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CLASSIFICATION OF NUCULID PELECYPODS (1)

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**Introduction.**

When one reviews the various schemes for the classification of bivalve mollusks, such as those by Da Costa (1776), de Blainville (1825), Lamarck (1835), Menke (1830), Deshayes (1839), Bronn (1849), Woodward (1880), Neumayr (1884), Pelsener (1889, 1906, 1911), Dall (1895), Stenta (1908), Douvillé (1912), March (1912), Haas (1929), and Davies (1933) (3), one is forced to the realization that the early arrangements were merely aids in the identification of specimens — really in the nature of artificial keys — and that they were not phylogenetic classifications. Nor have later efforts met with outstanding success. The reason for this failure is clear: it is due to the attempt to integrate undigested data of varying quality. That is to say, some groups have received extensive investigation, others little; consequently some families are defined by narrow limits and others are scarcely defined at all. Neither are we ready to say what morphologic characters should be accorded the greatest weight, nor to

(1) A preliminary report on this subject was read before the Pacific Coast Section of the Palaeontological Society of America, Los Angeles, California, 8 April, 1933.

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(3) Dates in parentheses refer to the bibliographic references on pages 60-68.

assert that the soft parts constitute a final court of appeal in matters of zoologic taxonomy. If agreement or a compromise could be reached as to where generic and family lines should be drawn, we should then be in a position to deal with groups of integrated units that could be moulded ultimately into a genetic classification. My aim in this paper is to attempt to define one molluscan family, the Nuculidae, by the use of shell characters alone (4).

Much information has been assembled that may be of use to systematists who, before adding to the already formidable list of generic, subgeneric, sectional, subsectional, and specific names, should take into account those names and those arrangements already proposed. This information presents numerous problems that may be solved only by a study of suites of specimens of the same species (5).

Although I have dissected live nuculids in the laboratory and have studied many shells ranging in age from early Paleozoic to Recent, and although I have discussed the classification of nuculids in particular and of pelecypods (6) in general with many zoologists and paleontologists, I have neither seen a sufficient number of specimens nor gained a sufficiently exhaustive fund of data to warrant dogmatic conclusions and to coordinate satisfactorily divergent opinions. Nevertheless, in view of the fact that *Nucula* is the radicle for many proposed phylogenies of the pelecypods, and since the family Nuculidae is obviously so little understood, even a preliminary report such as this is warranted.

(4) A general summary of the anatomy of the nuculids and nuculoids, with the description of additional material, is being prepared by Professor Harold Heath, of Stanford University, California.

(5) The illustrations of several hundred of the species of the Nuculidae are worthless and of many others incomplete. Such a magnificent monograph, for example, as that by Prasad (1932) contains excellent views of the *exterior* of several species, but not one of the *interior*.

(6) In my unpublished paper on *Acila* I have discussed the use of the word « pelecypod ». Those who consider « lamellibranch » more fashionable are welcome to employ that term (or any one of the dozen or more others) for the mollusks dealt with in this note. By « nuculid » I mean a member of the family Nuculidae; « *nuculoid* », on the other hand, is less precise: it refers to something that is *Nucula*-like but not necessarily a member of the Nuculidae.

### Review of the literature.

To the family Nuculidae various writers have assigned many genera, subgenera, sections, and even subsections. Representatives of some of these taxonomic units are illustrated in the accompanying plates. Any attempt to define a family must, of course, take into account such forms as have been allocated to it. A review of all of the publications in which one finds mention of nuculoid mollusks though desirable is not feasible. The literature cited herein shows how the pendulum of concepts of taxonomic units swings from one extreme — very broadly defined categories — to the other extreme — minutely defined units.

That the nuculids comprise but a fraction of the genus *Arca* of Linné was recognized by Lamarck (1805). He observed, also, that the nature of the hinge characterizes the nuculids.

De France (1825) separated the species of *Nucula* into two groups: (A) those having a smooth margin and (B) species with a denticulate margin. The latter division included a newly-described species, « *Nucula? Hammeri* » from Gundershofen — a species that later was selected as the type of a new subgenus.

The genus *Nucula*, according to Rang (1829), should be classified in the same family as *Cucullaea*, « *Archa* », « *Pectunculus* », and *Trigonia*; and to the family « *Arcacea* », Müller (1836) allocated the genera *Arca*, *Byssoarca*, « *Pectunculus* », and *Nucula*.

D'Orbigny (1844) regarded as members of the family Nuculidae (« *Famille des Nuculidae* ») *Nucula*, *Nuculina* (type, *Nucula miliaris* Deshayes) and *Pectunculina* (type, here designated, *Pectunculina guerangeri* d'Orbigny). The last named two genera would not be considered members of the family by most modern systematists. The genus *Nucula* he proposed to divide into three divisions :

1. The *Laevigatae*, for the smooth, oval or rounded species such as *N. obtusa*, *albensis*, and *ovata*.
2. The *Rostratae*, for species that we would to-day place in the family Nuculanidae (« *Ledidae* »).
3. The *Pectinatae*, for the generally oval or triangular species having transverse striae, such as *Nucula pectinata*.

The family « *Arcadae* », as viewed by Forbes and Hanley (1853), was a large one, comprising *Nucula*, *Leda*, *Arca*, and « *Pectunculus* ».

Pictet (1855) in his ninth family — « *Arcacides* » — placed

not only *Arca*, *sensu stricto*, but also « *Pectunculus* », *Limopsis*, *Nucula*, *Nucunella*, « *Leda* » and others. He stated (pp. 542-543) that the family is characterized, among other things, by its dentition and by an external ligament, but he recognized that the majority of conchologists of his day agrees in separating the nuculids from the arcids (7) because of the internal ligament in the case of the former and because of certain characters of the animal. Yet he did not adopt this division for he was of the opinion that its value is debatable, in view of the facts that the characters selected do not have family value and that the nuculids are very variable.

H. and A. Adams (1858) separated the family Nuculidae (*Nucula* and *Acila*) from the family « *Ledidae* » (8).

An opinion similar to that expressed by Pictet was held by Jeffreys (1863). *Nucula*, he was convinced, should be placed in the same family — « *Arcidae*, Lowe » — as « *Leda* », *Limopsis*, « *Pectunculus* », and *Arca*. His subdivisions of *Nucula* are as follows :

A. Inner margin notched.

*Nucula sulcata* Bronn, *N. nucleus* Linné, *N. nitida* G. B. Sowerby.

B. Inner margin plain.

*Nucula tenuis* Montagu.

Récluz (1869) was specific in his reasons for separating the family Nuculidae from the « *Ledidae* ».

On the other hand, Hörnes (1870), a contemporary of Récluz, assigned to the family Nuculidae the genera *Nucula* Lamarek, *Nucunella* Wood, and *Leda* Schumacher, although he did differentiate *Limopsis*, « *Pectunculus* », and *Arca* as the family « *Arcacea* ».

Stoliczka (1871), having defined the family Nuculidae, subdivided it into the subfamily Nuculinae, comprising *Nucula* and *Acila*, and the subfamily Sareptinae, including *Sarepta* and *Ctenodonta*.

(7) The word « arcid » is here used as a general term for members of the family Arcidae.

(8) The family name was corrected to Nuculanidae in the table of errata accompanying the volume.

## EXPLANATION OF PLATE I.

Representatives of some of the genera that have been referred to the family Nuculidae by various authors. According to the views expressed in this paper only those marked by an asterisk are allocated to the family. These figures are somewhat generalized.

1. *Neilo cumingii* A. Adams. (Modified after H. & A. Adams, *The Genera of Recent Mollusca*, London, 1858, pl. 126, fig. 3a.) Scale not given.

2. *Nuculana pernula* (Müll.) (Modified after H. & A. Adams, *op. cit.*, pl. 126, fig. 4a — as *Leda*.) Scale not given.

3. *Cadomia typa* de Tromelin. (Modified after Douvillé, *Bull. Soc. Géol. Fr.*, 1912, 4 sér., t. 12, p. 439, fig. 6.) Scale not given.

4. *Yoldia limatula* (Say). (Modified after Verrill & Bush, *Am. Journ. Sci.*, vol. 153, 1897, p. 60, fig. 12.) Length of shell, 51.0 mm.

\*5. *Acila* (*Acila*) *divaricata* subsp. nov. (original sketch). Length, 43.0 mm. Recent; Japan.

6. *Tindaria callistiformis* Verrill & Bush. (Modified after Verrill & Bush, *op. cit.*, p. 61, fig. 21.) Length, 6.9 mm.

7. *Lyrodesma* sp. (Modified after Douvillé, *op. cit.*, p. 439, fig. 7.) Scale not given.

\*8. *Nucula nucleus* Linné. (Modified after H. & A. Adams, *op. cit.*, pl. 126, fig. 3a.) Scale not given. Recent; Europe.

9. *Isoarca cordiformis* Ziet. (Modified after Dall in Zittel, *Text-Book of Paleontology*, Eastman Ed., 1913, p. 443, fig. 664.) Length, 23.5 mm.

10. « *Pleurodon* » *ovalis* Wood. (Modified after E. A. Smith, *Challenger Report, Zool.*, vol. 13, 1885, pl. 19, fig. 1a — as *Nuculina*.) Length, 2.7 mm. The genus is *Nucinella* S. Wood 1850.

## EXPLANATION OF PLATE II.

Representatives of some of the genera that have been referred to the family Nuculidae by various authors. According to the views expressed in this paper only those marked by an asterisk are allocated to the family. These figures are somewhat generalized.

11. *Ledella messanensis* (Seguenza). (Modified after Verrill & Bush, *op. cit.*, p. 60, fig. 13.) Length, 5.8 mm.

12. *Sarepta abyssicola* E.A. Smith. (Modified after Smith, *op. cit.*, pl. 20, fig. 6a.) Length, 5.1 mm.

13. « *Palaeoneilo* » *hopensacki* de Vern. (Modified after Douvillé, *op. cit.*, p. 439, fig. 6.) Scale not given.

14. *Redonia* sp. (Modified after Douvillé, *op. cit.*, p. 441, fig. 15.) Scale not given.

15. *Limopsis marionensis* Smith. (Modified after Smith, *op. cit.*, pl. 18, fig. 2a.) Length, 28.0 mm.

16. « *Glomus* » *nitens* Jeffreys. (Modified after Verrill & Bush, *op. cit.*, p. 60, fig. 2.) Length, 3.0 mm. The generic name should be *Pristigloma*.

17. *Actinodonta obliqua* Phillips. (Modified after Douvillé, *op. cit.*, p. 440, fig. 10.) Scale not given.

18. *Malletia obtusa* (Sars). (Modified after Verrill & Bush, *op. cit.*, p. 60, fig. 9.) Length, 2.9 mm.

\*19. *Nuculopsis girtyi* Schenck, n. n. for *Nucula ventricosa* Hall. Sketch of a specimen 12.3 mm. long from the late Paleozoic of North America.

\*20. *Palaeonucula hammeri* (De France). (Modified after W. Quenstedt, *Geol. u. Palaeont. Abh.*, Jena, 1930, Neue Folge, Band 18, Heft 1, Tafel II, fig. 9.) Length, 17.7 mm. Jurassic; Europe.

An early work on the nuculids is that by Bellardi (1875). His classification, summarized, was as follows :

#### Family Nuculidae GRAY.

##### Subfamily Nuculinae.

Genus *Nucula* LAMARCK.

##### Subfamily Ledinae.

Genus *Leda* SCHUMACHER.

Genus *Yoldia* MÖLLER.

##### Subfamily Malletinae.

Genus *Malletia* DESMOULINS.

Genus *Neilo* H. and A. ADAMS.

Genus *Tindaria* BELLARDI.

The name *Jupiteria* Bellardi, 1875 (type, *Nucula concava* Bronn, 1831) was shown by Sacco (1898) to be a subgenus of *Portlandia* and hence needs no further consideration.

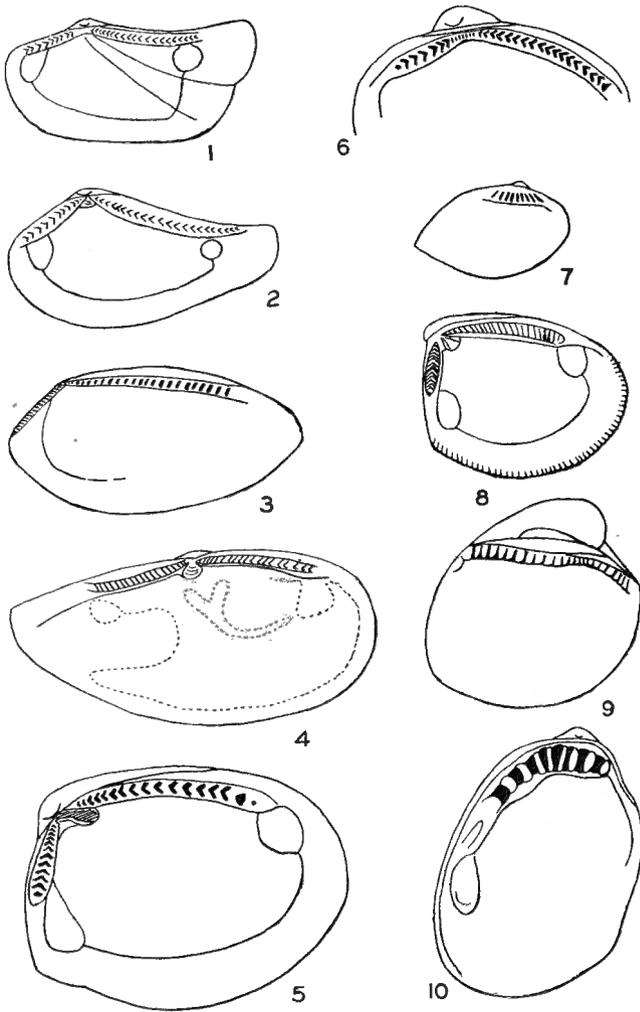
Seguenza (1877) recognized that the Tertiary nuculids fall into the following categories :

A. Margin crenulated or denticulate; surface smooth or nearly so. Examples: *Nucula placentina* Lamarck, *Nucula nitida* Sowerby.

