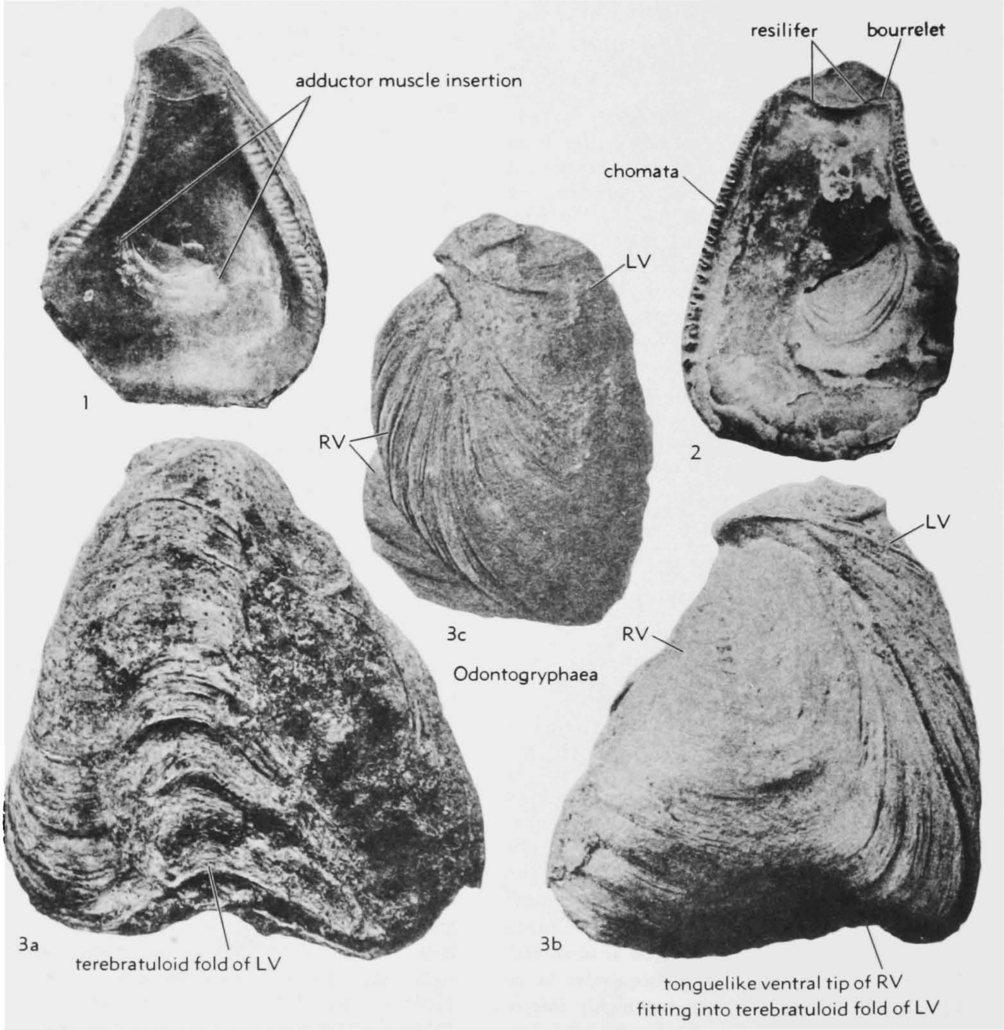

Fig. J127. Ostreidae (Ostreinae) (p. *N*1153-*N*1154).

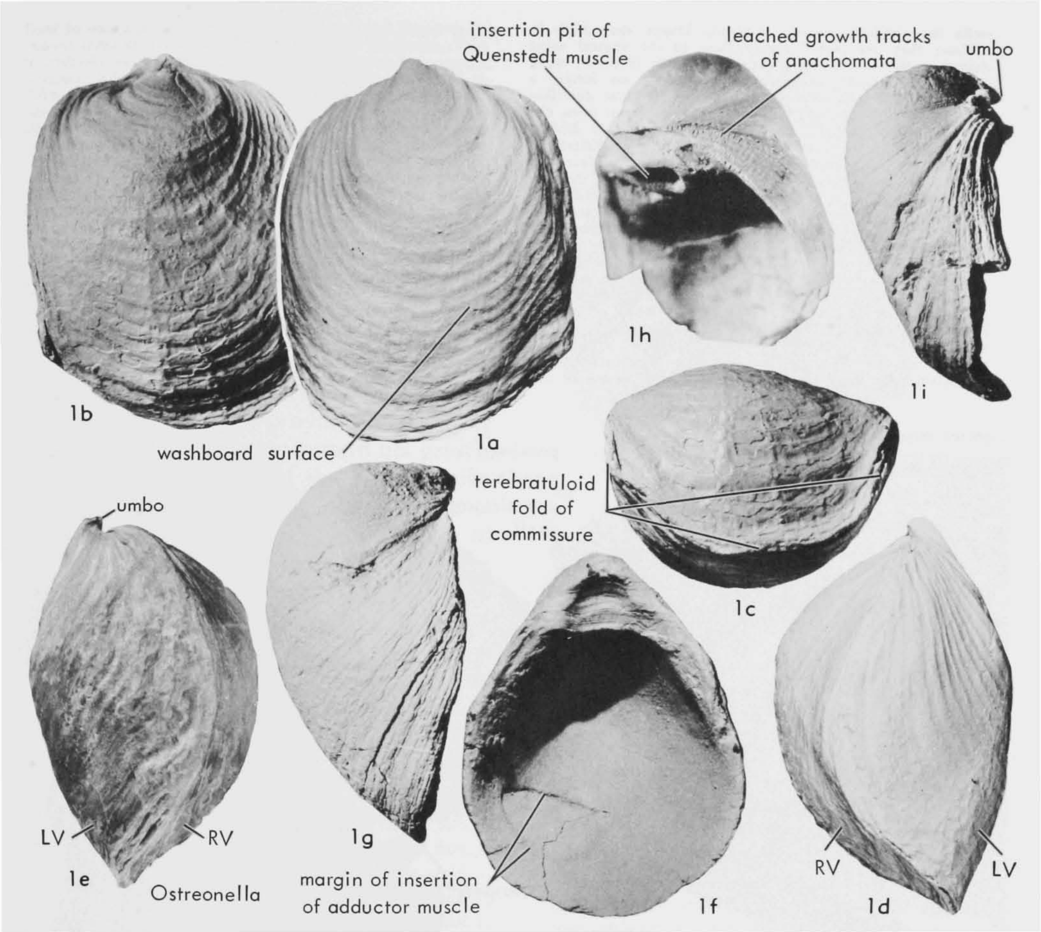

FIG. J128. Ostreidae (Ostreinae) (p. *N*1154-*N*1157).

spaced, separated from each other by smooth concentric bands that have sigmoidal profiles; growth squamae so delicate that they are mostly broken off. As a result the successive smooth concentric bands appear to merge forming a wavy "wash-board" surface. Chomata present. In old individuals the shell wall is very thick from the umbo to the adductor muscle. *U.Cret.(Campan.),* USSR (Gissar Mt. Range, near Shirabad town, Uzbek.)-C.Asia.——FIG. 128,*1.* **O. prima,* Gissar Mt. Range, USSR; *1a-e,* both valves, left and right sides, ventral, ant., post. views; *1f,g,* LV int., post.; *1h,i,* RV oblique post. and ant. views of an extremely humped and thick-walled individual, all ×1.3 (Stenzel, n). [All figures except *1e* whitened for photography; specimens by courtesy of KH. KH. MIRKAMALOV, Tashkent, and D. P. NAIDIN, Moscow State Univ., SSSR.]

[The genus is monotypic and so unusual that ROMANOVSKIY remarked that it does not have much resemblance to *Ostrea.* He is to be commended for recognizing that it is an ostreid genus. BORNEMAN, BURACHEK, & VYALOV (1934, p. 255) noticed that the convexity of the right valve, which ROMANOVSKIY had regarded as a generic character setting the genus apart, was fairly variable and ranged from very strong to weak. Therefore, they felt justified in doubting its value as a generic character setting *Ostreonella* apart from other smooth-shelled oysters. VYALOV in his elaborate scheme of classification of the Ostreidae (1936, p. 18; 1948a, p. 35) lowered the rank of *Ostreonella* to that of a section and placed it under *Liostrea* (*Liostrea*) DOUVILLÉ (1904a, p. 273) in the subfamily Ostreinae VYALOV, 1936. This arrangement has been followed by other authors in the USSR but is nonetheless faulty both as to nomenclature and phylogenetic systematics. First, it conflicts with *Code* Art. 23(e)(i). A subgenus or section of a genus dating from 1890 cannot legally be placed under a genus dating from 1904. If the two taxa are truly so closely related that one must be placed under the other, *Ostreonella,* having nomenclatural priority, would have to stay as a genus and *Liostrea* would have to be subordinated as a subgenus or possibly as a section. Second, *Liostrea* and *Ostreonella* are not at all closely related, notwithstanding the opinions and arguments of VYALOV (1936; 1948a) and BOBKOVA (1961, p. 42). Aside from the convexity of the RV, *Ostreonella* has several other generic features separating it from *Liostrea.*——Comparison of the type species of the two shows the following definitive differences: *Liostrea* has orbicular muscle imprints situated halfway between hinge and ventral valve margins, or even nearer to the hinge; although the shell and its valve commissure are variable and somewhat irregular, in average the valve commissure is a flat plane and chomata are absent on the commissural shelves. It is one of the Gryphaeinae as redefined by STENZEL (1959, p. 16). In contrast, *Ostreo-*

nella has reniform muscle imprints, longer than high in outline; they are placed rather close to the ventral valve margins. Its valve commissure, particularly in older, more inflated individuals, is heteroclite, that is, no longer a flat plane. For this reason, the valve commissure describes an "S" curve (Bobkova, 1961, p. 40), when seen from the posterior side. A broad semicircular terebratuloid fold is well shown on older, more inflated shells. The differences between *Liostrea* and *Ostreonella* in regard to outline and position of the adductor muscle imprints are proof that the internal soft anatomies of the two were quite different. Furthermore, *Ostreonella* has valves approaching equal convexities so that the general shell shape in younger individuals is like a biconvex lens and in older, more inflated individuals it approaches globose. The umbonal half of the shell, extending from umbo to region of the adductor muscle, has greatly thickened (15 mm.) shell walls, whereas the other, ventral, half of the shell has walls of normal thickness (2 mm.). Without doubt *Ostreonella* is one of the Ostreinae as redefined (Stenzel, 1959, p. 16) and a member of the *Flemingostrea* stock.——Vyalov's scheme of classification fails to take notice and make use of any of internal features of the shell, such as structure of shell walls, outline and position of the adductor muscle imprints, and morphology of the ligamental areas. Rather, it is based on external morphology alone. For this reason it places side by side genera having superficial external similarities but not really related. *Liostrea* and *Ostreonella* are examples. The position Vyalov gave to *Ostreonella* served only to obscure its true relationships. Recognition of these had to wait until a better, objective, detailed redescription of its type species became available. In providing this, however, Bobkova (1961, p. 39-43, pl. 3, fig. 1-5, pl. 4, fig. 1-5) chose to follow Vyalov's classification and again called it "*Liostrea*" *prima* (Romanovskiy), but she pointed out that two North American species, "*Liostrea*" *thirsae* (Gabb, 1861) (see Heilprin, 1884, p. 311, pl. 63, fig. 3-6; Stenzel, 1959, fig. 9, 15-16, 18-19; see Fig. J34 and J64) and "*L.*" *oleana* (Stephenson, 1945, p. 72-74, fig. 1-7), are quite similar to it. Although Bobkova relegated these two species to *Liostrea* they furnish important clues to true affinities of *Ostreonella*. Bobkova may be credited as the first to recognize close relatives of *Ostreonella prima* and to open the way for the present

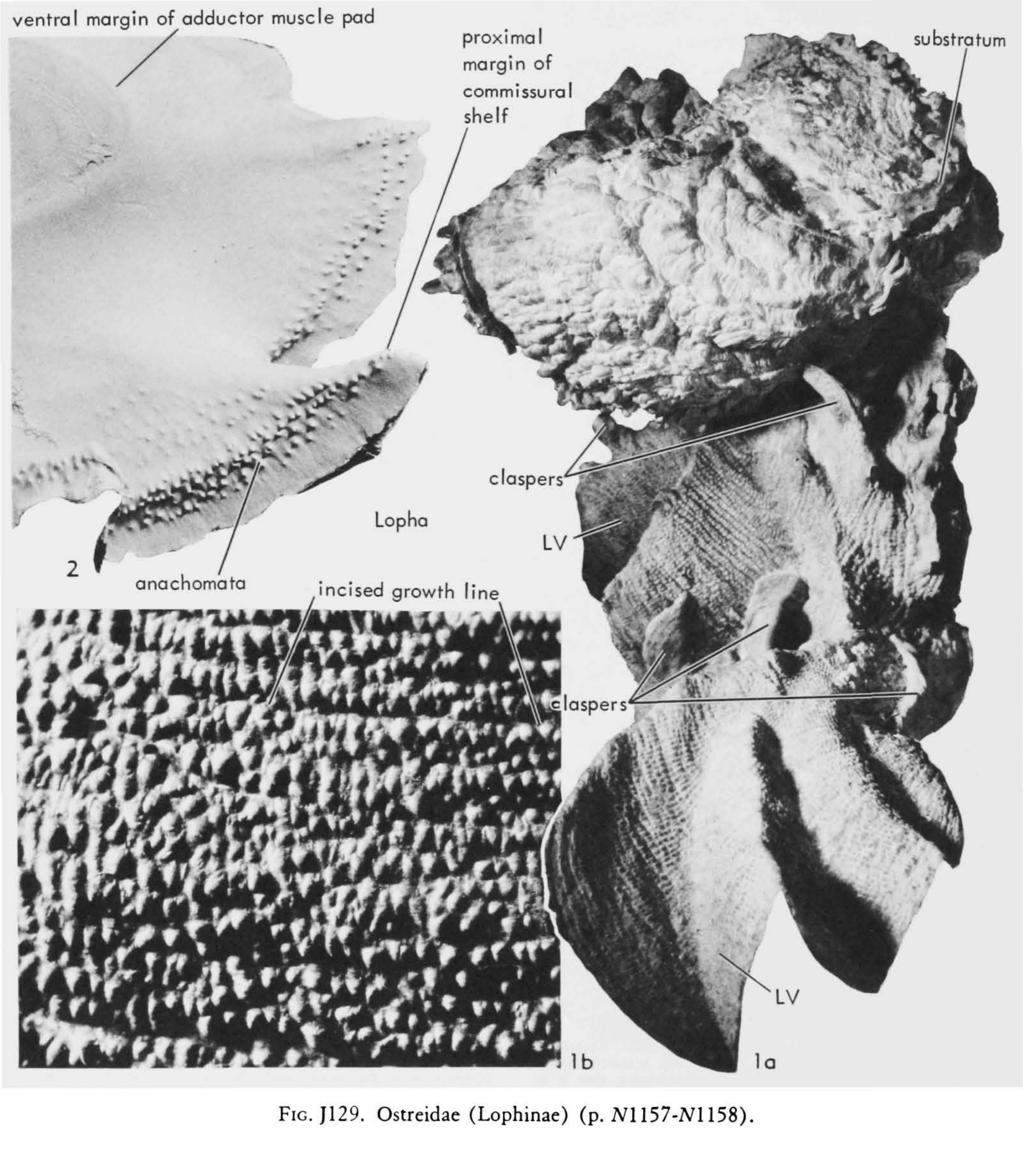

Fig. J129. Ostreidae (Lophinae) (p. *N*1157-*N*1158).

evaluation of this baffling genus. Fortunately, several specimens were kindly furnished to me by Prof. Kh. Kh. Mirkamalov of Tashkent.——The two North American species have been critically re-examined (Stenzel, 1945a,b; 1959, p. 32-33, fig. 3-19). The former was found to be a species of *Odontogryphaea* Ihering, 1903, and is rather similar to its type species; the latter was found to fit in the genus *Flemingostrea* Vredenburg, 1916.]

Subfamily LOPHINAE Vyalov, 1936

[Lophinae Vyalov, 1936, p. 19]

Incubatory. Attachment area medium-sized to large; some genera provided with shelly claspers that grow out at intervals to lock onto substrate. Valves subequal in size and convexity, and with similar rib patterns consisting of regular, subequal, fairly sharp-crested plicae which produce a regularly plicate valve commissure; pattern not greatly variable in individuals of the same species. Innumerable very small, slightly elongate tubercles are scattered over interior faces of valves, especially near their margins (Fig. J129,*2*). *U.Trias.-Rec.*

Lopha Röding, 1798, p. 168 [**Mytilus cristagalli* Linné, 1758, p. 704; SD Dall, 1898, p. 672] [=*Alectryonia* Fischer de Waldheim, 1807, p. 269 (type, *A. rara,* =*Mytilus cristagalli;* SD Gray, 1847, p. 201); *Alectrionia* Fischer de Waldheim, 1808, Tab. 5 *(nom. van.); Dendostrea* Swainson, 1835, p. 39 (type, *Ostrea folium* Linné, 1758, p. 699; SD Herrmannsen, 1847, v. 1, p. 378); *Dendostraea* Sowerby, 1839, p. 38 *(nom. van.); Dendrostraea* Swainson, 1840, p. 389 *(nom. van.); Dendrostrea* Agassiz, 1846, p. 118 *(nom. van.); Alectronia* Logan, 1898, p. 485 *(nom. null.); Actryonia* Dollfus, 1903, p. 271 *(nom. null.); Alcetryonia* Böse, 1910, p. 105 *(nom. null.); Alectryouia* Strausz, 1928, p. 277 *(nom. null.); Ostrea (Pretostrea)* Iredale, 1939, p. 397 (type, *O. (P.) bresia,* =*Lopha cristagalli* (Linné)); *Alekҭryonia* Vyalov, 1948a, p. 29 *(nom. null.); Alectryossia* Salisbury & Edwards, 1959, p. 128 *(nom. null.)*]. Small to medium-sized (to about 11 cm. long); both valves convex, subequivalve, with 6 to more than 50 sharp radial plicae the pattern of which is not greatly variable in each subgenus. *Trias.-Rec.,* mostly trop. and partly subtrop., worldwide.

L. (Lopha). The subgenus has two distinct ecomorphs. Ecomorph 1 [commonly called *Lopha cristagalli* (Linné) (=*Lopha s.s.* Auctt.)] grows on mangrove or on each other or on other bivalves, for example, *Chama.* Shell small to medium-sized (to 11 cm. long); both valves convex, equivalve; shape roughly globular to irregular with 6 to 9 or even 12 deep sharp radial plicae, angles of which decrease from near hinge to point farthest away from it according to Rudwick's rule (see Rudwick, 1964, and p. *N*1025-*N*1026). Surface of both valves roughened by countless small, low, rounded, almost equal-sized protuberances, which are elongate and arranged in obscure parallel radial rows disposed at right angles to incised growth lines (Fig. J129,*1*). No imbricating growth squamae. Hollow recurved compressed hyote spines arise intermittently from crests of some plicae; some spines recurved as claspers for support of LV on substrate. Ecomorph 2 [called *Dendostrea folium* (Linné), 1758, p. 699, by some authors] grows on stems of Gorgonacea or sea fans (Fig. J47). Small (to 8.5 cm. high); both valves convex, equivalve; shape lanceolate to ovate, with many sharp radial plicae. Surface without any protuberances, but with many fine, closely set growth squamae; hollow recurved hyote spines arise intermittently from crests of plicae, several of them serving as claspers for LV embracing stem of gorgonacean. Many individuals with xenomorphic sculpture consisting of rounded longitudinal ridge extending from umbo to opposite end of RV, corresponding to gorgonacean substrate. *Mio.-Rec.,* trop. and partly subtrop., worldwide.——Fig. J129,*1,2. L. (L.) folium* (Linné, 1758), ecomorph 1, called *L. cristagalli* (Linné, 1758), living, Indo-Pac.; *1a,b,* specimens from Ponape I., Carolines, growth group on *Chama* shell *(1a),* surface sculpture on ext. *(1b),* ×0.7, ×3; *2,* specimen from Guam showing band of small tubercle-shaped anachomata along margin of commissural shelf of RV, ×1.3 (Stenzel, n). [Specimen by courtesy of

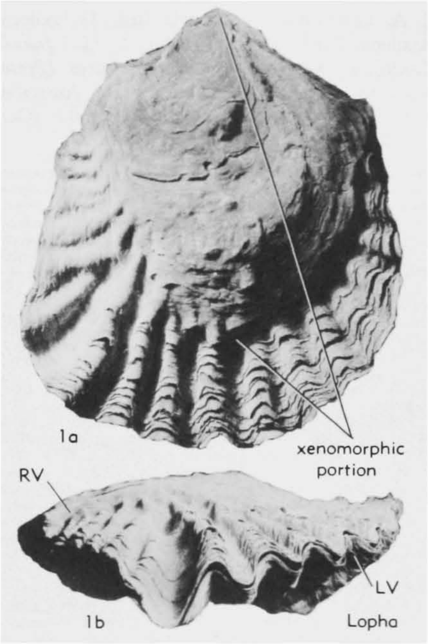

Fig. J130. Ostreidae (Lophinae) (p. *N*1157-*N*1158).

H. A. Lowenstam, California Inst. Technology, Pasadena, Calif.]——Fig. J130,*1. L. (L.) folium* (Linné, 1758), ecomorph called *Ostrea (Pretostrea) brezia* by Iredale, 1939, living, Australia; *1a,b,* right side, posteroventral view, ×0.8 (Carter, 1968). [*See* also Fig. J47.]

[Many authors, Swainson included, mistook the gorgonacean stems on which ecomorphs 2 grow for mangrove roots, hence the name tree oyster or *Dendostrea* Swainson, 1835 (an obvious error *pro Dendrostrea*). Indeed, when kept in a museum and dried out, the stems are blackish and wrinkled, resembling tree stems or roots with wrinkled blackish bark. Thomson, 1954 (p. 146-149, and letter of 14 Dec. 1966) was the first to discover that *Ostrea folium* Linné, *Mytilus cristagalli* Linné, and *Ostrea (Pretostrea) bresia* Iredale, 1939, are names for morphs of the same polymorphic species. Although his idea is in opposition to those expressed by many other workers (Lamy, 1929, p. 244-246, 254-256; Dodge, 1952, p. 190-191, 205), it is accepted here, because his work is based on extensive observations made on live oysters. According to Thomson the morphs generally identified as *Lopha cristagalli* live in intertidal situations and those identified as *Ostrea folium* live subtidally on Gorgonacea (Fig. J47). The former are found in the tropical Indo-Pacific; the latter are found, in addition, in the tropical and subtropical W. Atlantic, Caribbean, and Gulf of Mexico. If Thomson's interpretation and synonymization are accepted, the three above-given species names become subjective synonyms. Thomson as the first reviser of this situation selected *Lopha folium* (Linné) as the name designated for the biologic species, because it has priority and page precedence over the other two names. Thus the three genus-group names are subjective synonyms from a nomenclatural point of view. Present-day rules (*Code,* 1964) do not support the conclusion of Stenzel (1947, p. 177) that *Lopha* is unavailable as of 1798 and that *Alectryonia* Fischer de Waldheim, 1807, must be used in its stead. Until Ranson (1941) corrected the generic assignment, *Hyotissa hyotis* (Linné) had been regarded as a *Lopha* (see Hirase, 1930, p. 23). However, there is no question that *Hyotissa* is not closely related.]