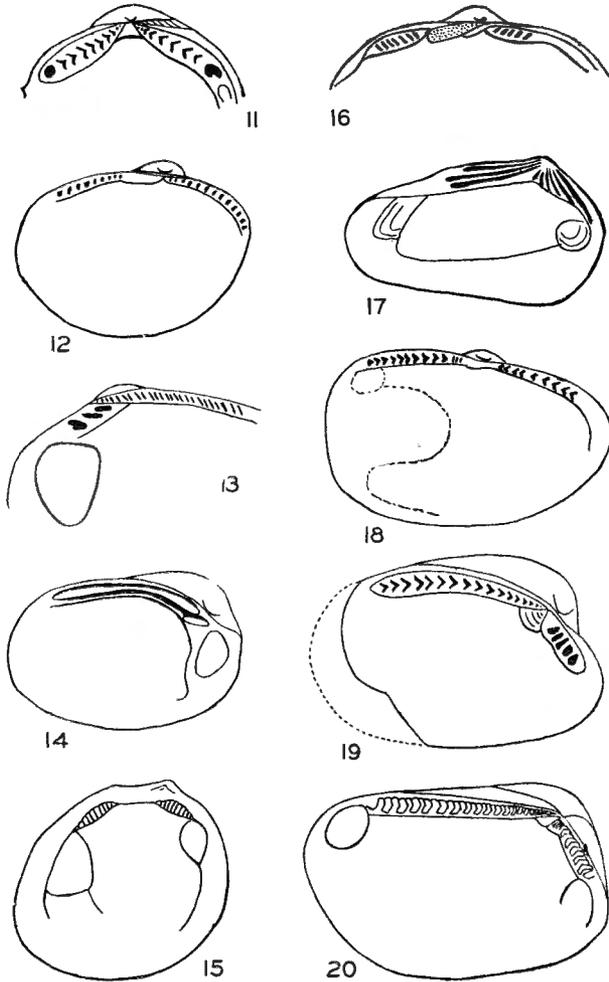
B. Shell transversely costate or corrugated; margin denticulate. Examples: *Nucula sulcata* Bronn, *Nucula jeffreysii* Bellardi.

C. Surface smooth; margin lacking denticulations. Examples: *Nucula decipens* Philippi, *Nucula glabra* Philippi, *Nucula corbuloides* Seguenza.

## PLATE L



1. *Neilo cumingii*; 2. *Nuculana pernula*; 3. *Cadomia typa*; 4. *Yoldia limatula*; 5. *Acila divaricata* subsp. nov.; 6. *Tindaria callistiformis*; 7. *Lyrodesma*; 8. *Nucula nucleus*; 9. *Isoarca cordiformis*; 10. « *Pleurodon* » *ovalis*.



11. *Ledella messanensis*; 12. *Sarepta abyssicola*; 13 « *Palaeoneilo* »  
*hopensacki*; 14. *Redonia*; 15. *Limopsis marionensis*; 16. *Pristi-*  
*gloma nitens*; 17. *Actinodonta obliqua*; 18. *Malletia obtusa*;  
 19. *Nuculopsis girtyi*; 20. *Palaeonucula hammeri*.

The family « Arcadae » in Woodward's (1880) manual comprises *Arca*, *Cucullaea*, « *Pectunculus* », *Limopsis*, *Nucula*, *Isoarca*, « *Leda* », *Solenella*, and ? *Solemya*.

James Hall (1884) placed in the family Nuculidae the genera *Nucula*, *Nuculites*, *Pyrenomoeus*, *Yoldia*, « *Leda* », *Palaeoneilo*, and *Tellinomya* (9). Of these forms only *Nucula* would to-day be considered a member of the family.

Fischer's (1887) arrangement of the family is as follows:

1. Nuculinae, with a single genus, *Nucula*.
2. Cucullellinae, with *Cucullella*, *Palaeoneilo*, *Ctenodonta*, and *Cardiolaria*.
3. Sareptinae, with *Sarepta*.
4. Ledinae, with « *Leda* » and *Yoldia*.
5. Malletiinae, with *Malletia* and *Tyndaria*.
6. Lyrodesmatinae, with *Lyrodesma*, *Actinodonta*, *Babinka*, *Cytherodon*, and *Phaseolus*.
7. Genera whose positions are not well defined: *Myoplusia*, *Ptychostolis*, and *Pyrenomaeus*.

What Fischer took to be family characters may be judged from one paragraph on page 981, freely translated:

« The shape of the palps and of their curious appendages, the disposition of the foot, and the absence of a byssus distinguish the *Nuculidae* from the *Arcidae*. »

It is worthy of note, in passing, that Cossmann (1887) separated the Nuculanidae (« *Ledidae* ») from the Nuculidae because each species of the latter family lacks a pallial sinus.

Bigot (1889), describing some Silurian pelecypods, expressed the belief that the genus *Cadomia* de Tromelin, 1876 (type: *C. typa* de Tromelin) should be placed in the family Nuculidae. A species of this genus is shown in Pl. 1, fig. 3. Although I have not seen specimens of the type species, the fossil, judging from Bigot's figures, seems to lack a chondrophore, and for this and other reasons I think that the genus belongs to another family.

Barrois (1891) placed in the « Famille des Nuculidae » the Paleozoic genus *Actinodonta* Phillips, 1848, a species of which is here figured (Pl. II, fig. 17). The genera *Lyrodesma* Conrad,

(9) *Tellinomya* is figured in the 10th Ann. Report of the Regents of the University of the State of New York for the year 1856, p. 183 (1857).

1841 (Ann. geol. Rep. N. Y., p. 51); *Redonia* Rouault, 1851 (Bull. soc. géol. France, 2<sup>e</sup> sér., t. 8, pl. 362, figs. 1-2); *Ctenodonta* Salter, 1851 (Rept. Brit. Assoc., p. 63); *Nuculites* Conrad, 1841 (Geol. Surv. N. Y. Ann. Rep. 1841, p. 49); and *Nuculana* Link, 1807 (Beschr. natur. Samml. Rostock), were all assigned to the family Nuculidae, but I doubt if there are many living qualified systematists who would agree to this arrangement. Why one should place in the same family a genus with a hinge like that of *Actinodonta* and one like that of *Nucula* I cannot understand.

Von Koenen (1893) considered both *Nucula* and « *Leda* » as belonging in the Nuculidae, but he excluded those forms typified by *Pleurodon ovalis* Wood, that is to say, those forms that have been variously assigned to *Pleurodon* S. Wood, *Nuculina* d'Orbigny, and *Nucinella* Wood.

Bernard (1896) separated the Nuculidae from the « Ledidae » presumably on shell characters.

*Diabolica diabolica* was named by Jousseume (1897) as a nuculid, but Lamy (1926) assigned the species to *Nucinella* S. Wood, 1850. I have examined Jousseume's types in the Muséum National d'Histoire Naturelle in Paris and I agree with Lamy that the species is certainly not related to *Nucula*.

Reasons for separating *Nucula* and *Nuculana* were advanced by Hind (1897). He placed in the family Nuculidae not only these two genera but also *Ctenodonta* Salter 1851.

In their « Revision of the Genera of Ledidae and Nuculidae of the Atlantic Coast of the United States », Verrill and Bush (1897) stated that the latter family differs from the former « mainly in having no siphon tubes, the mantle edges being completely disunited. » Their arrangement of the family Nuculidae is this :

#### Family Nuculidae d'ORB.

##### Subfamily Nuculinae.

Genus *Nucula* LAMARCK.

Genus *Nuculina* d'ORBIGNY, 1845.

##### Subfamily Glominae.

Genus *Glomus* JEFFREYS (10).

(10) Dall (The Nautilus, vol. 14, 1900, p. 44), pointed out that the name for the mollusk *Glomus* Jeffreys, 1876, was preoccupied by *Glomus* Gistel, 1848 (a beetle) and substituted for the mollusk the name *Pristigloma*.

In the following year, these authors (1898) placed the genus « *Glomus* » (type designated *G. nitens* Jeffreys) in a new family, Glomidae, distinct from Nuculidae. They recognized (p. 849) that fossil species referred to *Palaeoneilo* agree in « nearly all essential characters » with the living genus *Tindaria*, and they said (p. 850) that « it is probable that *Nuculites* and several related genera belong near this division, for they have an external ligament and no resilium ».

Their diagnosis of the family Nuculidae, as given on page 884, is as follows :

« Shell not gaping, short-ovate, subtrigonal, or rounded ; posterior end without a rostrum ; beaks usually curved backward ; no siphon tubes or pallial sinus. »

Hedley (1902) described *Pronucula* as a new genus belonging to the Nuculidae.

Borissjak (1904), describing the Nuculidae of the Jurassic of European Russia, considered that the family was made up of the genera « *Palaeoneilo* » Hall, *Nucula* Lamarck, *Leda* Schumacher, and *Phaenidesmia* Bittner. He subdivided the Jurassic *Nuculas* as follows :

Group *Nucula Eudorae* d'Orbigny, including several species, such as *Nucula calliope* d'Orbigny.

Group *Nucula Sana* Borissjak, among which is *N. pseudo-Menkii* Lor., well figured by the author.

Group *Nucula* (?) *circuliformis* Borissjak.

*Nuculoma* is a name proposed by Cossmann (1907) as a section of *Nucula*, the type species being *Nucula castor* d'Orbigny.

Girty (1911) erected the genus *Nuculopsis* (11) typified by *Nucula ventricosa* Hall, non Hinds.

Pelseneer's revised views on the phylogeny of bivalves were published in 1911, documented with numerous references to the literature. That such forms as *Nucula* with two adductor muscles are archaic is to him a demonstrated basic principle, and he is equally certain that the gills afford the most important

(11) Not of Rollier, Ab. Schweizer. Paläeon. Ges., vol. 38, part 2, p. 64, 1912. (No type designated ; illustrations poor). Renamed *Isonuculana* by Cox. The following note is supplied by L. R. Cox (March 23, 1934). « *Nuculopsis* Rollier was renamed *Rollieria* by Cossmann (Rev. crit. Paléozool. XXIV, p. 82, 1920) and this fact was overlooked by Rollier himself when he renamed it *Isoleda* (also preoccupied) and by myself when I renamed it *Isonuculana*. The type, *N. palmae* Sow., is a Carboniferous Limestone species wrongly attributed to the Lias by Dumortier and others ».

criteria for the « genetic » classification which he represents graphically on page 123. The family Nuculidae is separated from the families « Lediidae », « Pectunculidae » and Arcidae. One remark (p. 121), freely translated, is as follows :

« In the ascertaining that *Nucula* is the most archaic of living lamellibranchs, one finds a rare example of the perfect agreement of the phylogenetic results of conchologists (Neumayr, Bernard, Jackson) and of morphologists. »

I cannot express here all the reasons I have for believing that Pelseneer was too optimistic in this « perfect agreement ». Much depends upon how one defines *Nucula*, and even more upon what is the actual paleontologic record. To date I have seen no *Nucula*, *sensu stricto*, in rocks of Paleozoic age.

Douvillé (1912) attached importance to the character of the shell, that is, whether the interior is nacreous or porcellanous. Thus, all nuculids are nacreous, taxodont bivalves. Moreover, to the family Nuculidae he assigned those forms in which the teeth converge towards the center of the valve. Besides *Nucula*, he grouped in the same family the genera *Ctenodonta* Salter, *Cudomia* de Tromelin, and *Palaeoneilo* (Consult fig. 13, Pl. II). Except *Nucula*, none of these has a chondrophore. Furthermore, one gathers the impression that the ligament is external in the three genera, whereas it is internal in the case of *Nucula*.

The discussion of the classification of pelecypods by March (1912) emphasized hinge characters, since the author is convinced that « a gill classification must necessarily exclude all fossil forms, and so do away with the possibility of forming a phylogenetic classification » (p. 91). The paper is largely an exposition of ideas expressed by Bernard, whose works are cited. The family Nuculidae is placed in an « order Pleurodonta », a name which « refers to the definite proof of the evolution of the taxodont teeth from internal ribs ».