L. (Abruptolopha) Vyalov, 1936, p. 20 [**Ostrea abrupta* d'Orbigny, 1842, p. 59; OD]. Medium-sized (to about 10 cm. high), outline pyriform, both anterior and posterior valve margins concave, but each surmounted by short, subequal auricle; valves subequal and with same pattern of plicae, consisting of many (more than 50) narrow angular even-crested radial plicae which diverge from umbones and are interrupted at 3 to 5 places by abrupt angulations of shell profile where valves stopped growing in height but continued to accumulate wall thickness. *Cret.,* S.Am. (Colom.).——Fig. J131,*1.* **L. (A.) abrupta* (d'Orbigny, 1842), Maastricht.; *1a-c,* types of d'Orbigny, RV ext., profile, profile, ×0.7 (d'Orbigny, 1842).

L. (Actinostreon) Bayle, 1878, explanation to pls. 132, 143 [**Ostrea solitaria* J. Sowerby, 1824, v. 5, p. 105, pl. 468, fig. 1; SD Douvillé, 1879]. Shell size small to medium, about 6-10 cm. high. Shell close to equivalve, outline mostly elongately oval and slightly crescentically curved, a slight posterior auricle is common; adult shells have about 25 narrow, dichotomous slightly curved plicae with narrow but not angular crests. *Jur.-Cret.,* W.Eu.-N.Am.——Fig. J132,*1.* **L. (A.) solitaria* (J. Sowerby), U.Jur.(Sequan., *Trigonia clavellata* Beds, Glos Oolite Series), Eng. (Weymouth, Dorsetshire); *1a-h,* topotypes, RV, LV, ant. view of both valves, LV, RV, post. view of both valves, LV, RV, ×0.5 (Arkell, 1933).

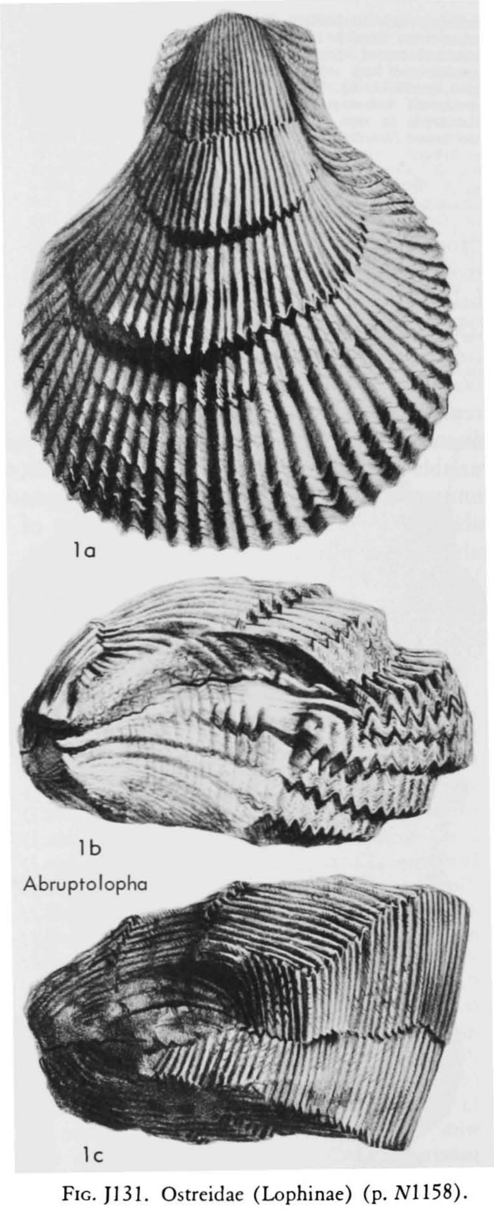

Fig. J131. Ostreidae (Lophinae) (p. *N*1158).

Agerostrea Vyalov, 1936, p. 20 [**Ostracites ungulatus* von Schlotheim, 1813, p. 112 (=*Ostrea larva* Lamarck, 1819, p. 216); OD]. Small to medium-sized (to 12 cm.), outline falcately curved, flanks tapering gently from umbo to opposite end; anterior flank convex, posterior one concave, both nearly vertical to generalized commissural plane; auricles at either end of hinge present or absent. Commissure folded into high and narrow plicae (up to 4 cm. high), ending in acute or rounded points (up to 20). Central field of valves flat, lacking costae or plicae. Many small rounded tubercles on commissural shelf. Adductor muscle imprint comma-shaped, situated close to hinge. *U.Cret.(Campan.-Maastricht.)*, worldwide.——FIG. J133,*1*. *_A. ungulata_ (VON SCHLOTHEIM), Maastricht., Neth.(St. Pietersberg near Maastricht); *1a-e,* LV ext., LV int., ant. side, RV int., LV int., all ×1.5 (adductor muscle insertion is outlined by pencil line on *1b*) (Stenzel, n).

[*Agerostrea* seems to be connected by transition species with *Arctostrea,* which is probably its ancestor. It differs

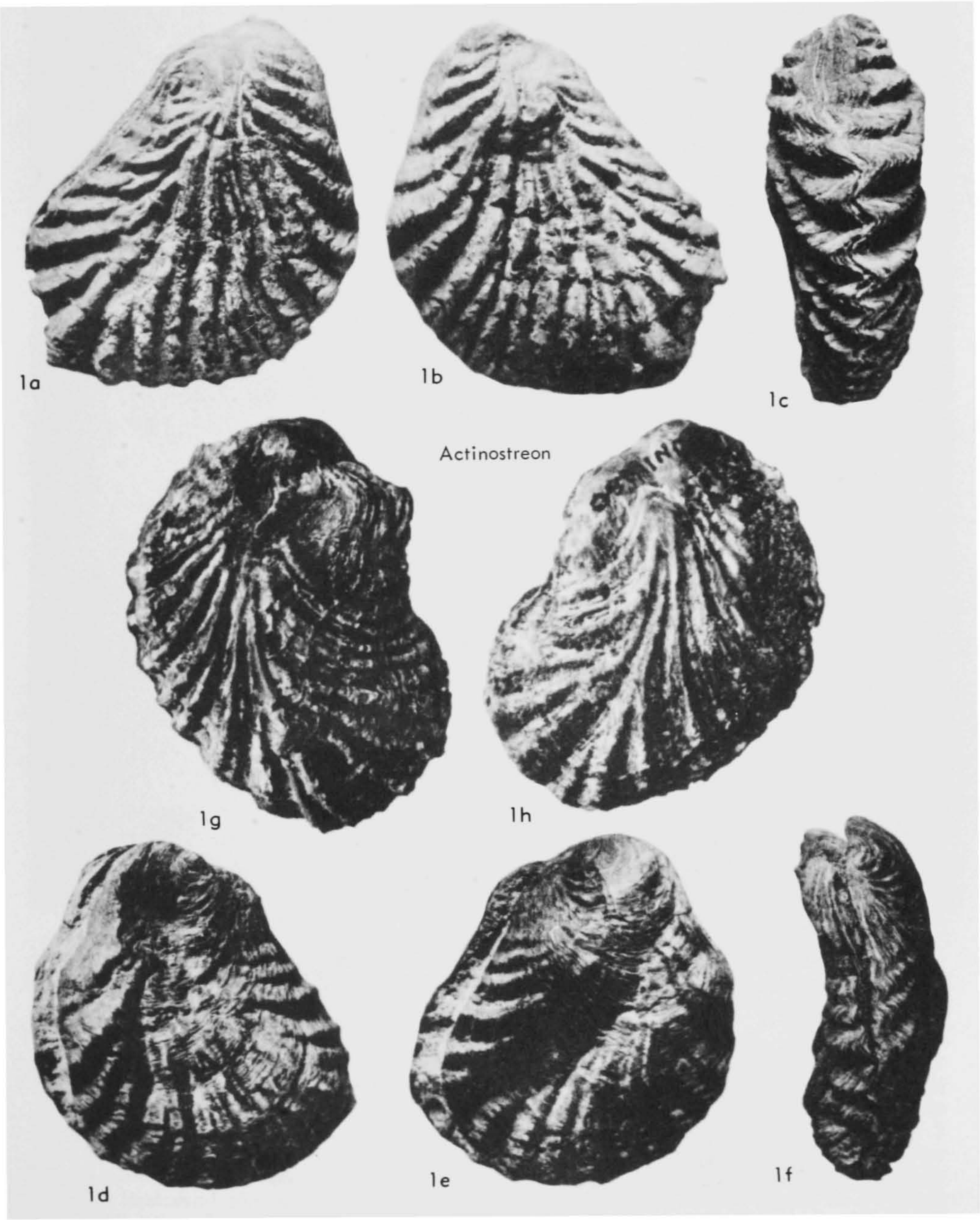

FIG. J132. Ostreidae (Lophinae) (p. *N*1158).

from the latter in lacking ribs or plications on the central fields of the valves, in lacking hyote spines arising from crests of the plicae, and in being less compressed from one flank to the other. The lineage appears to have died out with the end of the Maastrichtian.]

Alectryonella Sacco in Bellardi & Sacco, 1897a, p. 99 [**Ostrea plicatula* Gmelin, 1791, p. 3336, no. 111; OD]. Small (up to 9 cm. long), outline semicircular or crescentic so that outside curve, from hinge to branchitellum, approximates semicircle or well-curved loop, and distance on posterior side from hinge to branchitellum is very short. Highly inequivalve; LV deep, RV flat or rarely slightly convex; attachment area large to very large, in many individuals showing imprints