Cossmann and Peyrot (1912), attached great importance to the chondrophore, which feature they claimed varies not only in its dimensions but also in its inclination, its projection into the « umbonal cavity », and in other ways. But as for *Acila*, they were sceptical of its validity because the hinge does not appear to present any peculiarity. This opinion was based upon an examination of specimens of only one species — *cobboldiae*, as Professor Peyrot informed me by letter — and thus their opinion cannot be considered seriously.

Another attempt to classify the nuculids is that by Williams

and Breger (1916), who erected the subgenus *Nuculoidea*, distinguished principally by a nonpectinated (not crenulated) ventral margin, as seen on the interior of the shell.

Gillet (1924) proposed to group the nuculas into four « branches » (12) as follows :

1<sup>re</sup> Section : — Lisses.

1° Rameau : Ovatae ; type *N. planata* Desh. and var. *Corneuliana* d'Orb.

2° Rameau : Impressae ; type *N. simplex* Gardner.

2° Section : Pectines ; type : *N. pectinata*.

3° Section : Acilae ; type : *Nucula bivirgata* Sow.

There is little to recommend this medieval arrangement. Her ideas regarding the geographic distribution of the living nuculids are immature, and she accepted the widely-quoted but unproven opinion that the genus *Nucula* has been recognized in rocks as old as the Silurian.

The genus *Nucunella* d'Orbigny (1849) as emended and defined by Em. Vincent (1922), obviously does not belong in the family Nuculidae, though it has been so classified (13).

The name *Nuculopsis*, twice before proposed for a pelecypod, was again applied to a nuculid by Woodring in 1925.

Quenstedt's (1930 \*) opinions concerning the nuculids and nuculoids cannot be passed over briefly, for not only does he pre-

(12) The taxonomic category « rameau » (translated « branch ») is not generally accepted and has no legal standing. See also footnote 15, page 14, regarding « subsection ». The International Rules of Zoological Nomenclature have received wide circulation and have recently been reprinted by Karl Krejci-Graf (1932), together with Opinions 1-123, inclusive. The paper by Frizzell (1933) should also be in the hands of all systematists.

(13) Dr. W. P. Woodring was good enough to examine a specimen of *Nucunella nysti* that I sent him and he reported (letter to me dated 11 December, 1933) that he doubts if it is closely allied to *Postligita* Gardner (1916) (Upper Cretaceous vol. Maryland Geol. Survey, p. 543, pl. XXI, figs. 7-9). « Both have prosogyrate beaks and opisthodetic ligament, but the plan of the two series of teeth is different, and in *Postligita* the ligament grooves are strongly oblique and extend up under the beak. »

Attention is here directed to the fact that the original spelling *Nucunella* has been changed by various writers after d'Orbigny. The original orthography should be retained.

(\*) The bibliography on pages 114-119 of this monograph contains many useful citations not included in the present paper.

sent a formal scheme of classification, with the proposal of new names, but he also makes the definite statement (p. 108) that *Acila* is not a « natural » group, since (freely translated) :

« When you finally see how divaricate sculpture is acquired independently in the most varied shells (*Leda pella*) (14) in a more or less similar manner as in *Acila*, then it is very probable that the phenomenon in the different groups of *Nucula* arose at different times. In other words, *Acila* is not a genetic entity but is a polyphyletic compilation (*Sammelbegriff*) — a convergence phenomenon. »

Structure and sculpture are independent of each other (p. 108) and divaricate ribs, he maintains, represent merely a new development of a radially sculptured *Nucula* of the *N. nucleus* group. At some time between the Devonian and Jurassic, he holds (p. 89), bifurcation began, and it developed as a result of the forward motion of the animal; this type of sculpture offers a more efficient aid in softening the dorso-ventral « recoil » of the shell during its movement. Concentric ribbing is, consequently, a primitive character in contrast to the more specialized radial and divaricate ribbing. Another result of movement is the enlargement of the foot and the attendant acquisition of opisthogyrous beaks. In brief, Quenstedt offers a mechanistic explanation for the morphologic features exhibited by the nuculids, and his ideas color his views on classification.

Notwithstanding his philosophical considerations and his repeated assertions that *Acila* is a « makeshift », he recognized it as a section of *Nucula* (p. 112), as may be seen from the following summary of his arrangement :

Genus *Nucula* (type: *N. nucleus* Linné).

I. Subgenus *Nucula*.

1. Section *Nucula* (*s. s.*).

a. Subsection (15) *Nucula* (*s. s.*)

(14) Quenstedt overlooked the fact that « *Leda* » *pella* Lamarck (1819, p. 58) is the type of the subgenus *Lembulus* Risso, 1826. (See Bucquoy, Dautzenberg, and Dollfuss, *Les Mollusques Marins du Roussillon*, T. II, Fasc. V, Pélécytops (Fasc. 18), April, 1891, p. 218). I have examined Lamarck's holotype in the Muséum National d'histoire Naturelle in Paris and there is no doubt that the species is a member of the family Nuculanidae, and not Nuculidae. Quenstedt's objection to *Acila* is not cogent, since characters of generic rank in one family may have no classificatory value in another.

(15) Systematists are still waiting for a definition — not to men-

- b. Subsection *Pectinucula* (Type: *N. pectinata* Sowerby).
2. Section *Leionucula* (Type: *N. albensis* d'Orbigny).
  3. Section *Acila* (Type: *N. divaricata* Hinds).
- II. Subgenus *Palaeonucula* (Type: *N. hammeri* (De France) (Bronn)).
1. Section *Palaeonucula* (*s. s.*).
  2. Section *Nuculoidea* (Type: *N. opima* Hall (= *Randalli* Hall).

Although the position and character of the beaks is of some importance, the major differences, as seen by Quenstedt, are internal. For instance, he lays emphasis upon the « *Bandgrube* », which judging from his figure 11, plate 2, is the chondrophore. Behind the chondrophore in *Nucula*, but not in *Palaeonucula*, according to Quenstedt, is a « chondrophore tooth » (*Bandgrubenzahn*).

Some of the species of *Acila* (*cobboldiae* and *picturata*) he classed (p. 110) with *Leionucula*; some (*shumardi* and *conradi*) go with *Nucula*, *s. s.*, and *Acila bivirgata* is placed in the subsection *Pectinucula* along with *Nucula pectinata* Sowerby. Thus, although all of the species of *Acila* would be placed in the subgenus *Nucula* and none in the subgenus *Palaeonucula*, Quenstedt would apparently place some species in sections other than *Acila*, *s. s.*

The generic name *Protonucula* was given by Cotton (1930) to a small nuculoid from west of Eucla, Australia; the type species lacks a chondrophore.

*Ennucula* and *Deminucula* were proposed as new genera by Iredale (1931), with *Nucula obliqua* Lamarck and *Nucula praetenta* Iredale (new name for *N. umbonata* Smith) respectively as types. Under a discussion of *Nucula tenisoni* Pritchard, Singleton (1932) remarked :

« In its smooth inner ventral margin, oblique chondrophore, and hinge dentition, *N. tenisoni* agrees with *N. obliqua*, genotype of *Ennucula* Iredale (1931, p. 202), but these characters... seem to be of sectional rather than of generic importance. »

J. Marwick (1931) proposed the name *Linucula* as a subgenus of *Nucula*.

My preliminary arrangement of the divaricate nuculids appea-

tion legal recognition — of a section. Now they have an additional problem — a subsection!

red in 1931, in the monograph by Grant and Gale (1931) (16). Accepting *Nucula divaricata* Hinds as the type species of *Acila*, *sensu stricto*, the name *Truncacila* was applied to the truncate group of *Acilas*, with the type species designated as *Nucula castrensis* Hinds.

In 1933, Jaworski (17), reviewing the abstract of my preliminary report on « Bivalves of the Genus *Acila* », accepted W. Quenstedt's evidence for rejecting *Acila* as a « natürliche Einheit ». This evidence is stated by Jaworski as follows :

« Aus dem Indischen Ozean ist eine noch nicht beschriebene Art bekannt, bei der die divaricate Berippung erst auf dem Vorder- und Hinterteil der Schale, aber noch nicht auf der Schalenmitte vorhanden ist. Die divaricate Berippung ist nachweisbar von verschiedenen Nuculiden-Gruppen unabhängig voneinander erworben worden. »

This undescribed species might fall into the category named *Linucula* by Marwick in 1931. In any event it certainly does not invalidate the taxonomic position of *Acila* whatsoever.

Even to-day some authors insist on placing *Otenodonta* « *Leda* », and *Yoldia* in the family Nuculidae. As thus defined, Hennig (1932) gives the range of the family as from Cambrian to the present (\*).

Prashad (1933) defined the family Nuculidae and the genus *Nucula*; he perpetuated the unproven belief that the genus ranges in time from the Ordovician to Recent.

The high esteem I have for Professor Johannes Thiele is not diminished by his recent (1934) treatment of the « Familia Nuculidae » in his valuable handbook. His statements therein illustrate what a gigantic task it is for any one person to compile the names of described genera and subgenera of the bivalve mollusks, not to speak of the difficulties in store for him who strives to evaluate the names by an examination of specimens. The author's arrangement of the family is this :

(16) The abstract of my paper presented before the Pacific Coast Section of the Paleontological Society of America appeared under the title « Bivalves of the Genus *Acila* » in Bull. Geol. Soc. Amer., vol. 43, pp. 288-289, 1932.

(17) JAWORSKI, E. (1933), Neues Jahrbuch f. Min., Geol., und Paläon. Referate, III, 1933, 5. Heft, pp. 1054-1055.

(\*) Some of the Paleozoic fossils called taxodont mollusks may actually belong to another phylum. Specimens of *Leperditia hisingeri* Schmidt, a Silurian ostracode, show what might be taken for taxodont dentition; these crustaceans are not unlike some nuculoids in shape.

Genus *Nucula* Lamarck 1799 (Synonym *Nuculana* Link 1807 (18).

Subgenus *Brevinucula*, n. subgen. (Type by monotypy, *Nucula guineensis* Thiele.)

Subgenus *Leionucula* W. Quenstedt 1930. (Synonym *Ennucula* Iredale.)

Subgenus *Acila* H. & A. Adams 1858.

« Sectio » *Truncacila* Grant & Gale, 1931 (19).

Subgenus *Nucula*, s. s.

The genus *Protonucula* Cotton he says « ist von *Tyndaria* nicht wesentlich verschieden » and that « *Deminucula* Iredale 1931 dürfte nicht verschieden sein ». I agree with both these statements, for reasons expressed before reading Professor Thiele's book.

It is not clear from the discussion how Thiele would classify *Pronucula* Hedley, but he informs me, in a letter dated 5 March, 1934, that he considers *Pronucula* Hedley doubtfully a « Section » of *Nucula*.

The important monograph by Pfab (1934) appeared after this paper was submitted for publication. The family Nuculidae is said to include the following Silurian genera: *Otenodonta* Salter; *Praeleda* Pfab, nov. gen.; *Praenucula* Pfab, nov. gen.; and *Pseudocyrtodonta* Pfab, nov. gen. I would exclude all of these from the family. His ideas of the phylogeny of the taxodonta are based on the assumption that *Nucula* occurs in the Devonian.

(18) L. R. Cox comments as follows (March 23, 1934): « I think that the argument that *Nuculana* was an emendation of the name *Nucula* and therefore a synonym was brought forward in the first place by Dall. »

(19) It is expressly stated in the monograph by Grant and Gale that Schenck is the author of the name *Truncacila*. In my opinion, the authorship of this name is fully covered by the International Rules of Zoological Nomenclature, but Thiele and at least one other of the leading systematists in Europe hold the view that the author of a name is the author of the note in which that name is published. They maintain that if the name of the author of the unpublished manuscript is cited, it might lead to a fruitless search by subsequent workers among that author's papers (if any) in an attempt to find the original description. This objection is not serious, because the author's name may be given in addition to the name of the author of the published note; e. g. *Truncacila* Schenck MS in Grant & Gale, 1931.

**Taxonomic units eligible for selection as Members  
of the family Nuculidae.**

Modern workers agree that the divisions 2-7 of Fischer's classification, that is, the Cucullellinae, Sareptinae, Ledinae, Malleitiinae, Lyrodesmatinae, and *Myoplusia*, *Ptychostolis*, *Pyronomaeus*, and « *Glomus* » Jeffreys are not members of the family Nuculidae. There is no reason to place in the family those forms that lack taxodont dentition and a chondrophore. Nor should the family include those forms that possess a pallial sinus (20), or those genera whose representatives have definite siphons, such as *Nuculana* (« *Leda* »), since present-day qualified zoologists are in accord with conchologists in placing this genus in another family than the Nuculidae. We eliminate from consideration, therefore, those genera figured on Pl. I and II, except numbers 5 (*Acila*), 8 (*Nucula*), 19 (*Nuculopsis* Girty), and 20 (*Palaeonucula*). We need not consider many of the other genera, such as *Otenodonta*, mentioned on the preceding pages. The taxonomic units that cannot be so summarily dismissed will be arranged for convenience under four main headings: (A) those having shells with denticulate ventral margins; (B) those having smooth inner ventral margins; (C) those with divaricate sculpture and (D) systematic position uncertain.

(A) FORMS WITH DENTICULATE VENTRAL MARGINS :

(1) NUCULA Lamarck, 1799. (Type by monotypy: *Arca nucleus* Linné.)

Pl. I, fig. 8; Pl. III, fig. 2; Pl. IV, figs. 4, 4a, 4b; Pl. V, figs. 1, 1a.

Lamarck, Mém. Soc. d'Hist. Nat. de Paris, p. 97, 1799.

The following is Lamarck's (1799) original description of *Nucula* :

« 104. Nucule. *Nucula*.

Coq. presque triangulaire, inéquilatérale; charnière en ligne brisée, garnie de dents nombreuses, transverses, parallèles; une dent cardinale oblique, en gouttière et hors de rangs; les crochets contigus; tournés en arrière.  
*Arca nucleus*. Lin. »

(20) Presence or absence of a pallial sinus may not be a character of family importance.

Bucquoy, Dautzenberg, and Dollfuss aptly remarked (21) that the diagnosis of « *Arca* » *nucleus* Linné given in the « *Systema Naturae* » is so incomplete that it is impossible to recognize the species to which it refers. This is the description in the 10th edition of « *Systema Naturae* », p. 695 :

« *A. testa oblique ovata laeviuscula, natibus incurvis, margine crenulato, cardine arcuato ciliari.*

*Habitat in Europa.* »

It is likely that the figures accompanying the Roussillon monograph cited above (pl. 37, figs. 15-21) are of the type species.

The figures presented here on Plates III, IV and V are of specimens furnished by Dr. Ph. Dautzenberg, with the accompanying remarks (22) :

« *L'Arca Nucleus* a été si mal défini par Linné et son habitat : « in Europa » est si vague, qu'il est impossible de connaître non seulement l'habitat précis de son type, mais même de savoir si les auteurs ont eu raison d'employer comme ils l'ont fait le nom *Nucula nucleus*. Tout en acceptant cette interprétation à cause de sa longue tradition, il serait prudent de l'attribuer à : (Linné) auctorum. »

The following is a brief characterization of these shells :

Shell closed, not gaping ; profile ovate-trigonal ; a « pouting » of the escutcheonal area, which the radial ribs do not cross ; beaks opisthogyrate, appressed ; prodissoconch unornamented ; radial ribs faint, low, wide and flat, often difficult to see on the middle part of the shell, but they are more distinct near the ventral margin where they form the « pectinate margin » ; interspaces narrow, about one-tenth the width of the ribs ; interior nacreous ; pallial line simple ; two subequal adductor muscle scars and additional muscle scars ; longer (anterior) row of teeth arched, with  $16 \pm$  to  $24 \pm$  teeth ; the shorter (posterior) row straight with  $7 \pm$  to  $11 \pm$  ; axis of chondrophore forms an arc of a circle of which the arcuate dorsal margin is a part ; dimensions of some of the specimens are given in Table I, page 20.

European conchologists are not in accord on the subject of the

(21) BUCQUOY, E., DAUTZENBERG, Ch. and DOLLFUSS, G. (1891), *Les Mollusques marins du Roussillon*, t. 2, Pélécy-podes, p. 212, April, 1891.

(22) Letter from Dautzenberg to me, dated Paris, December 16, 1933.

TABLE I

Dimensions of some Recent specimens of *Nucula nucleus* (Linné)  
from Europe (23).

Locality	Specimen Number	Length in mm.	Height in mm.	Thickness (2 valves) in mm.	Umbonal angle in degrees	Ratio of height to length in percent
Arcachon, au large, France (Atlantic) (Drag haul)	1	2.0	4.5	4.0	—	75
	2	3.6	2.6	4.7	—	73
	3	4.0	2.8	1.8	—	70
	4	4.7	4.0	2.5	93	83
	5	5.3	4.0	2.5	95	76
	6	6.2	5.8	3.5	97	94
	7	8.0	6.4	3.7	92	80
	8	9.9	8.0	5.3	105	80
Port Vendres France (Mediterranean)	1	7.6	6.3	4.4	96	86
	2	8.0	6.4	4.2	98	80
	3	8.7	7.3	5.0	96	84
	4	8.8	7.2	5.2	98	82
	5	10.7	8.8	5.7	96	82
St Pair, Channel (Atlantic)	1	9.6	8.2	5.5	91	86
	2	10.5	9.2	—	92	87
Astan, near Roscoff, France (Atlantic)	1	6.0	5.0	3.3	—	84
	2	8.2	6.9	4.5	98	84
	3	8.8	7.2	4.6	96	82
	4	10.5	8.0	4.8	93	77
Baie de Quiberon, France (Atlantic)	1	10.4	8.3	4.8	102	80
	2	11.5	9.6	6.2	99	84
	3	12.0	9.8	6.2	93	—
Baie Alilas Ile de Zante, (Mediterranean)	1	7.7	6.3	4.6	97	82
	2	7.8	6.2	4.2	95	80
	3	9.4	7.4	—	102	79
	4	10.8	8.6	—	98	80
	5	11.0	8.6	—	100	78

(23) Specimens supplied by Ph. Dautzenberg to the Musée royal d'Histoire naturelle de Belgique.

identity of *Nucula nucleus*, to judge from the determinations of specimens in the museums that I have visited. I did not find Linné's type of « *Arca* » *nucleus* in the collections in Sweden. The original description of the species, however, leaves no doubt that the type is a form with a denticulate ventral margin.

Dr. Nils Odhner suggests (Oral communication) that the following are appropriate terms for the scars other than the adductor muscle scars :

The narrow, elongate scar clearly outlined in fig. 4, Plate III, and figures 1 and 1a, Plate V, may be called the *median muscle scar*. The small, oval or round scar below the long one may be termed the *central muscle scar*. The numerous small scars between these two and the anterior adductor muscle scar may be designated the *punctiform scars*.

To determine how many of the species assigned to-day to *Nucula*, *sensu stricto*, actually belong there is an enormous task. I select as an illustration of morphologic differences certain species from the Tertiary of Belgium.

I have seen several hundred specimens of *Nucula haesendonckii* Nyst and Westendorp, 1839, from the upper Miocene (Anversian) sands near Bolderberg, Edegham, from mines at Houthaalen, etc. It is a species ranging in length up to 26 mm. in length, in height up to 20 mm. and in thickness (two valves) up to 20 mm. Especially characteristic is its form, high degree of inflatedness, impressed lunule and escutcheon, and *Inoceramus*-like concentric ribs. The dentition is peculiar: commonly the ends of several posterior teeth merge to form a sort of button under the proximal part of the chondrophore. Some of the shells exhibit numerous elongate muscle scars near the pallial line between the adductor muscle scars. The posterior adductor scar is often deeply impressed and bordered anteriorly by a ridge. Despite the fine radial ribs, the inner ventral margin is smooth, even on small individuals.

Exceptionally large nuculas are those from the Chattian (upper Oligocene) of Belgium, known as *Nucula compressa* Philippi (24). The largest shell I have examined is from mines at Houthaalen and measures 29.3 mm. in length, 22.2 mm. in height, and 14.7 mm. in thickness. The ventral margin is distinctly crenulate and low radial ribs cross the disk. Unworn shells ex-

(24) The identification of the specimens is based upon the illustrations by Speyer (1884, pl. XVI, figs. 9-16). I have not seen the original description of the species.

hibit distinct concentric undulations. I have seen no well-preserved hinge, but one individual has a chondrophore that is not as wide distally as in the case of *N. nucleus*.

*Nucula duchastelii* Nyst (1835, p. 16) (25) from the Rupelian clay (middle Oligocene) of Boom is a form with a crenulate ventral margin and weak radial ribs, but is specially characterized by strong concentric ribs. The species ranged during the middle Oligocene as far north as Denmark, if the identification by Ravn (1907, p. 254-255) is correct. Such sculpture aids in distinguishing this species from shells called *Nucula comta* Goldfuss from the lower Rupelian (middle Oligocene) near Berg, in the vicinity of Kleyn-Spauwen, province of Limbourg, as recorded by van den Broeck (1883, p. 73, etc.). The type of *comta* (often spelled « *compta* ») « kommt zu Bünde und Astrupp vor », and according to Speyer (1884, pl. 16, fig. 17-26) it is an Oligocene species with radial ribs; it is closely related to *duchastelii*. I have not had a chance to make a direct comparison of specimens of *duchastelii* with *Nucula rugosa* Odhner (Arkiv för Zoologi, Bd. 12, n° 6, pp. 23-24, pl. II, figs 15-18, 1919), a Recent species from Tamatave, Madagascar.

*Nucula tumulata* Nyst, 1845, a common upper Eocene species near Brussels, has been redescribed by Vincent (1925, p. 15-16). The radial ribs are low and wide, as in the case of *N. nucleus*; the two species are also similar in profile and hinge characters. The chief difference is the greater « pouting » in the escutcheonal region, well figured by Nyst. Hence, there can be no doubt that *Nucula*, *sensu stricto*, occurs in rocks of Eocene age, and judging from the description of *N. gaultina* Gardner presented by Henry Woods (1899, pp. 25-26) the time range of the subgenus must be extended from the Recent as far back as the Cretaceous, at least; on the other hand I have seen no radial-ribbed nuculids from Jurassic or older formations.

(2) PRONUCULA Hedley, 1902. (Type: *P. decorosa* Hedley.)

Pl. III, fig. 3.

Hedley, Australian Museum, Sydney, Mem. IV, Pt. 5, p. 290. 29 July, 1902. Recent, Australia.

This name was proposed for a new genus which « differs from

(25) The spelling of the specific name in the original description is here followed. Nyst (1843) seems to have changed the orthography to « *Chastelii* » and in this was followed by von Koenen (1868, p. 92), Ravn (1907), and others.

*Nucula* by having the hinge line arched instead of angulated, the rows of teeth do not meet or overlap beneath the umbones, but are distant from the chondrophore, which is not oblique as in *Nucula*, but perpendicular. Briefly, the constituents of the hinge, which in *Nucula* are much compressed and perhaps slightly rotated, are here wide spread. The shell has not the trigonal contour of *Nucula*, is far thinner and the radial sculpture more pronounced than in that genus ».

The length of the holotype is only 2.5 mm. The original figures are copied here on Pl. III, fig. 3.

Marwick (1931) accepted this genus and described a new species from the Tertiary of New Zealand. Cotton has described several Recent species.

(3) PECTINUCULA Quenstedt, 1930. (Type: *Nucula pectinata* (Sowerby).)

Pl. III, fig. 1, 1a, 1b, 1c.

Quenstedt, Geol. u. Palaon. Abh. n. f. Bd. 18 (der ganzen Reihe Bd. 22), Heft 1, p. 112, 1930. Cretaceous, Europe.

The type of this « subsection » is the well-known European Cretaceous species (26) with strong radial ribs. Forty-eight representatives of this species from the Gault of Folkestone, England, are in the Musée royal d'Histoire naturelle de Belgique in Brussels. Table II, page 25, gives the dimensions of some of these topotypes.

Although the valves of nearly all of the specimens are in the attached position, broken specimens show clearly that the ventral margin is denticulate. The elevated radial ribs, however, do not cross the escutcheonal region; that is, the area posterior and ventral to the beaks lacks the distinct radial ribs that cross the major part of the disk. Many of the specimens have a beaded sculpture. The ill-defined lanceolate lunule is also without radial ribs. In width the ribs and interspaces are approximately equal.

British Museum specimens L-4969, from the Gault of England, exhibit the numerous muscle scars observed in the case of *Nucula nucleus* and other nuculids. A specimen that shows the hinge is in the Musée royal d'Histoire naturelle de Belgique from the Gault of Epothémont, near Brienne-le-Château (Aube), France; this shell is here illustrated as fig. 1c, Pl. III. The anterior (long) series of teeth of the right valve terminates

(26) Described by Sowerby in Min. Conch., vol. 2, 1812, p. 209, pl. 192, figs. 6, 7. « Sussex, Folkestone and Dover », England.

against a tooth posterior and ventral to the bounding wall of the chondrophore.

*Nucula archiacana* Nyst (1843) (27) is a synonym of this species. The holotype was presumed by Nyst to come from the « Argile de Boom » (Oligocene) of Baesele, Province of Antwerp, Belgium. This type (N° 24) is in the Musée royal d'Histoire naturelle de Belgique in Brussels and agrees in every detail with topotypes of the earlier-named *pectinata*. It seems to me that Nyst's collection was mixed. E. Vincent (MS) recognized this identity between Nyst's and Sowerby's species. Von Koenen (1868, p. 94) accepted Nyst's species as one from the middle Oligocene, and I have seen in the collection at the University of Liège two specimens (N° 4296) said to come from the Rupelian clay at Boom. The largest is a slightly crushed individual 28 mm. long with distinct radial ribs. If Nyst's holotype actually comes from the Rupelian clay at Baesele, as he claimed, then the range of the species *pectinata* is appreciably lengthened.