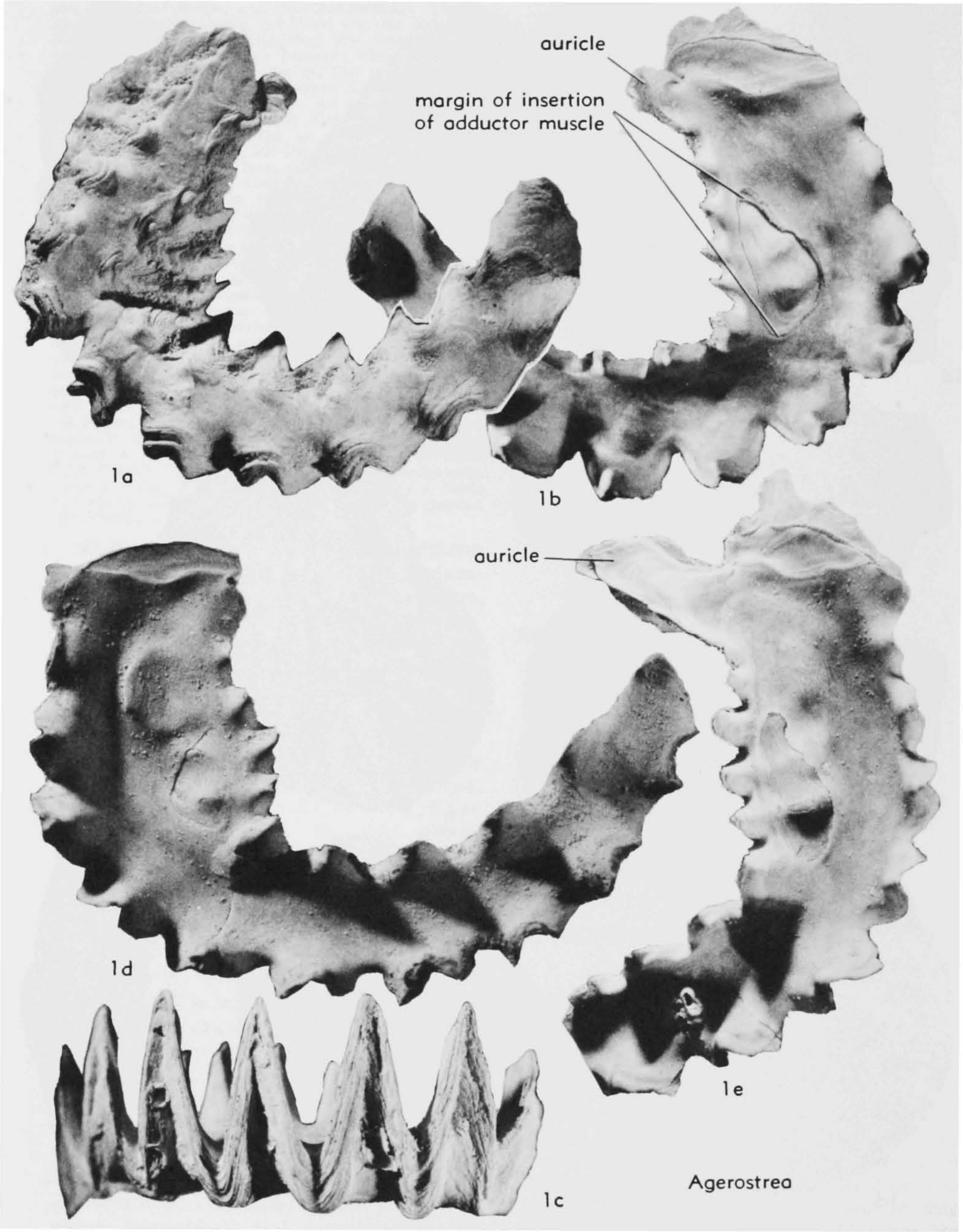

Fig. J133. Ostreidae (Lophinae) (p. N1158-N1160).

FIG. J134. Surface configuration on patches of fingerprint shell structure on RV of *Alectryonella plicatula* (same as Fig. J135,*1d*), ×5.5 (Stenzel, n). [Specimen whitened for photography.]

of compound corals. Both valves have about 14 to 22 continuous, commonly well-rounded, very nearly equal radial plications separated by interspaces of same size and equally well rounded, most plications not anastomosing, but widening toward the valve margins, and accompanied by a very few intercalated plications; growth squamae very few but irregular concentric growth wrinkles numerous. Adductor muscle imprint somewhat higher than long, obliquely distorted, and slightly concave at its dorsal margin, both of its horns well rounded and not prominent. RV margins bearing slightly elongate pustules in band 3 to 5 mm. wide; LV margins without pits except near hinge. Many individuals have an umbonal cavity in LV. Quenstedt muscle imprint in pit placed less than 1 mm. from ventral margin of ligament. Fingerprint shell structure often visible on internal

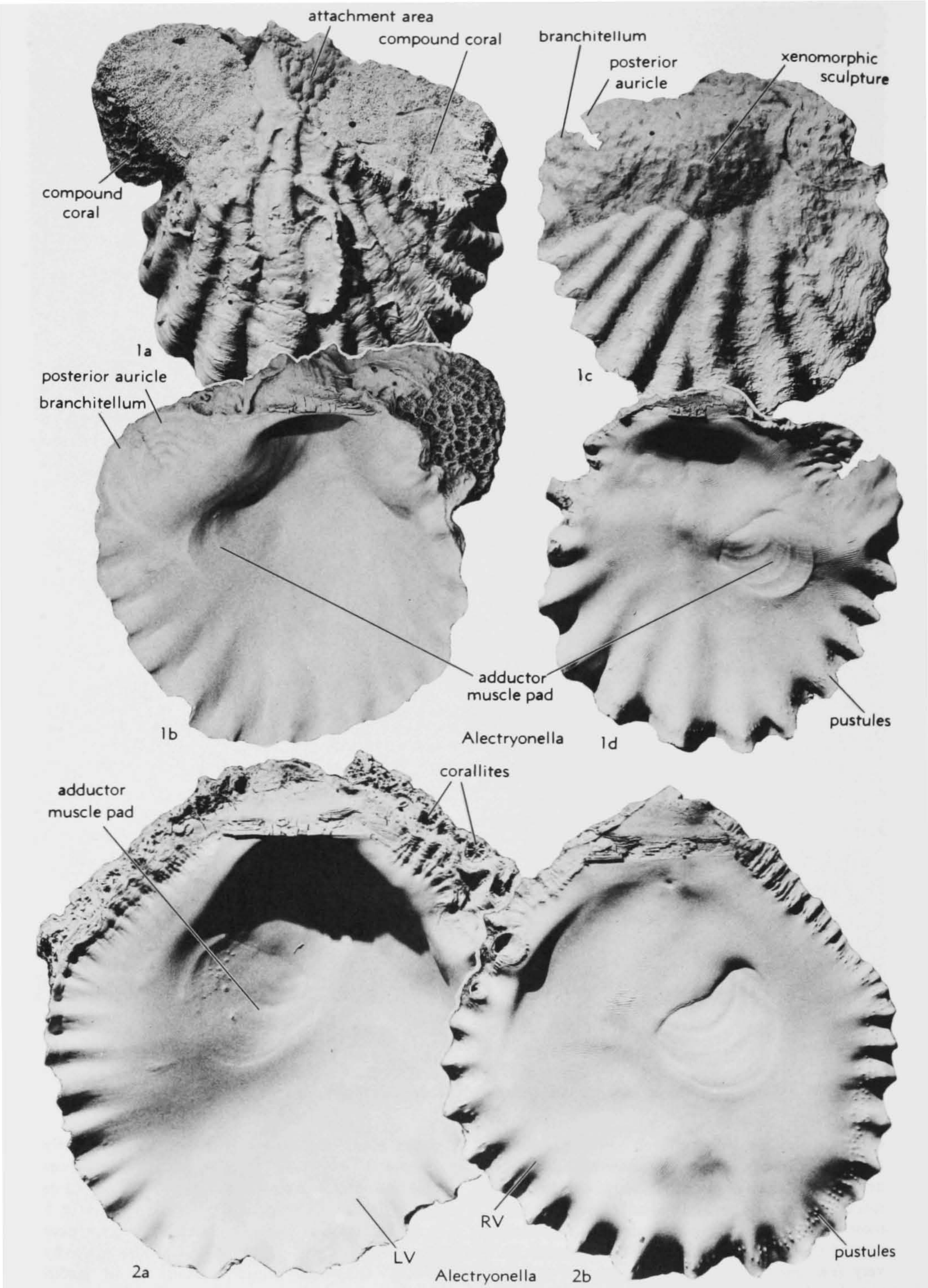

FIG. J135. Ostreidae (Lophinae) (p. *N*1160-*N*1161, *N*1163-*N*1164).

surfaces of the valves (Fig. J134). *?Mio., Plio.-Rec.,* tropical SW.Pac.——Fig. J135,*1,2*. **A. plicatula* (Gmelin), growing on compound hexacoral, Madag.(Nosi-Bé); *1a-d,* LV ext., int., RV ext., int., ×0.75; *2a,b,* LV int., RV int., ×0.75 (Stenzel, n). [Specimens by courtesy of R. Tucker Abbott, formerly of Acad. Nat. Sci. Philadelphia; all whitened for photography.] [*See* also Fig. J29.]

[Interpretation of this genus depends entirely on understanding of the type species, which is attainable in manner explained as follows. When Sacco (1897a) selected *"Alectryonella plicatula* (Gm. Lk.)" as the type species of his new subgenus *Alectryonella,* he made it quite clear through the authorships indicated that the particular species he had in mind was Lamarck's interpretation of *Ostrea plicatula* Gmelin (1791, p. 3336, no. 111). Lamarck's concept of this species can be analyzed, because fortunately the specimens studied by him are preserved at the Laboratoire de Malacologie of the Muséum National d'Histoire Naturelle in Paris. There they were studied by me in September 1962 with the generous aid of Gilbert Ranson. The six type lots of *Ostrea plicatula* Lamarck (1918, p. 211) contain several different species. Which one of the species should retain the name *plicatula* Lamarck can be solved only by a judicious selection of a lectoholotype from among his specimens. Lamarck himself recognized that more than one so-called variety were represented among his types, for he closed his description with the words: "It . . . offers a quantity of varieties which to distinguish would be more detrimental than useful to science." Some of the type lots are labeled var. [b], var. [c], and var. [d], and these designations apparently go back to Lamarck. If a lectoholotype is to be selected, it is evident that all the type lots which are labeled var. [b], var. [c], and var. [d] were regarded by Lamarck as atypical and should be excluded from consideration at the start. This restriction narrows the selection down to one stiff cardboard to which are glued two well-preserved bivalved specimens. This same cardboard was listed by Lamy (1929-30, p. 82-89) as the "ler carton" and bears two labels *"ostrea plicatula"* and *"huitre plicatule/ostrea plicatula"* in Lamarck's handwriting attached to its back; in addition, the front of the cardboard is labeled *"Ostrea/Ostrea plicatula* Lamk/Nelle Hollande (individus nommés par Lamarck)." The two specimens are much alike and certainly are of the same species. Also, they correspond to the figure given by Chemnitz (1780-95, v. 8, pl. 73, fig. 674), as Lamy has pointed out. This fact is rather important, because Gmelin had not illustrated his species, but had defined it by a short Latin description and two references to illustrations in older publications, one of which was this figure in Chemnitz. By restricting Lamarck's specific name to the two types of the "ler carton" of Lamy, one succeeds in establishing the identity of "Die faltenvolle Auster" of Chemnitz with *Ostrea plicatula* Gmelin and with *O. plicatula* Lamarck. At the same time one takes into account Lamarck's own revision of his type materials as implied by the way in which he had separated the materials into several so-called varieties. The larger one of the two type specimens of the "ler carton" is herewith selected as the lectoholotype of *Ostrea plicatula* Lamarck, 1819. Its dimensions are: largest dimension 7.66 cm., dimension at right angles to the largest 6.11 cm., and width 2.66 cm. These dimensions, measured in 1962, are somewhat different than those given by Lamy, who probably did not use calipers. The peculiar finger-print shell structure is visible on the inside of both valves in both specimens. The structure is believed to be a definitive feature of this species, even though it was not noticed, or at least not mentioned by Chemnitz, Gmelin, Lamarck, Lamy, and several other authors. The same structure was seen in the following additional museum specimens, which are regarded as representing *Ostrea plicatula* Gmelin, 1791: (1) *Ostrea lactea* G. B. Sowerby (1871, pl. 21, figs. 48 a-b), 1 specimen, Acad. Nat. Sci. Philadelphia. (2) *O. cumingiana* Dunker (Dunker in Philippi, 1845-47, *Ostrea* issue, p. 81-82, and pl.), 10 specimens from Indochina, Mus. Natl. d'Histoire Nat. (Paris). Dunker's own description mentions this peculiar structure, and it is obvious that the 10 specimens are correctly identified as Dunker's species. The Philadelphia specimen is most likely correctly identified and may have been identified originally by Sowerby himself, because some of the older specimens at Philadelphia were obtained from Sowerby or Reeve. Gilbert Ranson agreed in September 1962 that the 10 specimens labeled *O. cumingiana* are the same species as the two types of the "ler carton" of *O. plicatula* Lamarck, 1819. The type species is incubatory (Amemiya, 1929).] [Circumstances relating to designation and identification of the type species of *Alectryonella* Gmelin as recorded and interpreted by Sten-