It should be remarked in passing that the Oligocene species *piligera* Sandberger is a *Pectinucula*, as is the Miocene form *notabilis* Mayer.

To regard *Pectinucula* as a subgenus of *Nucula* has much in its favor, and it is thus regarded here. *Nucula subredempta* Böhm (1891), from the Cretaceous (with *Baculites*, etc.) of Bavaria, belongs to this category, as does *Nucula tenera* J. Müller, originally described from the Cretaceous near Aix-la-Chapelle, but well figured by Pervinquière (1912) from the Maestrichtian (Upper Cretaceous) of Sidi Ahmor, Tunis. The Swedish Cretaceous species, *Nucula truncata* Nilsson, 1827, refigured by Henning (Kongl. Fysiogr. Sällskapet i Lund. Handl. Ny fölljd. Bd. 8, pl. 3, fig 30, 1897), is represented by poorly preserved material, as far as I have seen, but it is probably a *Pectinucula*.

The geographic distribution of Cretaceous species identical with or related to *pectinata* is very wide. Dr. L. W. Stephenson, of the U. S. Geological Survey, showed me, while I was in Washington, D. C., some North American specimens and I have also examined numerous specimens from France (Revigny, Epothémont, Clermont en Argonne, Dienville, Pargny, etc.).

(27) Nyst, P. H., (1843), Description des Coquilles et des Polyptiers fossiles des terrains tertiaires de la Belgique. Mém. Cour. et Mém. des Savants Etrangers, Acad. Roy. de Bruxelles, t. 17, 1843, p. 234, N° 190, pl. 24, figs. 1b, 1c.

TABLE II

Dimensions of topotypes (28) of *Nucula pectinata* Sowerby from the Gault of Folkestone, England.

Specimen Number	Length (1) in mm.	Height in mm.	Thickness in mm.	Umbonal angle in degrees	Ratio of height to length in percent
1	8.5	6.8	5.0	102	80
2	1.04	8.1	5.5	101	78
3	14.0	40.3	7.2	116	74
4	15.3	42.0	8.6	93	79
5	17.2	42.4	9.4	106	72
6	18.0	44.2	10.1	98	79
7	18.4	43.8	9.5	114	76
8	19.4	44.3	10.3	109	74
9	20.7	45.4	11.4	103	74
10	21.3	45.5	12.4	105	73
11	22.7	45.3	13.0	110	67
12	23.2	46.4	—	—	70
13	24.9	47.1	13.9	103	69
14	26.6	48.6	14.8	108	70
15	26.— (2)	49.0	14.3	109	73
16	26.8	47.4	—	—	63

(1) Length measured with the shell held so that the dorsal margin is horizontal.

(2) Anterior end slightly broken.

(4) LINUCULA Marwick, 1931. (Type: *Nucula ruatakiensis* Marwick.)

Marwick, Palaeon, Bull. 13, New Zealand Geol. Survey, p. 49, 1931. Miocene, New Zealand.

This name was introduced as a subgenus of *Nucula*. The following is the original characterization :

« Shell small; sculpture of numerous weak radials; lunule and escutcheon with much finer, divaricate radials. »

The type species of *Linucula*, as described and figured by Marwick (1926, p. 327, pl. 75, figs. 7, 9), was based on a speci-

(28) Specimens in the Musée royal d'Histoire naturelle de Belgique in Brussels; Belgium.

men 5.1 mm. in height and 5.5 mm. in length. Through his kindness, I have had the privilege of seeing the holotype of *Nucula ruatakiensis* and in addition paratypes of *N. tutamoensis* and *waipao*, also assigned to *Linucula*. As he pointed out to me (letter dated January 5, 1934), the word « divergent » is a more descriptive term than « divaricate » for the characteristic sculpture on the lunule and escutcheon.

The hinge of the holotype (a single valve) of *ruatakiensis* is broken, and I cannot be sure of the nature of the chondrophore (resilifer), if there is one. The teeth number about 12 on each side of the beaks. The entire margin of the shell on the interior is finely crenate, except immediately under the beaks, and the ventral margin is distinctly pectinate. Details of the various muscle scars cannot be made out. Paratypes of *waipaoensis* exhibit nacreous interiors, as does the type of *ruatakiensis*. Though preservation is imperfect, I believe that these paratypes have a very small chondrophore. The holotype of *tutamoensis* shows muscle scars in addition to the adductors and the long, narrow scar situated in the umbonal region is relatively deeply impressed, as in the case of *ruatakiensis*.

The distinctive sculpture and profile of these fossils, coupled with the hinge characters, force me to the belief that *Linucula* should not be classed as a subgenus of *Nucula*, though it is probably a member of the family Nuculidae. Better preserved material may prove that it merits recognition as a genus.

(B) FORMS WITH SMOOTH INNER VENTRAL MARGINS.

(5) NUCULOMA Cossmann, 1907. (Type by monotypy: *Nucula castor* d'Orbigny.)

Pl. IV, fig. 5, 5a, 5b, 5c.

Cossmann, VI<sup>e</sup> Con. Assoc. Franc-Comtoise (Vesoul), Soc. Agric., Let., Sci., Arts de la Haute-Saône, p. 56, 1907. Jurassic, France.

*Nuculoma* was proposed by Cossmann (1907, p. 56) as follows :  
 « Cependant, l'aspect lithodomiforme de *N. Castor* est particulièrement remarquable et ses stries régulières la caractérisent encore davantage. Il y a loin de cette forme secondaire aux Nucules typiques des terrains tertiaires, et il est probable que, surtout à cause de la disposition du cuilleron, et de son crochet enroulé, cette coquille pourra être prise comme génotype d'une Section distincte que je proposerais de dénommer *Nuculoma*. »

The following is a free translation of a part of Cossmann's (1924) discussion of this « section » :

« Always lithodomiform, they belong to the section *Nuculoma* — that I proposed in 1907 — characterized by its enrolled and terminal umbones as well as by its narrow chondrophore, which resembles a small comma; the serial teeth of the posterior side are more crowded near this chondrophore, whereas the most separated ones are very thick; there are only fifteen teeth up to the chondrophore, but the series continues above the chondrophore with six or seven punctiform teeth up to under the umbones, so that the numbers that I have indicated successively in my diagnoses (and which seem to be contradictory) are found to be exact according to the point where one stops counting. These four large anterior teeth are lodged obliquely under those that are punctiform; the locking of the valves is therefore very complicated. »

The types of the species *castor* are in the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle (N° 3349) in Paris. I have studied these and 16 specimens from the collection of the Institut de Géologie Appliquée of the Université de Nancy, supplied through the courtesy of M. Fallot. Of these, two are here figured. For a discussion and figures of d'Orbigny's types, consult the monograph by Cottreau (1925).

The description of the species here presented is based upon an examination of the types from Montsec (Meuse) and specimens from the localities mentioned in the accompanying Table III, page 28.

Shell roughly trigonal in profile; anterior extremity bluntly rounded; posterior extremity truncate; ventral margin gently convex; valves tightly closed, not gaping. Umbones rise high above dorsal margin; beaks strongly inturned. Escutcheon area depressed; degree of pouting in the area variable. No radial ribs, but strong, evenly-spaced concentric ribs. Inner ventral margin smooth. The left valve shows a longer (anterior) row of teeth gently arched, with  $20 \pm$  teeth; the shorter (posterior) row with  $4 \pm$  teeth; adductor muscle scars subequal; chondrophore narrow, oblique. Measurements of the specimens are given in Table III.

That this species should be differentiated from *Nucula*, *sensu stricto*, is, in my opinion, evident. The clearly developed concentric ribs, character and position of the umbones, lack of radial sculpture, and the peculiar hinge characters are distinctive fea-

TABLE III

Dimensions of Jurassic (lower Callovian) specimens of *Nucula castor* d'Orbigny from France. The fossils are in the collection of the Institut de Géologie Appliquée de l'Université de Nancy and in the Muséum National d'Histoire Naturelle, Paris.

Repository	Locality in France	Specimen number	Length in mm.	Height in mm.	Thickness (2 valves) in mm.	Umbonal angle in degrees	Ratio of height to length in percent.	
Muséum National Paris	Montsec	Holotype	14.2	10.3	8.2	84	72	
		Paratype	11.4	8.4	7.6	90	74	
	"	Paratype	12.6	9.5	8.0	85	75	
	"	Paratype	12.7	9.2	7.5	—	74	
	"	Paratype	13.4	10.2	9.1	—	77	
	"	Paratype	13.5	9.2	8.2	—	68	
	"	Paratype	13.7	10.5	8.4	—	78	
	"	Paratype	14.6	9.7	—	—	66	
	"	Paratype	14.8	10.1	9.5	—	69	
Université de Nancy	Montsec	1	12.3	9.0	7.8	95	73	
		2	15.4	10.6	8.0	—	70	
		3	16.3	11.3	—	—	70	
	Marault	1	10.8	9.2	—	80	85	
		2	15.7	12.0	—	—	77	
		3	18.0	12.4	—	—	69	
	Brainville	1	18.8	12.8	11.0	87	68	
		2	18.6	12.6	10.9	116	68	
	Puxe	1	20.0	12.8	11.9	112	64	
		2	22.0	15.4	—	—	70	
		3	22.0	15.4	—	—	70	
	Poix	1	1	13.7	10.5	—	—	77
			2	14.0	10.4	—	—	74
		3	1	14.5	9.6	8.0	108	66
			2	14.6	9.9	—	—	68
3			14.7	11.7	—	—	79	

tures, and I believe there is more to be gained by recognizing *Nuculoma* as a genus than by leaving it a section of *Nucula*. For some of the occurrences of *N. castor*, consult the monograph by Corroy (1932).

(6) NUCULOPSIS Girty, 1911. (Type : *Nucula ventricosa* Hall 1858, not of Hinds, 1843.)

Pl. II, fig. 19, Pl. IV, figs. 2, 2a, 2b.

Girty, Ann. N. Y. Acad. Sci., vol. 21, p. 133, 1911. Late Paleozoic, America (29).

The photographs of *Nucula ventricosa* Hall (Geol. Survey Iowa, vol. 1, part II, Paleontology, p. 716, pl. 29, figs. 4, 5a, 5b, 1858) are apparently schematic. His fig. 4 is of the interior and shows a shell without a chondrophore, which, I feel sure, is an error. The illustrations show that the beaks are opisthogyrate.

*Nuculopsis* was proposed as a new genus for the reasons that (1) « the dentition consists of a continuous series of taxodont denticles not apparently interrupted by a chondrophore »; (2) Girty supposed that the short side of the shell is anterior; and (3) because he believed that there was an external ligament.

An examination of a number of Recent specimens of *Nucula* that have lunular areas like that of the type of *Nuculopsis* proves to my satisfaction that the ligament of the Paleozoic species was internal. The reason presented by Chao (1927) for distinguishing *Nuculopsis* from *Anthroconeilo* is therefore not valid, though they are easily separated by other criteria.

Hypotype N° 5646 (Stanford Univ. Paleo. Type Coll., California) is from the late Paleozoic (Pennsylvanian) of the state of Iowa, U. S. A. The specimen is figured here as fig. 19, Pl. II. That a *chondrophore* is present cannot be doubted.

I am convinced that one of Girty's (30) figures (his fig. 6) of the hinge is inexact and that the other (fig. 7) is incomplete. In view of the fact that *Nucula ventricosa* Hall agrees morphologically with Recent species of known orientation, there is no reason for believing that the short side of the shell is anterior

(29) Dr. James S. Williams, of the United States Geological Survey, supplied the following information (letter dated February 6, 1934): The catalog of types of the American Museum of Natural History shows that this species was described from near Rush Creek, Indiana. (This needs verification. H. G. S.)

(30) GIRTY, G. H., (1915), U. S. Geol. Survey Bull. N° 544, pl. XV, figs. 6, 7, 1915.

in the case of *Nuculopsis*. Thus, the erection of the new genus when based upon such imperfect observations and assumptions was a gamble. The name, however, has value, (31) since it is the earliest one to be applied to Paleozoic nuculids with a smooth ventral margin, and, as far as I can tell, without definite concentric ribs, as in *Nuculoma*.

*Nucula ventricosa* Hall, 1858, is a homonym of *Nucula ventricosa* Hinds, 1843 (Proc. Zool. Soc., XI, p. 100). I propose, therefore, the following nomenclatural change :

*Nuculopsis girtyi* Schenck, new name for *Nucula ventricosa* Hall, 1858, not of Hinds, 1843, nor of Pchelintsev, 1927.