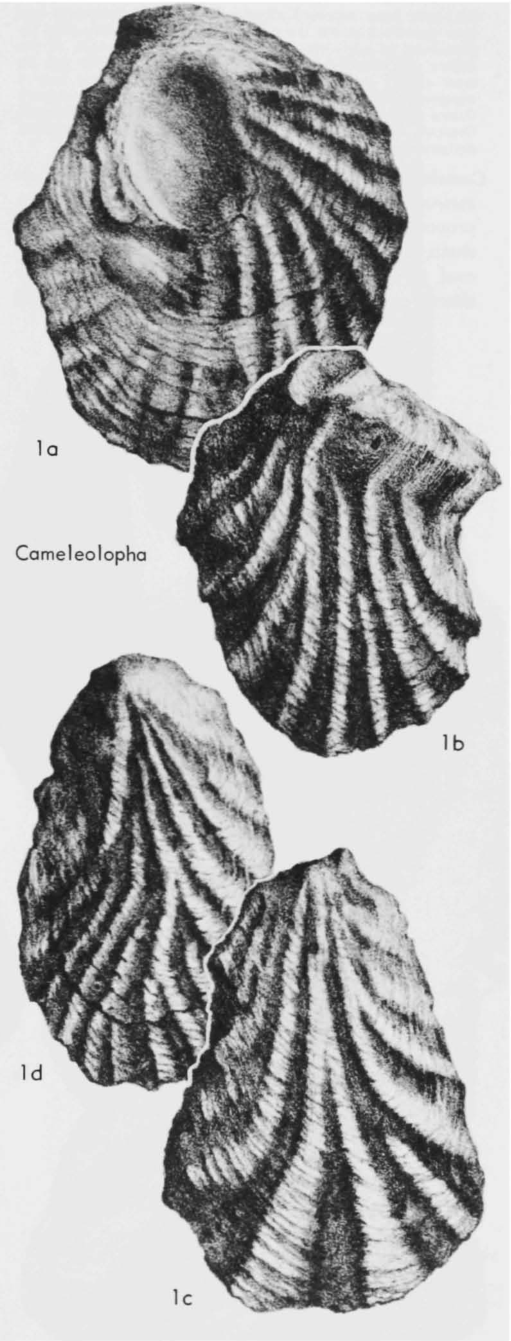

Fig. J136. Ostreidae (Lophinae) (p. *N*1164).

ZEL have been reported clearly by him in foregoing text now published at his insistence. STENZEL, thinking that his discussion is adequate, has not accepted suggestion of the Editor that the systematic fixation of *Alectryonella* can be most simply and firmly established by designating now a neotype specimen—say from one of the lots of LAMARCK's *Ostrea plicatula* (1819)—to serve as holotype of *O. plicatula* GMELIN, 1791, type species of *Alectryonella* by original designation.—R. C. MOORE.]

Cameleolopha VYALOV, 1936, p. 20 [**Ostrea cameleo* COQUAND, 1869, p. 149; OD]. This taxon proposed as a section of *Lopha s.s.* includes small shells (to 6 cm. high) with outlines orbicular or oval to spatulate and rounded; auricles generally absent, never large. Both valves have 12 to 20 angular, narrow-crested, dichotomous and intercalating radial ribs that continue to commissure. RV flat, LV convex to gibbous. *U.Cret.(Ceneman.),* N.Afr.(Alg.).——FIG. J136,*1*. **C. cameleo* (COQUAND), Bou Sâada, Subdivision de Sétif; *1a-d,* outlines of 4 individuals, ×1 (Coquand, 1869).

Nicaisolopha VYALOV, 1936, p. 20 [**Ostrea nicaisi* VYALOV, 1936, *nom. null.* (=*O. nicasei* COQUAND, 1862=*O. elegans* BAYLE in FOURNEL, 1849, p. 366, *non* DESHAYES, 1832, v. 1, p. 361); OD]. Medium-sized (to 10 cm. long and 11 cm. high),

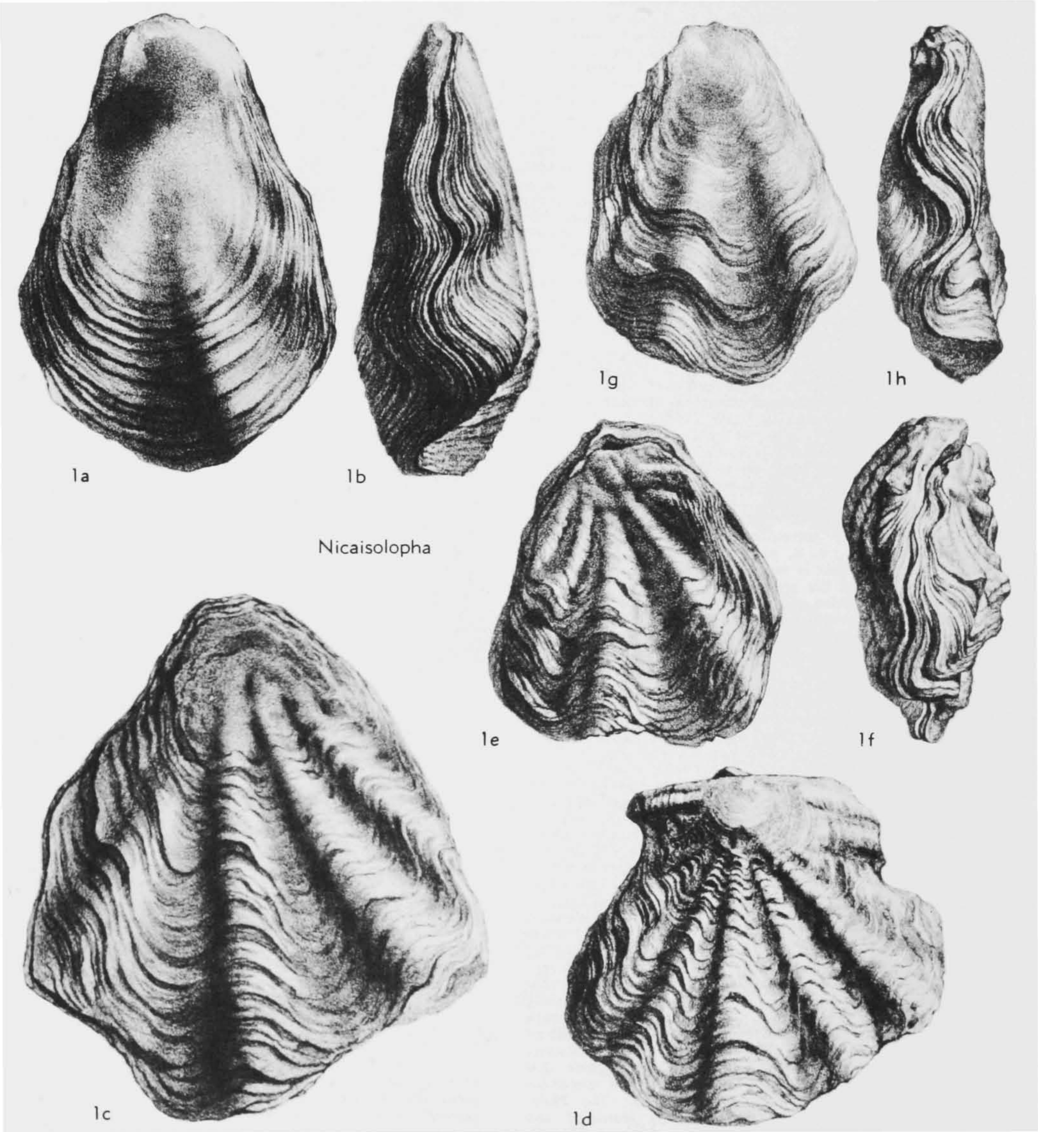

FIG. J137. Ostreidae (Lophinae) (p. N1164-N1165).

outline orbicular or ovate to spatulate, with greatest length very near ventral margin and height about 110 to 130 percent of length; flattish, width 25 to 40 percent of height, and subequivalve; LV very similar to RV but slightly more convex and capacious. Attachment area variable, very small to large; neanic part of shell smooth, orbicular, and only slightly convex at diameter of 2 to 4 cm.; marginal commissural folds beginning to develop at end of this growth stage, such folds few (4 to 7 large ones at ventral margin, small ones elsewhere), well rounded at their crests. Radial folds similar on both valves, not dichotomous, undulatory, round-crested and separated by equal, rounded interspaces, ending at commissural folds. Growth squamae slightly raised in later growth stages. Adductor muscle imprint reniform, deeply concave at its dorsal margin, about twice as long as high, placed slightly ventral of valve center. Ligamental area low and long, its height is about 40 percent of length; LV resilifer shallowly excavated and slightly longer than bourrelets; RV resilifer flat. No chomata. [*Nicaisolopha* was defined by Vyalov as a section of *Lopha s.s.* as follows: "Sculpture consists of vague folds."] *U.Cret.(Turon.-Maastricht.)*, Eu. (Port.) - N.Afr. (Alg. -Tunisia-Egypt) - Mexico-S.Am. (Peru).——Fig. J137,*1*. **N. nicasei* (Coquand, 1869), Campan., Alg. (M'zâb-el-Messai and other local.); *1a-h*, 5 individuals, ×0.7 (Coquand, 1869).

Rastellum Faujas-Saint-Fond, 1799 [?1802], p. 167 [**Ostrea macroptera* J. de C. Sowerby, 1824, v. 5, p. 105; SD Winkler, 1863-67, p. 251] [=*Rostellum* Pervinquière, 1910a, p. 119 *(nom. null.)* (*non* Mörch, 1850, p. 26)]. Small to large (largest diameter up to 24 cm.), almost equivalve, sculpture same on both valves, outlines crescentic to triangular-crescentic, latter accompanied by large triangular auricles anterior and posterior to ligament producing long straight hinge line; posterior auricle commonly larger one. Shells with crescentic outline long-tapering, curved like comma or hook, semicircular or almost full circle, with convex anterior and concave posterior flanks that tend to be vertical to commissural plane or nearly so, resulting in narrow roof along mid-axis of valves. Attachment area mostly large. Adductor muscle large and subtriangular to comma-shaped in cross section, located rather close to hinge, i.e., less than half of shell height from hinge. Roofs of valves with many branching dichotomous costae, subdued to well-developed; costae turn into sharp plicae on reaching steep flanks and descend straight down flanks without any dichotomy. Crests of plicae either smooth or raised at intervals into narrow hyote spines. Valve commissure has many (100 or more) interlocking zigzags, the tips of which are acute-angled; grooves between plicae end in projecting acute tips and plicae end in corresponding recesses. *M.Jur.(Callov.)-U.Cret.(Maastricht.)*, worldwide.

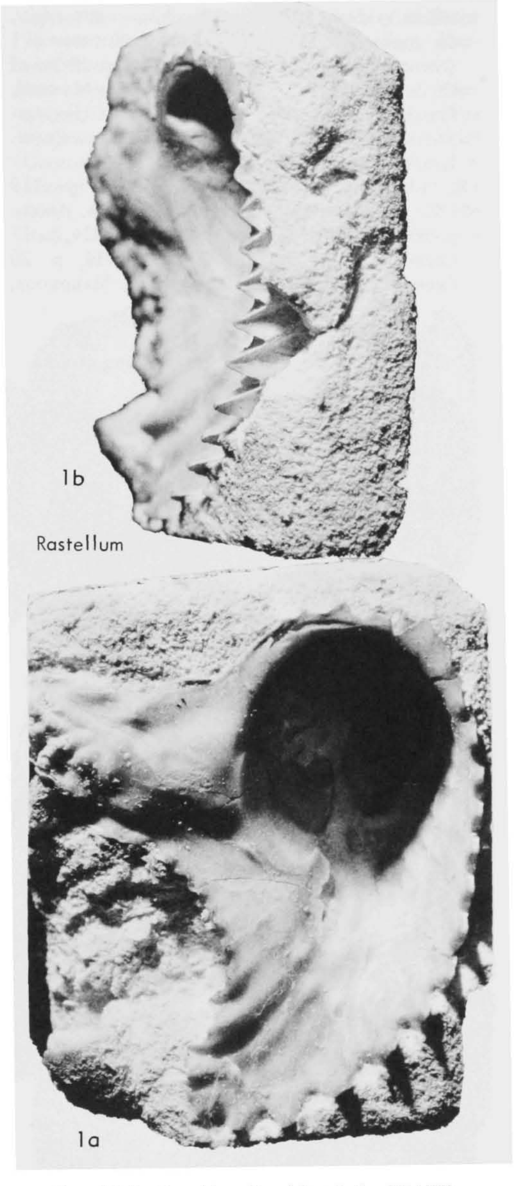

Fig. J138. Ostreidae (Lophinae) (p. *N*1165).