The stratigraphic distribution of *Nuculopsis girtyi* Schenck in the States of Kansas, Missouri, Oklahoma, and Texas is given by Morgan (1924) as « *Nuculopsis ventricosa* (Hall) ». The areal extent and stratigraphic position of the Graham formation are presented by Plummer and Moore (1922). That this formation is « approximately equivalent in age to the Kansas City formation of the Kansas section » is a view expressed by Moore and Plummer (1922). No matter how finely these late Paleozoic (Pennsylvanian) formations may be subdivided, it is unlikely that they are as old as the Dinantian of the European sequence. *Nucula gibbosa* Fleming, 1828, figured by Hind (1897, pl. 14, figs. 4-15), from the « Carboniferous » of England probably belongs to *Nuculopsis*.

(7) NUCULOIDEA Williams and Breger, 1916. (Type: « *Cucullea* » *opima* Hall, 1843.)

Williams and Breger, U. S. Geol. Survey Prof. Paper 89, p. 173, 1916. Lower Devonian, North America.

Williams and Breger proposed *Nuculoidea* as a subgenus of *Nucula* for Paleozoic species having nondenticulate ventral margins. The authors state that :

« The distinguishing marks of *Nuculoidea* are a distinct cartilage pit, as in *Ctenodonta albertina* Ulrich, of the Upper Ordovician, and a nonpectinated ventral margin, which differentiates them from the true *Nuculas* of the Paleozoic. The species *Nucula opima* Hall = *N. randalli* Hall and authors....., is taken as the type of the group. The persistent absence of the denticulate ventral margin in the early and frequently large *Nuculas* and its persistent development in the Recent *Nuculas* furnish a ready

(31) My original opinion that *Nuculopsis* Girty deserves no recognition is thus changed.

TABLE IV

Dimensions of specimens of *Nuculopsis girtyi* Schenck, n. n., from the Upper « Carboniferous » of the United States. The fossils are in the paleontological collection of Stanford University, California, of the British Museum (Natural History), and in the Musée royal d'Histoire naturelle de Belgique.

Locality and formation	Specimen Number	Length in mm.	Height in mm.	Thickness (2 valves)	Ratio of height to length in percent	Ratio of thickness to height in percent
Graham formation, state of Texas.	1	13.0	8.6	8.8	66	102
	2	13.1	8.5	—	64	—
	3	13.2	9.0	8.6	68	96
	4	13.3	9.4	9.2	71	98
	5	13.7	9.4	9.2	68	98
	6	13.7	10.0	9.7	75	97
	7	14.1	10.1	10.3	72	102
	8	14.2	9.5	7.8	67	82
	9	14.6	10.3	10.6	70	103
	10	15.8	10.7	10.5	68	99
Wewoka formation, near Bixby, Oklahoma.	1	17.0	11.3	10.8	67	96
	2	17.4	11.4	11.3	66	99
Boggy formation, Oklahoma.	1	9.0	5.8	5.0	64	86
	2	13.7	9.1	8.2	66	90
	3	14.3	9.2	8.4	64	91
	4	14.5	10.0	8.0	69	80

and easy distinction. The nondenticulate and earlier form is here designated *Nuculoidea*, from its resemblances to *Nucula*. Some of the Triassic and Jurassic *Nuculae* may possibly belong in the same group. »

The following were proposed as subdivisions of *Nuculoidea* (p. 174) :

« Group (32) of *Nuculoidea opima* (Hall). Umbones twisted to a vertical position or actually faintly prosogyrate; the anterior end usually longer and semilunulate under the beaks.

« Group of *Nuculoidea aquisgranensis* (Beuschen). Umbones opisthogyrate; anterior end convexly rounded and usually larger; posterior outline semi-lunuliferous. This group includes shells having the common cordate, ovate, or veneriform *Nucula* expression.

« Group of *Nuculoidea* (?) *notica* (Hall). Umbones opisthogyrate; posterior margin truncate, nearly vertical; anterior margin also nearly straight, producing a characteristic vertically triangular outline. »

The photographs of « *Cucullea* » *opima* Hall (Geology of New York, part IV, page 197, Text figure 78 (3) and plate 40, fig. 3, 1843) are of an inflated fossil, trigonal in profile. The exterior only is illustrated, and it is therefore impossible to determine its proper family. The figures presented by Williams and Breger are also exterior views, but they expressly state « hinge features unknown » for the species they describe. Not having had the opportunity to examine specimens, I can offer no useful remarks concerning the validity of the taxonomic unit *Nuculoidea* (\*).

(32) « Group » is another taxonomic unit that needs definition. As here used, it is a *section*.

(\*) After this paper went to press, I examined through the courtesy of Dr. P. Dienst in Berlin, the types of the following lower Devonian species from the Rhineland: *circularis*, *cornuta*, *curvata*, *decipiens*, *decipiens aequalis*, *drevermanni fornicata*, *grandaeva*, *lieseri*, *lieseri similis*, *lodanensis*, *macrorhyncha*, *primaeva*, *trigona* and *tumida*. These specimens (in the coll. of the Preussische Geologische Landesanstalt in Berlin) are all poorly preserved. Although some show concentric ribs, none has radial ribbing. On none can be seen the details of the hinge and muscle scars, but on the types of *Nucula circularis* Spriesterbach and *N. lieseri* Spriesterbach there are traces of a chondrophore. One should note the muscle scars shown on the dorsal margin of *fornicata*, figured by Beushausen (1895, t. 4, fig. 9). Some of the fossils from the Upper Coblenzian at Daleiden show another small pair immediately below the beaks; these are in addition to the adductor muscle scars. Professor Quenstedt called my

(8) « NUCULOPSIS » Woodring 1925. (Type : *Nucula hilli* Woodring.)

« *Nuculopsis* » Woodring, Carnegie Inst. Wash. Publ. 366, 1925, p. 15, pl. 1, fig. 2, 3. Miocene, Jamaica.

The following is Woodring's (op. cit., p. 14) diagnosis of the section « *Nuculopsis* » :

« Shell medium-sized, subelliptical, inequilateral; sculpture consisting of a strong concentric rugae; chondrophore long, narrow, oblique, deeply excavated; anterior series of teeth more than twice as long as posterior series; anterior teeth reduced in size toward chondrophore, posterior teeth not reduced; interior of valve subnacreous; lower inner margin of valve smooth. »

He remarked further that :

« The outline and sculpture of *Nuculopsis* and *Nucula* s. s. are strikingly different. The chondrophore is more detached from the anterior series of teeth than in *Nucula* s. s., and the anterior teeth above the chondrophore are much smaller... »

The category named by Woodring in 1925 probably should be recognized. In a letter to me dated April 9, 1934, Dr. Woodring stated that he prefers to let me propose a new name. I do not care to do this, however, until I have studied representatives of the type species.

(9) LEIONUCULA Quenstedt, 1930. (Type : *Nucula albensis* d'Orbigny.)

Pl. III, figs. 5, 5a, 5b.

Quenstedt, Geol. u. Palaon. Abh. n. f. Bd. 18 (der ganzen Reihe Bd. 22), Heft 1, p. 112, 1930. Cretaceous, Europe.

This name was proposed as a « section » of *Nucula*, *sensu stricto*, for those forms which are characterized by (translated freely) the « chondrophore tooth generally present, the connecting piece of the hinge plate seldom lacking; shell edge smooth, and therefore the boundary between the shell's upper surface and the nacreous layer is smooth ». Quenstedt assumed the time range to be from Cretaceous to Recent.

attention to the middle Devonian fossil he discussed (1930, p. 64) and an examination of the specimen verifies the existence of a chondrophore. The significance of these remarks is that I do not doubt that the family Nuculidae has Devonian representatives, but I insist that the Paleozoic specimens that I have studied are not closely related to the type species of *Nucula*, s. s.

The following is the original description of the type species, *Nucula albensis* (33):

« *N. testâ ovato-compressâ, laevigatâ, inaequilaterâ, latere anali elongato; latere buccali brevi, subexcavato; lunulâ subnullâ; labro laevigato.*

« *Dimensions.* Longueur, 13 millim. — Par rapport à la longueur: largeur, 78/100; épaisseur, 42/100; longueur du côté anal., 79/100. — Angle apical, 105°.

« *Localité.* Elle caractérise le gault ou terrain albien du bassin parisien. Elle a été recueillie à Dienville, à Gérodot et à Ervy (Aube), par MM. de Vibraye, Dupin et par moi; aux Côtes-Noires, près de Saint-Dizier (Haute-Marne), par moi. Elle y est rare. »

Besides the type specimens, I have seen four imperfect specimens of this seemingly rare species. One is from the Cretaceous of Revigny, France, 16.6 mm. long, 13.7 mm. high, and 9 mm. thick; umbonal angle 101°, and is the specimen shown in fig. 5a, Pl. III.

The type specimens of *albensis* are N° 5984 in the Muséum National d'Histoire Naturelle in Paris, from Dienville, France. They are quadrangular ovate; dorsal margin gently convex, sloping abruptly to form a bluntly pointed anterior extremity; ventral margin convex; posterior extremity truncate; shell compressed. On the dorsal part of the shell is the low furrow illustrated by d'Orbigny. The escutcheonal area is slightly depressed, owing to the fact that the valve-sides change abruptly at the posterior extremity of the disk, producing a ridge-like boundary of the escutcheonal area, and behind this low ridge is a shallow furrow running from the ventral margin to below the opisthogyrate beaks. Although there are concentric growth stages, the shell is without definite ribs. Interior not exposed. Dimensions are given in Table V, page 35. The specimens in Cossmann collection are from Moeslains (Maelin or Malain). All material examined is from the Albian stage of the Cretaceous (\*).

(33) ORBIGNY, A. d' (1844), Paléon, française, Terrains Crétacés, t. 3, 1844, p. 172-173, pl. 301, fig. 15-17.

(\*) After this paper went to press, Professor Quenstedt kindly placed at my disposal a left valve of *albensis* from the Cretaceous of Blackdown. The arched anterior row of teeth has about 25 teeth; the straight posterior series about 10. A chondrophore tooth is present; the chondrophore is oblique.

TABLE V

Dimensions of specimens of *Nucula albensis* d'Orbigny in the Muséum National d'Histoire Naturelle and in the Laboratoire de Géologie à la Sorbonne in Paris.

Specimen number	Length in mm.	Height in mm.	Thickness (2 valves) in mm.	Umbonal angle in degrees	Ratio of height to length in percent
Holotype	13.0	40.0	5.7	108	77
Paratype	9.7	7.6	4.5		79
Specimen N° 5984-C	18.0	14.2			79
Cossmann Collection 9567 a	12.5	9.4	5.6		76
9567 b	49.8	16.1	40.7		82

Having seen no hinge, I am unable to evaluate the systematic position of *Leionucula*. It may prove to be closely related to *Ennucula* Iredale.

10) PALAEONUCULA Quenstedt, 1930. (Type *Nucula hammeri* De France.)

Pl. II, fig. 20, Pl. IV, figs. 1, 1a, 1b.

Quenstedt, Geol. u. Palaeon. Abh. n. f. Bd. 18 (der ganzen Reihe Bd.22), Heft 1, p. 112, 1930. Jurassic, Europe.

The following is a free translation of Quenstedt's diagnosis of the « subgenus » *Palaeonucula* (supra cit., p. 112) :

« Beaks not at all or only moderately strongly opisthogyrate. Chondrophore wide, short, not curved, directed either straight dorso-ventrally or only gently inclined from behind anteriorly or from the anterior to the posterior, not at all or only slightly spoonshaped and projecting into the cavity of the shell. Behind the chondrophore, between it and the posterior part of the row of teeth, neither a « chondrophore tooth » nor a plain connecting piece (*Verbindungsstück*) of the hinge plate. The anterior part

of the row of teeth straight; ventral edge of the valve moderately strongly curved. Seldom present is an area bounded by a ridge followed by a furrow running posteriorly. Ventral margin always smooth » (\*).

I have examined a specimen of *Nucula hammeri* in the United States National Museum (Acq. N° 74728), from the Upper Lias (Whitbian) of Lincoln, England; four specimens in the collection of the University of Louvain from the Upper Lias of Gundershofen; and 17 specimens in the collection of the Ecole des Mines (Paris) from the same locality (\*\*). All have opisthogyrate (but not strongly incurved) beaks. Mr. L. R. Cox informed me (in a letter dated December 1, 1933) that the specimens of this species in the British Museum from the Upper Lias have beaks that are opisthogyrate. The topotypes display no distinct and sharp concentric ribs although there are traces of low concentric sculpture on the less worn shells. The hinge is exposed on three specimens and the taxodont dentition and chondrophore can be distinguished readily. A « chondrophore tooth » is present, and the chondrophore projects into the cavity of the shell as in *Nucula*, *sensu stricto*. The two large, subequal, adductor muscle scars are deeply impressed.

It is true that the beaks of « *Nucula* » *hammeri* to judge from the specimens studied, are less strongly opisthogyrate than in the case of *Nuculopsis girtyi* Schenck, otherwise the two species are similar. That *hammeri* is more closely related to *girtyi* than to the type species of *Nucula*, *sensu stricto*, is obvious, but exactly how to evaluate the systematic position of *Palaeonucula* is not so apparent. My opinion is that *Palaeonucula* Quenstedt is a subgenus of *Nuculopsis* Girty.