[The confused nomenclatural history of this generic name has been discussed by Pervinquière, 1910a, 1911, and Stenzel, 1947. (See also discussion herein, p. N1201.)]

R. (Rastellum). Shell outline tending more to triangular crescentic than to crescentic with parallel flanks. Plicae mostly without hyote spines. *M.Jur.(Callov.)-U.Cret.(Maastricht.)*, worldwide.——Fig. J138,*1*. **R. (R.) macropterum* (J. de C. Sowerby), Maastricht. (Tuffeau de Maestricht), Neth. (St. Pietersberg, S. of Maastricht.); *1a,b,* LV int., LV oblique ant. view, on rock matrix of Maastricht grainstone, ×1 (Stenzel, n). [Specimen loaned by courtesy of C. O. van Regteren Altena, Teyler's Museum, Haarlem, Neth., no. 11046, type of Faujas-Saint-Fond [?1802], pl. 28, fig. 7, as *Rastellum*. *See* also Fig. J153,*4-5*.]

R. (Arctostrea) Pervinquière, 1910a, p. 119 [**Lopha (Arcostrea) carinata* Lamarck, 1806a, p. 166; OD] [=*Arctostraea* Jourdy, 1924, p. 17 (*nom. van.*); *Artostrea* Vyalov, 1936, p. 20 (*nom. null.*); *Arcostrea* Charles & Maubeuge, 1951, p. 114 (*nom. null.*)]. Shell outline tending to crescentic with both flanks parallel and very steep; outlines long-tapering and curved like comma, hook or semicircle to almost full circle; steep flanks (up to 5 cm. tall) on each valve. Plicae rise at their crests at intervals to form slender hyote spines, which in some grow into long tubules. Commissure very serrate; serrae as many as 3 per cm. of commissure length. Tips of zigzags sharp-pointed, long, and narrow. [Distinction between *R. (Rastellum)* and *R. (Arctostrea)* is uncertain.] *Cret.(U.Alb.-L.Cenoman.),*

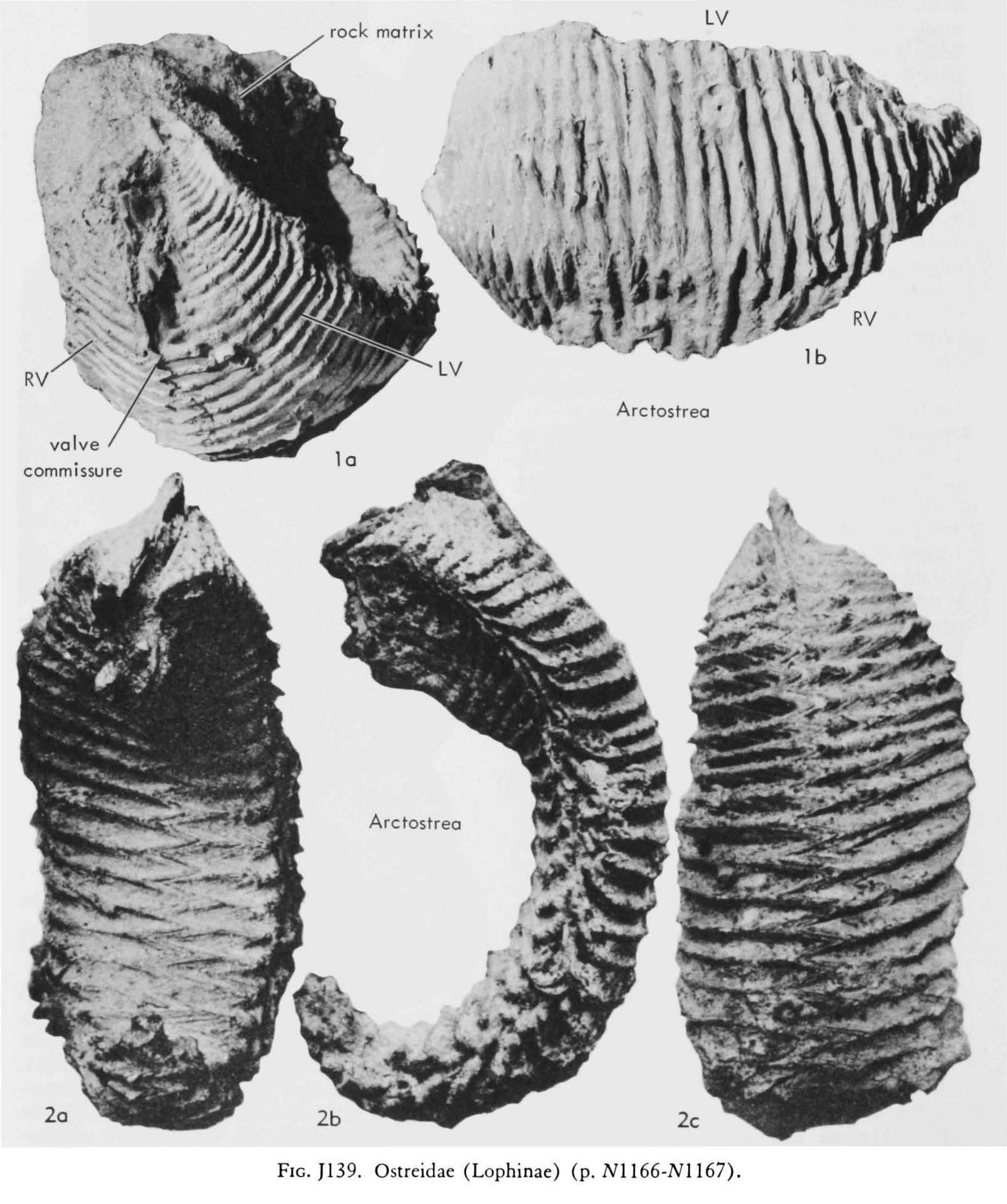

Fig. J139. Ostreidae (Lophinae) (p. *N*1166-*N*1167).

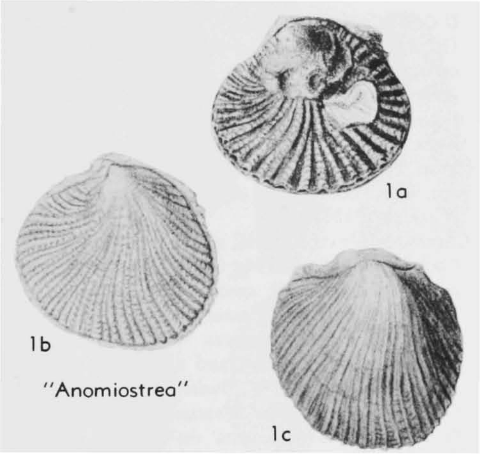

FIG. J140. Genera Uncertain (p. *N*1167).

worldwide.——FIG. J139,*1*,*2*. **R. (A.). carinatum* (LAMARCK), Cenoman., France; *1a-b,* oblique umbonal view, ant., ×1; *2a-c,* LeMans, both valves post., right side, ant., ×1 (holotype) (*1,* Stenzel, n; *2,* Pervinquière, 1910b). [Specimen loaned by courtesy of Naturhist. Museum, Basel, Switz.]

[An interesting study of the functional morphology of *Arctostrea* was made by CARTER, 1968.]

NOMINA DUBIA AND GENERA OF DUBIOUS TAXONOMIC VALUE OR POSITION

Listed below are generic names published for Ostreidae AUCTORUM which were obscurely described and are difficult to recognize or interpret. Their type species were not available for this study.

Anomiostrea HABE & KOSUGE, 1966, p. 323 [**Osstrea pyxidata* ADAMS & REEVE, 1848, p. 72 (*non* BROCCHI, 1814, p. 579, =*O. pyxidata* BORN, 1778, p. 93); OD]. Described as follows: "The shell is small, thin, orbicular, dark green to pale yellow, inequivalve. The upper valve is flat, divergently ribbed and has the ovate white muscular scar situated near the center of its inner surface. The lower valve attached to the coral is deeply concaved, forming a cup-shape and crenulated at the margin by the ribs on the surface and its muscular scar is distinctly elevated by the white callus. The ligament is small and short. This is a unique *anomia*-like oyster found on the branches of corals in the Philippines and rather commonly collected at Samboanga, Mindanao by Mr. Ichiro Yamamura. No related species has been reported until today." Figure and description given are not sufficiently informative.——FIG. J140,*1*. **A. pyxidata* (ADAMS & REEVE, 1850), Philip.I.; *1a-c,* both valves, seen from right(?) side, ×1 (*1a,* Adams & Reeve, 1850, pl. 21, fig. 19; *1b,c,* G. B. Sowerby, Jr., 1870-71, v. 18, *Ostraea* sp. 16). [All figures from copies furnished by courtesy of RUTH TURNER, Museum of Comparative Zoology, Harvard Univ., Cambridge, Mass.]

Anulostrea VYALOV, 1936, p. 19 [**Ostrea bourguignati* COQUAND, 1869, p. 86; OD]. Proposed as subgenus of *Liostrea.* All specimens figured by COQUAND have valves closed, so that nothing is known of the interior, and the affinities of this taxon remain unknown. General outline of the shell, approaching rectangular, well-developed

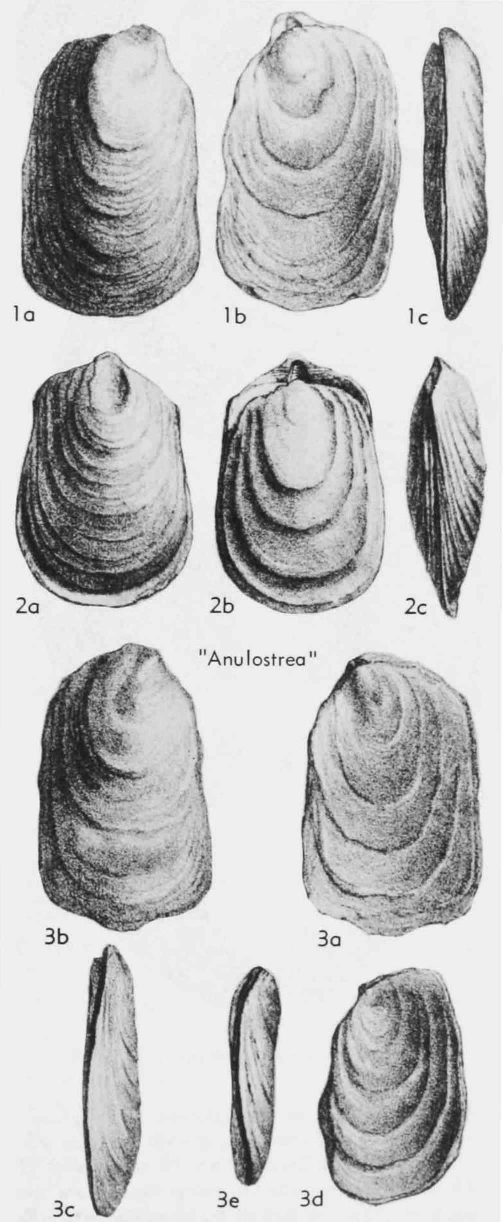

FIG. J141. Genera Uncertain (p. *N*1167-*N*1168).

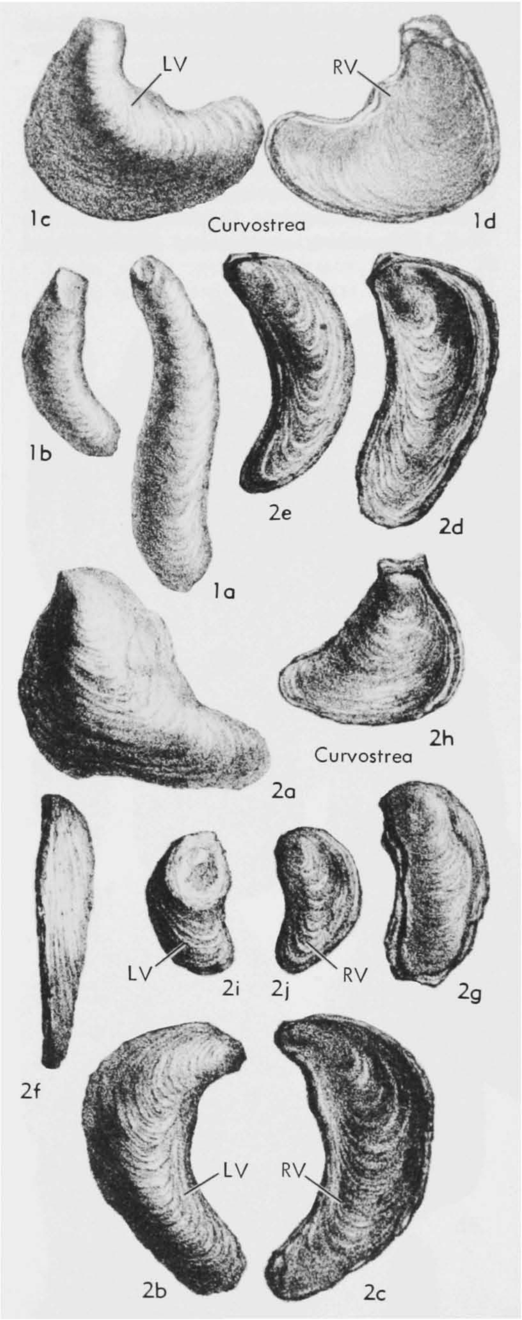

FIG. J142. Genera Uncertain (p. *N*1168).

shoulders at ends of the ligament, and regularly and widely spaced concentric growth squamae separated by smooth intervals are all reminiscent of *Flemingostrea,* but the specimens figured are too small to show the fold of the commissure at the venter of the shell, which would be diagnostic. *U.Cret.(Coniac.-Santon.),* N. Afr. (Tunisia) - Eu. (France).——FIG. J141,*1-3.* **A. bourguignati* (Coquand), Coniac.-Santon.; *1a-c,* Alg.(Sétif), both valves, left side, right side, ant. view, ×1; *2a-c,* France (Saint-Paterne), both valves, left side, right side, ant. view, ×1; *3a-e,* Tunisia (R'fana near Tebessa), both valves right side, left side, ant. view, both valves right side, post. view, ×1 (Coquand, 1869).

Curvostrea Vyalov, 1936, p. 18 [**Ostrea rediviva* Coquand, 1869, p. 154; OD]. All figured specimens of this small species have valves closed, so nothing is known concerning muscle imprints and other internal features. Thus the taxon remains largely unknown and cannot be classified. ——FIG. J142,*1,2.* **C. rediviva* (Coquand), U. Cret.(Cenoman.); *1a-d,* France (Saint-André near Goudargues, Département du Gard), LV ext., LV ext., both valves left side, right side, ×1; *2a-j,* Alg. (Bou-Sâada), LV ext., both valves left side, right side, both valves right side, both valves right side, ant. view, both valves right side, both valves right side, LV, RV, ×1 (Coquand, 1869).

Margostrea Vyalov, 1936, p. 20 [**Ostrea merceyi* Coquand, 1869, p. 93; OD]. Proposed as section of *Lopha s.s.* with the following definition: "Shell not incurved, with a very large median smooth surface; beyond, the sculpture presents only one undulation or crenelations at the shell margins." *U.Cret.(Santon.),* Eu.(France).——FIG. J143,*1,2.* **M. merceyi* (Coquand); *1,* Parnes, RV ext., ×1; *2a-g,* Tartigny, Département Oise, LV ext., int., RV ant., RV int., LV int., ext., RV int., ×1 (Coquand, 1869).

[Only one unlabeled specimen possibly referable to the type species was found in collections of the École des Mines in Paris. The central unribbed area of RV evidently is xenomorphic in this bivalved specimen, because its LV has a correspondingly large attachment area. It is also evident from figures published by Coquand that all specimens of the type species are young and grew on an elongate and convex, that is, more or less cylindrical, substrate. In these figures the RVs have an unribbed convex central area and the LVs have the corresponding concave attachment area. Therefore, the central unribbed areas are xenomorphic and cannot be diagnostic for supraspecific taxa. For this reason the species too remains unrecognizable; it is perhaps a lophine oyster. However, even that guess is dubious, because Woods, 1913, p. 381, listed *Ostrea merceyi* Coquand in the synonymy of *Ostrea semiplana* J. De C. Sowerby, 1825, =*Hyotissa semiplana* (J. De C. Sowerby, 1825). Thus *Margostrea* must be set aside as indeterminate.]

Notostrea Finlay in Marwick, 1928, p. 432 [**Ostrea subdentata* Hutton, 1873, p. 34; OD]. Only one valve, best illustrated by Boreham (1965, pl. 13, fig. 2-3, p. 48), has been figured. Contrary to statements by Finlay (1928b, p. 266) this lectoholotype is a LV, not RV. Descriptions given and material available so far are insufficient. Boreham's illustrations seem to show vermiculate chomata. If it turns out that the shell wall has vesicular shell structure, *Notostrea* would fall into the Pycnodonteinae as a rather unusual monotypic genus. *Low.Oligo.(Duntroon.),* N.Z.——FIG. J144,*1.* **N. subdentata* (Hutton), Broken River, Trelissick Basin; *1a,b,* holotype, LV ext., int., ×2 (Stenzel, n). [Plaster cast by courtesy of C. A.

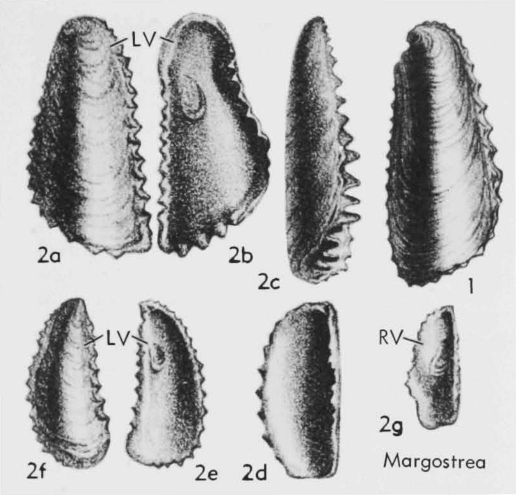

FIG. J143. Genera Uncertain (p. *N*1168).

FLEMING and Mrs. A. U. E. SCOTT, New Zealand Geol. Survey, Lower Hutt, N.Z.]

Pulvinostrea VYALOV, 1936, p. 17 [**Ostrea (Cymbulostrea) fluctuosa* MAYER-EYMAR, 1889, p. 3; OD]. Described as a section of the subgenus *Ostrea (Cymbulostrea):* "Beak pointed, shell high, the sculpture consists of some distant, interrupted costae." The type species was described but not figured by MAYER-EYMAR, who placed it in the "series of *Ostreae Polyphemi.*" It was redescribed by OPPENHEIM (1903, p. 32-33, pl. 1, fig. 12-12b) from a single LV which had been identified by MAYER-EYMAR and deposited at Munich. Although this is believed to be the type, or one of the types, some serious discrepancies between it and the description given by MAYER-EYMAR were noted by OPPENHEIM (p. 33), so that a mixup of labels is not improbable. Although MAYER-EYMAR described both valves, no RV was available to OPPENHEIM. *Eoc.,* Afr.(Egypt).——FIG. J145,*1*. *?P. fluctuosa?* (MAYER-EYMAR) (=*Ostrea (Cymbulostrea)* section *Pulvinostrea* VYALOV, 1936), Libyan, Nobka; *1a-c,* LV ext., int., post., ×1 (Oppenheim, 1903). [Labeled as a type specimen by MAYER-EYMAR, 1889, but possibly erroneously.]

[Because MAYER-EYMAR stated that the upper valve is devoid of ribs and the lower valve has 9 radial ribs, it is likely that this species falls into the general group of genera and subgenera that cluster around *Ostrea s.s.* For the rest, the material available to MAYER-EYMAR, OPPENHEIM, and VYALOV is too inadequate to permit one to establish a species firmly, let alone a supraspecific taxon.]

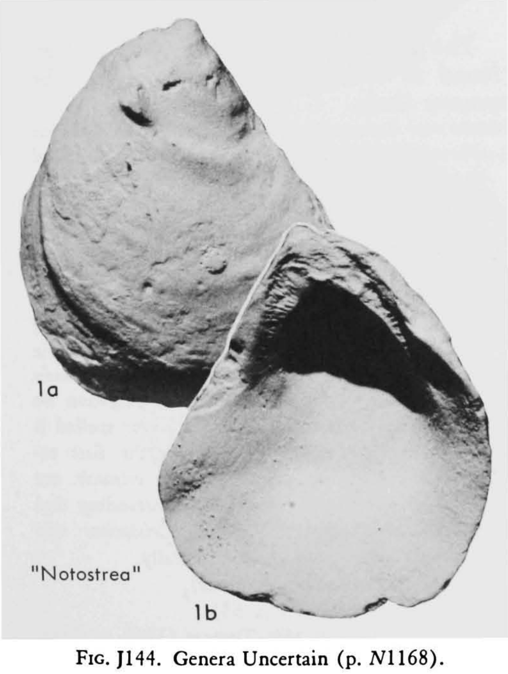

FIG. J144. Genera Uncertain (p. *N*1168).

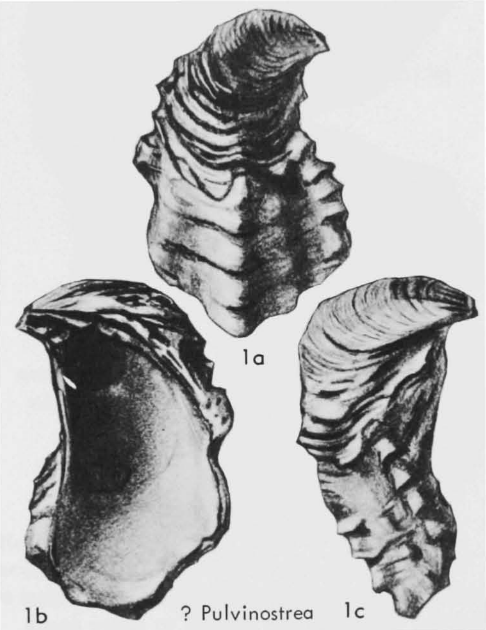

FIG. J145. Genera Uncertain (p. *N*1169).

Quadrostrea VYALOV, 1936, p. 18 [**O. tetragona* BAYLE in FOURNEL, 1849, v. 1, p. 367; OD]. Described as a section of *Liostrea (Liostrea):* "Beak slightly prominent, cardinal margin straight, shell angular." The holotype of the type species at the École des Mines in Paris is a bivalved specimen with valves closed and interior filled with matrix and inaccessible. Its systematic position remains unknown. *U.Cret.(Senon.),* Afr.(Alg.). —— FIG. J146,*1*. **Q. tetragona* (BAYLE), Campan., M'zabel-Messaï and other local.; *1a-c,* two individuals, ×1 (COQUAND, 1869).