Besides the occurrences recorded above, « *Nucula* » *hammeri* is reported by Kayser (1924) from the lower Dogger, or lower « brown Jura » of Swabia; by Goldfuss (1837) from the lower Oolite and Oxfordian clay of Streitberg and Württemberg, Ger-

(\*) The specimens figured by W. Quenstedt (1930, t. II, fig. 9) is a right valve 17 mm. long, slightly broken under the beaks. Although the drawing is somewhat schematic, the straight anterior row of teeth is accurately figured. Professor Quenstedt agrees with me that at least one of the shells from the same locality as his hypotype has a chondrophore tooth.

(\*\*) There are 15 topotypes of *hammeri* in the Sammlung des Geol.-Paläont. Inst. u. Mus. d. Universität Berlin. The largest has a length of 31.5 mm., and in the Sammlung für Paläontologie und historische Geologie in Munich, Germany, are several specimens. For dimensions, consult Table VI, p. 38.

many, and by Corroy & Gérard (1934) from the Upper Toarcian of France. There are two specimens (up to 25 mm. long) of *hammeri* in the Institut de Géologie, University of Liège, from the « Brown Jura » of Boll (Württemberg), Germany. In Morocco, Daguin (1927) found the species in the Upper Lias (Toarcian) of El Hamraoua and Tselfat. Among the forms either conspecific with or related to *hammeri*, that will extend the range of *Palaeonucula*, are *Nucula haussmanni* Roemer, *N. misolensis* Jaworski (1915), *N. crassa* Münster, and *N. strigillata* Goldfuss (well figured by Bittner, 1895).

(11) ENNUCULA Iredale, 1931. (Type: *Nucula obliqua* Lamarck.)

Pl. III, figs. 4, 4a, 4b. Pl. IV, figs. 3, 3a, 3b.

Iredale, Rec. Australian Mus., vol. XVIII, n° 4, p. 202, 29 June, 1931. Recent, Australia.

Iredale's method of introducing this generic name is as follows :

« The type species of *Nucula* is *nucleus* Linné, a European species which differs appreciably from antipodean shells so classed, the latter having a notably oblique chondrophore, above which the teeth become much smaller, and the angle of opposition of the two rows of teeth is scarcely marked; further, the edge of the European shell is strongly denticulate, whereas ours is practically smooth. »

No type was designated, and several species are named in the original description. Singleton, however, in 1932 designated the type species given above.

I have examined the holotype of Lamarck's species. It is a right valve in the Muséum National d'Histoire Naturelle in Paris, and is from « Cap aux Huitres, Nouvelle Hollande ». For the original description consult Lamarck (1819, p. 59). The specimen is figured here on Pl. III, figs. 4a, 4b. The inner ventral margin is « practically smooth » as Iredale remarked. No radial or concentric ribs are on the exterior. The dorsal margin is gently arched, anterior extremity rounded; ventral margin convex; and posterior extremity truncate. The beaks are opisthogyrate. There are  $24 \pm$  teeth in the anterior (long) series and 7 in the posterior. Measurements of this shell, and of specimens of the species in the Dautzenberg collection from Port Phillip, Victoria, and three individuals in the British Museum are given in the accompanying Table VII, page 39.

TABLE VI

Dimensions of *Nucula hammeri* De France from the upper Lias (Jurassic) of Gundershofen, Alsace. The specimens are in the paleontological collection at the University of Louvain, Belgium, at the Ecole des Mines, Paris, France, and in Munich, Germany.

Collection	Specimen number	Length in mm.	Height in mm.	Thickness (2 valves)	Umbonal angle in degrees	Ratio of height to length in percent.	Ratio of thickness to height in percent.
University of Louvain	1	27.0	18.0	16.2	100	67	90
	2	28.0	18.5	16.0	108	66	86
	3	29.4	16.5	15.3	115	56	93
	4	31.5	18.3	16.8	113	58	92
Ecole des Mines, Paris	1	19.3	12.5	—	—	66	—
	2	20.8	13.3	—	—	64	—
	3	25.5	15.8	—	—	61	—
	4	28.7	16.0	—	—	56	—
	5	29.4	18.0	—	—	61	—
Sammlung f. Paläont- und hist. Geolog. Munich.	1	12.0	8.5	6.6	106	71	78
	2	12.3	8.7	6.8	105	71	78
	3	12.4	7.8	6.3	101	64	80
	4	13.3	9.5	7.8	107	72	82
	5	18.5	12.4	10.5	110	67	83
	6	18.7	12.3	10.4	109	66	84
	7	21.0	13.7	12.3	108	66	89
	8	25.7	16.0	14.1	110	63	88
	9	27.2	18.2	16.4	114	67	90
	10	27.6	17.4	14.4	107	63	82

TABLE VII

Dimensions of specimens of *Nucula obliqua* Lamarck from Australia. The holotype is in the Muséum National d'Histoire Naturelle in Paris; the other specimens in the Dautzenberg collection, and in the British Museum.

Locality	Specimen	Length in mm.	Height in mm.	Thickness (2 valves) in mm.	Umbonal angle in degrees	Ratio of height to length in percent	Ratio of thickness to height in percent
Cap aux Huitres	Holotype	10.8	8.2	—	105	76	—
Port Philip	Dautzenberg 1	10.6	9.4	5.8	93	88	62
»	Dautzenberg 2	15.3	12.1	8.8	99	80	73
Arafura Sea	British Museum	27.6	20.0	—	109	73	—
Port Jackson	British Museum	19.0	14.3	—	106	75	—
»	British Museum	14.0	10.5	6.5	104	74	62

Descriptive terms for the muscle scars, other than the adductors, are given on page 21. These scars are illustrated in fig. 4, Plate III, but are not shown in the drawing of the holotype (fig. 4a, Pl. III).

Cotton (1930, p. 225) remarked that « apparently *N. obliqua* Lamarck does not occur in South Australia; specimens so diagnosed are much less ventricose and less solid, have smaller teeth, and a more acutely angled anterior margin. These should probably be named *N. subdilecta* Iredale. »

*Nucula obliqua* Münster (1841, p. 85), is a homonym of Lamarck's species and may need to be renamed, as is the case with three or four other forms called « *obliqua* ».

(12) BREVINUCULA Thiele, 1934. (Type by monotypy: *Nucula (Brevinucula) guineensis* Thiele.)

Pl. V, figs. 2, 2a, 2b, 2c.

Thiele, Handbuch der Systematischen Weichtierkunde, Dritter Teil, p. 786; Recent, Africa.

Proposed as a subgenus of *Nucula*, this unit is characterized as follows :

« Schale klein und verhältnismässig kräftig, kurz dreieckig, aussen glatt und glänzend, Schlossrand stark geknickt, der kleine Ligamentknorpel ragt nicht oder wenig nach innen vor und trennt die vordere von der hinteren Zahnreihe, hinten ist die Schale abgeflacht. »

Through the friendly cooperation of Professor Thiele, I have examined three individuals of the type species, and I present on Pl. V, figs. 2, 2a, 2b, 2c, drawings of two. The exteriors are smooth, polished, with faint concentric growth stages and without radial ribs. The ligament is internal and the interiors are nacreous. Other features are adequately treated in the original description of *Nucula guineensis* Thiele (1931, p. 194). Figure 2c, Pl. V, shows clearly the position of the two adductor muscle scars; the supplementary scars are faint. Thiele concluded, I judge from his description of the species, that the longest row of teeth is the anterior series. Although a dental pit lies on each side of the chondrophore, there are no teeth above it. The pallial line is simple and the inner ventral margin is smooth. The original description gives the length of the species as about 4 mm.; height, 4.3 mm., and thickness, 2 mm.

The types come from Station 71 (6° 18.7' S., 12° 2.1' E.,

44 meters). Dr. Thiele reports (personal communication dated March 13, 1934) that he has specimens from Station 56 (3° 10' N., 5° 28.5' E., 2278 m.) and Station 63 (2° N., 8° 4.3' E., 2492 m.). All three stations are in the Atlantic Ocean off the coast of west Africa.

Thiele aptly compared his specimens with *Nucula verrillii* Dall, a Recent species whose occurrences are given by Dall (1890, pp. 257-258) and whose possible relation to *Nucula dolabella* H. C. Lea from the Miocene of Virginia is suggested. To judge from the figure of the hinge of *verrillii* presented by Verrill and Bush (1898, pl. XCV, fig. 10), *guineensis* is congeneric if not conspecific with that species.

#### C. FORMS WITH DIVARICATE SCULPTURE.

(13) ACILA H. and A. Adams, 1848. (Type: *Nucula divaricata* Hinds.)

Adams, H. and A. Gen. Rec. Moll., vol. 2, p. 545, January 1858. Type designated by Stoliczka, 1871. Recent; Western Pacific Ocean.

A detailed treatment of *Acila* is to be published elsewhere, and reasons for considering this name to merit generic standing are there presented. Briefly, my reasoning is as follows :

No one will deny that *Acila* belongs to the family Nuculidae, nor is there any doubt that it is related to *Nucula*, *sensu stricto*. The critical question is whether divaricate sculpture has taxonomic value in this family. The geologic range of *Acila* (Cretaceous-Recent) proves that bifurcation is well-established in these mollusks, which are readily separated by other means from such genera of different families as have bifurcating ribs. Because some species of the family Lucinidae (or any other family) share a certain character with species of another family, one cannot conclude logically that such a morphologic feature has no taxonomic value in a given family.

The reasons for treating *Acila* as a genus are that its many species can be recognized with comparative ease; that the species have a definite distribution in time and a distinct phylogenetic development; and, finally, because the living forms are restricted to the Indo-Pacific.

*Acila*, *sensu stricto*, is typified by *Nucula divaricata* Hinds (Proc. Zool. Soc. London, Part II, 1843, p. 97; fig. in Zool. of the Voyage of H. M. S. Sulphur, vol. 2, 1843, pl. 18, fig. 4). *Nucula mirabilis* Adams and Reeve (Zool. Voy. Samrang, 1850,

p. 75, pl. 21, fig. 8) is a synonym of Hind's species. The time range of the subgenus is surely from early Miocene to Recent, and possibly from Oligocene. Recent species are restricted to the western Pacific and Indian Oceans, in contrast to the wider distribution of *Truncacila*. No *Acila* has been reported from depths in excess of 803 fathoms (34) and none is known to live in the intertidal zone. The majority of specimens comes from depths less than 500 fathoms.

The following are the described species that seem to be valid; omitted from the list are such forms as have some element of doubt connected with them.

Subgenus *Acila* H. and A. Adams.

*Acila (Acila) divaricata* (Hinds), 1843. (Synonym: *A. mirabilis* A. and R.)

*Acila (Acila) fultoni* (Smith), 1892.

*Acila (Acila) gettysburgensis* (Reagan), 1909.

*Acila (Acila) isthmica* (Brown and Pilsbry), 1911.

*Acila (Acila) semirostrata* (Grant and Gale), 1931.

*Acila (Acila) submirabilis* Makiyama, 1923.

(14) TRUNCACILA Schenck, 1931. (Type: *Nucula castrensis* Hinds).

Schenck, in Grant & Gale, Mem. San Diego Soc. Nat. Hist., vol. 1, p. 115, 3 November 1931. Recent, Eastern Pacific Ocean.

Originally proposed as a section of *Acila*, this name is now believed to be worthy of the rank of a subgenus. Reasons for this conclusion are expressed in another paper.

The following are the described species that seem to be valid; omitted from the list are such forms as have some element of doubt connected with them :

*Acila (Truncacila) bivirgata* (J. de C. Sowerby), 1836.

*Acila (Truncacila) blancoensis* Howe, 1922.

*Acila (Truncacila) castrensis* (Hinds), 1843.

*Acila (Truncacila) cobboldiae* (Sowerby), 1818.

*Acila (Truncacila) conradi* (Meek), 1864.

*Acila (Truncacila) dalli* (Arnold), 1908.

*Acila (Truncacila) decisa* (Conrad), 1855.

*Acila (Truncacila) demessa* Finlay, 1927.

*Acila (Truncacila) empirensis* Howe, 1922.

*Acila (Truncacila) granulata* (Smith), 1906.

(34) From « Albatross » station 5603, Gulf of Tomini, Celebes. Gorontalo pier N. 6° W., 5.7 m. (00° 24' 00" N., 123° 03' 45" E.).

*Acila (Truncacila) insignis* (Gould), 1861.

*Acila (Truncacila) muta* Clark, 1918.

*Acila (Truncacila) nehalemensis* G. D. Hanna, 1924.

*Acila (Truncacila) packardi* (Clark), 1925.

*Acila (Truncacila) paita* Olsson, 1931.

*Acila (Truncacila) shumardi* (Dall), 1909.

The time range of this subgenus is Cretaceous-Recent. The species *bivirgata* and *demessa* are surely Cretaceous, but *picturata* Yokoyama is Miocene. The holotype of the Japanese species is in the Paleontological Museum in Munich, and is an imperfectly preserved *Truncacila* about 18.5 (over) mm. long. The paratype has a marked area of obsolete radial ribbing. Modern representatives occur on both sides of the North Pacific Ocean and *Acila (Truncacila) jucunda* (Thiele) was described from off the coast of east Africa.