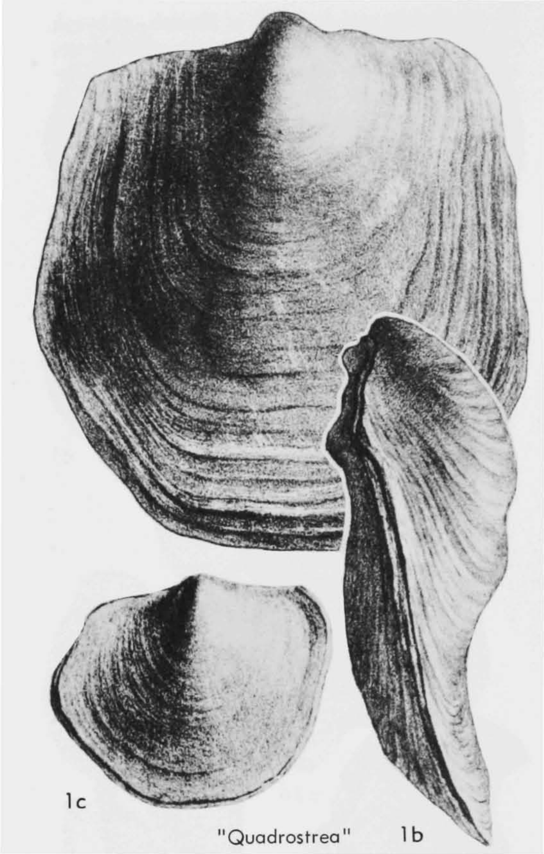

FIG. J146. Genera Uncertain (p. *N*1169).

GENERA ERRONEOUSLY ASSIGNED TO OSTREIDAE

The following genera originally were described as or suspected to be Ostreidae AUCTT., but found to belong to other families.

Heterostrea JAWORSKI, 1913, p. 192-195, pl. 6-7 [**Crassostrea (Heterostrea) steinmanni;* M]. *Heterostrea* was originally believed to be a primitive, dimyarian, ancestral stage (Stadium in German) of *Crassostrea.* It was found in the Jur. (M. Bajoc.) of Chunumayo, Peru. JAWORSKI (1951) later removed it from the Ostreidae and placed it in *Myoconcha* SOWERBY, 1824, p. 5, 103, near *M. unguis* WHIDBORNE (1883, p. 530, pl. 18, fig. 21), family Pleurophoridae, subfamily Myoconchinae NEWELL, 1957 (p. *N*547).——FIG. J147,*1.* **Myoconcha steinmanni* (JAWORSKI) [="*Crassostrea (Heterostrea)*"]; *1a-c,* RV int., LV int., ext., ×0.4 (Jaworski, 1913).

Holocraspedum CRAGIN (1893, p. 190-191) [**Osstrea anomiaeformis* ROEMER, 1849, p. 394; OD]. CRAGIN correctly placed this genus in the Anomiidae, although the type species had been described as an *Ostrea.* All the specimens of the type species that were available to CRAGIN are preserved at the University of Texas in Austin, Texas; they are all anomias and *Holocraspedum* is here questionably regarded by Cox as a junior synonym of *Placunopsis* (p. *N*380).

Lithiotis GÜMBEL, 1871, p. 48-51 [**L. problematica;* M]. Since GÜMBEL described it, believing it to be a lime-secreting alga, many authors have discussed its systematic position and some believed it to be an oyster close to *Crassostrea.* It is now placed in the Lithiotidae REIS, 1903, near the Spondylidae (*see* p. *N*1200).

Ostreinella COSSMANN in COSSMANN & PEYROT, 1914, p. 398-400 [**Liostrea (Ostreinella) neglecta* (MICHELOTTI), 1847, p. 81, pl. 3, fig. 6, not fig. 3; OD]. Originally described as a subgenus of *Liostrea* it was recognized by GLIBERT & VAN DE POEL, 1965, p. 6, as a member of the Vulsellidae [Malleidae] (see p. *N*331).——FIG. J148.*1.* **O. neglecta* (MICHELOTTI), Mio. (Burdigal.), SW. France (Aquitaine); *1a-d,* loose valves, ×2 (Cossman & Peyrot, 1913-14).

Palaeostrea GRABAU, 1936, p. 284-286, pl. 28, fig. 1 [**P. sinica;* OD]. This incompletely described fossil is wholly unidentifiable and probably not an oyster, see p. *N*1051. [*See* also Fig. J59,*4.*]

Praeostrea BARRANDE, 1881a, p. 147, pl. 3, fig. 1-2 and 3-4 [**P. bohemica;* M]. The taxon is now placed as a junior synonym of *Vevoda* BARRANDE, 1881, in the family Antipleuridae NEUMAYR, 1891, Superfamily Praecardiacea HÖRNES, 1884 (*see* p. *N*247, p. *N*1051). It has been restudied by KŘÍŽ, 1966. [*See* Fig. J59,*5.*]

UNAVAILABLE GENERIC NAMES

The generic names listed below have been found to be unavailable according to the present *Code.*

crist. VON SCHLOTHEIM (1820, p. 240-245). This abbreviation written in lower-case letters was used in connection with 9 species names of the genus *Ostracites.* The list was headed by the vernacular "D. Cristaciten. (Hahnenkämme)"; the abbreviation was not explained. Later VON SCHLOTHEIM (1823, p. 82) used "*cristacit.*" instead in connection with two of these species. STENZEL (p. *N*1210) has shown that these abbreviations stand for *Cristacites* and were meant to be a subgeneric name. *Cristacites* VON SCHLOTHEIM is a *nomen oblitum,* because until STENZEL's investigation no one had recognized it as a subgenus or spelled it out correctly. Because STENZEL is the first reviser, his conclusion that *crist.* and *cristacit.* are unavailable is to be followed notwithstanding that VOKES (1967), p. 193, listed *Cristacites* VON SCHLOTHEIM as valid nomenclaturally.

Acuminata ARKELL (1934, p. 64).

Bilobata ARKELL (1934, p. 64).

Corrugata ARKELL & MOY-THOMAS (1940, p. 404).

Cretagryphaea ARKELL (1934, p. 62).

Dilatata ARKELL (1934, p. 64).
Incurva ARKELL (1934, p. 64).
Jurogryphaea ARKELL (1934, p. 62).
Knorrii ARKELL (1934, p. 64).
Marcoui ARKELL (1934, p. 64).
Virgula ARKELL (1934, p. 64).

These ten names were proposed as "rationalised names" admittedly under disregard of the zoological Rules. They were called "name of the lineage," that is, they were meant to designate monophyletic groupings of some sort. However, each lacked definition or indication as required by the *Code* and remained unavailable.

Neogryphaea VYALOV & SOLUN (1957, p. 197).
Pseudogryphaea VYALOV & SOLUN (1957, p. 197).

These two names were proposed as hypothetical names for as yet undescribed genera. They lack species and definitions. Contrary to the listing by VOKES (1967, p. 196-197), they are unavailable.

Neogyra CHELTSOVA (1969, p. 9).

This name is a *nom. nudum* in CHELTSOVA. It

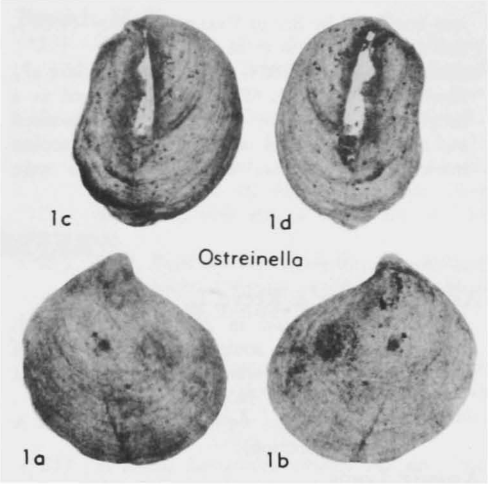

FIG. J148. Malleidae (*Ostreinella*) (p. N1170).

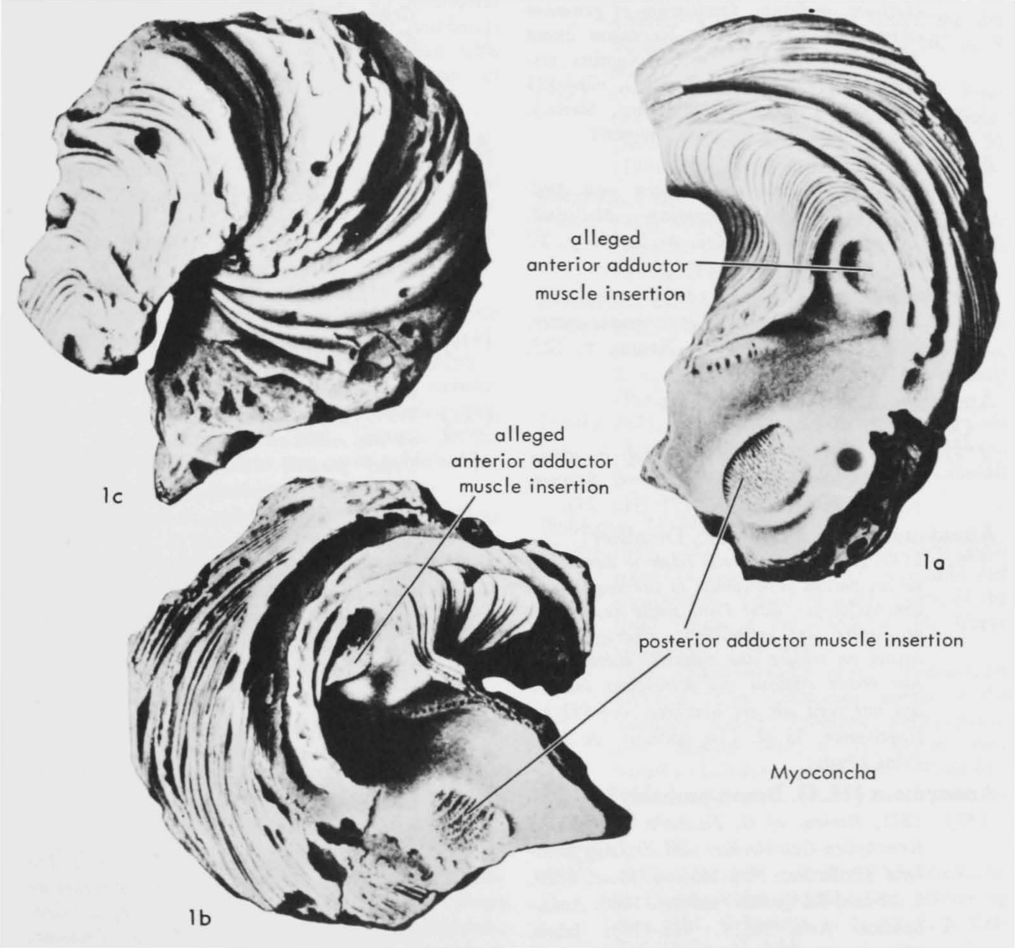

FIG. J147. Permophoridae (*Myoconcha*) (p. N1170).

was attributed by her to VYALOV & SOLUN (1957), but no such name is to be found there.

Sdikia DE GREGORIO, 1884, p. 48 [**Ostrea (Sdikia?) bonfornellensis;* OD]. *Sdikia* was proposed as a subgenus of *Ostrea;* the only species was described but not illustrated and was listed with a question mark as shown above. Species and genus were based on a single valve only and remain unrecognizable. In view of the question mark the species listed cannot be accepted as the type species (*Code,* Art. 67h). Thus *Sdikia* remains a nominal genus without included species, besides being unrecognizable. *?U.Mio.,* Italy (Buonfornello).

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