#### D. SYSTEMATIC POSITION UNCERTAIN.

(15) DEMINUCULA Iredale; 1931. (Type: *Nucula praetenta* Iredale, n. n. for *N. umbonata* Smith.)

Pl. V, figs. 3, 3a, 3b, 3c, 3d.

Iredale, Records Australian Mus., vol. XVIII, N° 4, p. 202, 29 June, 1931. Recent, Australia.

The following is the original description of this « genus »:

« I have noted that *Nucula praetenta* was not a *Pronucula* but was a *Nucula*, that was in the broad sense. Specimens from 800 fathoms, 35 miles east of Sydney, identical with Smith's species, have the surface radially rayed, the inner margin of the shell denticulate and the hinge line more angulate than it is in *Ennucula*, the teeth more distant, the chondrophore small and scarcely exceeded by any teeth. A new genus *Deminucula* is therefore introduced for it. »

The type species is *Nucula praetenta* Iredale (35), a new name for *Nucula umbonata* Smith (36), not Hall, 1885.

Smith remarked, in the original description of the species, that :

« This species is peculiar for its somewhat triangular form,

(35) IREDALE, T., (1924), Results from Roy Bell's Molluscan Collections : Proc. Linn. Soc. New South Wales for the year 1924, vol. XLIX, N° 197, Part 3, pp. 184-185.

(36) SMITH, E. A., (1891), Descriptions of new Species of Shells from the « Challenger » Expedition. Proc. Zool. Soc. London for the year 1891, p. 443, pl. 35, fig. 25.

prominent umbones, the fine radiating striae, and the denticulated inner margin of the valves. The lunule is not clearly defined, but the posterior dorsal area is narrow and bounded by a slight but distinct ridge. »

The accompanying figures (Pl. V, figs. 3, 3a, 3b, 3c, 3d.) are drawings of the original specimens, now in the British Museum (Natural History). Both of the valves figured have been examined under the microscope by Messrs. Tomlin and Vickery, and the latter informs me (letter dated 19 January, 1934) that they can find no vestige of a chondrophore. For this reason I doubt whether *Deminucula* should be assigned to the family Nuculidae.

(16) PROTONUCULA Cotton, 1930. (Type by original designation: *Protonucula verconis* Cotton.)

Cotton, Rec. South Australian Mus., vol. 4, N° 2, p. 223, fig. 1, 1930.

« This genus is proposed for *P. verconis* sp. nov., described below. While resembling *Pronucula* in shape, it differs in having the anterior and posterior teeth meeting below the umbo and forming one series, and no chondrophore. »

The type species is described as follows :

« Shell oval, thin, polished, concentrically lirate; umbos fairly prominent, the anterior and posterior teeth form an unbroken series; they attain the maximum size about the middle of the anterior set.

« Type, 120 miles west of Eucla, 300 fathoms. 3.5 mm. × 2.7 mm. In South Australian Museum (D. 10119).

» Loc. Cape Jaffa to 120 miles west of Eucla, 130 to 300 fathoms.

« The Cape Jaffa shells were those previously incorrectly listed as *Sarepta obolella* Tate. »

Through the courtesy of Mr. H. M. Hall, director of the South Australian Museum (Adelaide), I have had the opportunity to examine a paratype (a single valve 2.6 mm. long, 2 mm. high) of *Protonucula verconis* Cotton. Little need be added to the original description. The concentric ribs are evenly spaced and more pronounced than the protograph would lead one to believe. The interior is polished, and may be nacreous. There are two adductor muscle scars; no pallial sinus; and the position of the ligament is undetermined. That no chondrophore is present is certain. Six teeth constitute the short series, thirteen the long.

This species is probably more correctly allocated to *Tindaria*

Bellardi, 1875, and thus to a family other than the Nuculidae, than to a new genus. I hesitate in making a decision because I have not seen specimens of the type species of *Tindaria arata* Bellardi.

(17) *NUCULA TUBERCULATA* Gabb, 1873.

Gabb named the species *Nucula tuberculata* in 1873 (37). Dall (38) mentioned it as occurring in the Oligocene of Haiti; Pilsbry (39) described and figured a specimen as an *Acila*; Maury (40) stated that it occurs in the Dominican Miocene; and W. P. Woodring has informed me (41) that the species was not found by later collectors, and inasmuch as the Cercado and Gurabo formations have been rather thoroughly explored, Gabb probably collected it from the Baitoa formation (late lower Miocene).

This species should not be classed with *Acila*. This conclusion is based upon an examination of paratypes kindly supplied to me for study by Dr. Henry A. Pilsbry. The radial ribs, as shown by Pilsbry's figure, and by the specimens themselves, *do not bifurcate*. Although the tubercles give the appearance of divaricate sculpture, this is explained readily when the pustules are plotted at each growth stage. The result is a pseudo-divarication. Nevertheless, this sculpturing is distinctive and the erection of a new taxonomic unit might be worthwhile for specimens similar to Gabb's species.

#### Definition of the family Nuculidae.

The following is a tentative definition of the family Nuculidae based upon hard parts only :

Shells equivalve, up to 50 millimeters in length (\*); roughly

(37) GABB, W., (1873), Trans. Amer. Philos. Soc., n. s., vol. 15, p. 255, 1873.

(38) DALL, W., (1898), Trans. Wagner Free Inst. Sci., vol. 3, part 4, p. 573, 1898.

(39) PILSBRY, H. A., (1922), Proc. Acad. Nat. Sci. Phila, vol. 73, (1921), p. 401, pl. 38, fig. 5, Part II, 1922.

(40) MAURY, M., (1925), Bulls. Amer. Paleo., vol. 10, N° 42, p. 20, 1925.

(41) Written communication dated May 20, 1931.

(\*) The lengths of some of the largest nuculids that I have seen are as follows: (1) *Acila*, fig. 5, Plate I, 43 mm.; (2) *Nucula placentina*, 35 mm.; (3) *Nucula ovata*, 32 mm.; (4) *Nucula laevigata*,

trigonal or oval in outline; inequilateral; posterior side short, often truncate; anterior side longer than posterior, with anterior extremity rounded. Beaks posterior, opisthogyrate. A true lunule (behind the umbones) wanting; the pseudo-lunule, though sometimes lanceolate, is seldom well-defined. Below the beaks the escutcheon (occupying the position of the lunule of many pelecypods) is often heart-shaped. Prodissoconchs smooth. Sculpture, when present, consists of concentric ribs only, concentric ribs and radial ribs; bifurcating radial ribs, or modifications and combinations of these. Inner ventral margins smooth or denticulate (crenulate or pectinate). Dentition taxodont, with the longer row of teeth generally extending over the chondrophore (ligament-support). No external ligament, but an internal resilium. Pallial line entire. Shells with nacreous interiors (at least when the animal was alive); in many, if not all, species there is a differentiation of shell material, but no prismatic layer. Shells not gaping, and commonly each exhibits two sub-equal adductor muscle scars and additional muscle scars. The type genus is *Nucula* Lamarck, 1799.

The family may be subdivided tentatively as follows :

#### FAMILY NUCULIDAE D'ORBIGNY 1844.

Genus *Nucula* Lamarck, 1799.

Subgenus *Nucula*, *sensu stricto*.

Subgenus *Pectinucula* Quenstedt, 1930.

Subgenus *Ennucula* Iredale, 1931.

Subgenus *Linucula* Marwick, 1931.

Subgenus « *Nuculopsis* » Woodring, 1925.

Genus *Acila* H. and A. Adams, 1858.

Subgenus *Acila*, *sensu stricto*.

Subgenus *Truncacila* Schenck, *in* Grant & Gale, 1931.

Genus *Promucula* Hedley, 1902.

Genus *Nuculoma* Cossmann, 1907.

Genus *Nuculopsis* Girty, 1911.

Subgenus *Nuculopsis*, *sensu stricto*.

Subgenus *Palaeonucula* Quenstedt, 1930.

Genus *Brevinucula* Thiele, 1934.

31 mm.; (5) *Palaeonucula hammeri*, 33.6 mm.; (6) *Nucula compressa*, 29.3 mm.; (7) *Pectinucula pectinata*, 26.8 mm.; (8) *Ennucula obliqua*, 26.6 mm.; (9) *Nucula georgiana*, 30 mm.; (10) *Acila (Acila) divaricata* in the University of Berlin collection, 49 mm.

**Systematic Rank Unsettled.**

*Nuculoidea* Williams and Breger, 1916.

*Leionucula* Quenstedt, 1930.

**Systematic Position Uncertain.**

*Deminucula* Iredale, 1931.

*Protonucula* Cotton, 1930.

*Nucula tuberculata* Gabb, 1873.

**Size of the family Nuculidae.**

The size of the family may be defined, not as the total number of individuals in it, but as the amount of speciation within it. The determination of this amount of differentiation can be accomplished with any degree of accuracy only by examining all specimens, and to do this is an obvious impossibility. A means of making an estimate is to compile a list (see pages 48-55) of the specific names that have been used in conjunction with the generic name *Nucula*. There are 1044 names in the list I have prepared (42). The family Nuculidae does not comprise all of the species enumerated, as some would now be placed in genera belonging to other families. This loss of an appreciable number of names would not be balanced by those that have been applied to species incorrectly assigned to other genera, nor by such homonyms as might be valid species. But even though many of the names should be eliminated from the list, it is certain from their total number that the family, even as narrowly defined in this paper, is a large one.

(42) Many, but not all, of the names up to 1850 can be found from Sherborn's « Index Animalium », Part XXIX, June, 1932. This list carries a little more than one-third the number stated above.

LIST OF NAMES THAT HAVE BEEN USED WITH  
THE GENERIC NAME *NUCULA*.

This list has been compiled from Sherborn's « Index Animalium », the « Zoological Record », « Revue de Géologie », « Biological Abstracts », « Neues Jahrbuch f. Min., etc. » (Allgemeines Repertorium für das Decennium 1850-1859, Referate III, etc.), « Palaeontologisches Zentralblatt », « Index to the Nautilus... », the references cited in this paper, and from the synonymy under various species.

aalensis	antoniminensis	bellastriata
abbreviata	apicina	bellatula
abrupta	apiculata	bellistriata
accipiens	appenni	bellotii (? belloti)
acuminata	appenninica	belzonii
acuta	applanata	bengalensis
acutidens	aqualis	benoisti
acutula	aquisgranensis	bertrandi
adamsii	aracanensis	bettari
aegeensis (? = ageen- sis ? aegensis)	aralensis	beyrichi
aeolica	arata	beyrichia
aequalis	araucana	bicarinata
aequilatera	arcaeiformis	bicuspidata
aequilateralis	archiaciana (? = ar- chiacana)	bidorsata
africana	archiaci	bifida
agujana	arctica	biloba
ahrendi	arcuata	birostrata
alaskensis	arduennensis	bisulcata
albensis	argentea	bivirgata
albertina	arisaigensis	blancoensis
alpina	ascendens	blochmanni
amana	ashiyaensis	böckhi
amata	athabaskensis	boettjeri
ambrosia	atkinsoni	bohemica
amica	attenuata	boliuensis
amoena	aturensis	borsoni
ampla	australis	bouffeti
amygdalea	axiniformis	bowerbanki
amygdaloides		brevicultrata
analoga	baboensis	brevirostris
andina	baccata	brevitergum
anglica	barroisi	brongniarti
angulata	barrosi	bronni
angusta	bathybia	bruckmanni
anodontoides	beachportensis	bruxellensis
antipodum	beirensis	bullata
antiqua.	belcheri	burdigalica
antiquata	bella	bussacensis
		bushi

caecilia	clavata	cretacea
caeciliaeformis	claviformis	cretae
caelata	coarctata	crispa
cahuitensis	cobboldiae	crospyana
calcarensis	coelata	culebrensis
callicredemna	coërcita	cultelliformis
calloipe	coislinensis	cultrata
camchae	colliculus	cumingii (= cumingi)
cancellata	colombiana	cuneata
cantrainei	coloradoensis	cuneiformis
capillacea	commutata	cuneifrons
capillata	compar	curioni
capraeformis (? cap- saeformis)	complanata	curvata
capsiopsis	compressa	curvirostrum
carantana	compressinscula	cuspidata
cardara	compta (= compta)	cylindrica (? cylin- dricus)
cardiiformis	conca	cymella
cardioides	concentrica	cyrenoides
carinata	concinna	
carinifera	confluentina	dahmeri
carlottensis	confusa	daleidensis
carolinensis	conradi	dalli
carthusiae	consentanea	dalmasi
cascoensis	consobrina	darella
caseoensis	consors	dasa
castanea	contrastans	dautzenbergi
castor	convexa	decheni
castrensis	cooperi	decipiens
catalina	corbuliformis	decisa
catherina	corbuloides	declivis
caudata	cordata	decurtata
cecileana	cordiformis	decussata
cepha	cornueliana	deformis
certisinus	cornuta	defuniak
charlottensis	corticata	deglandi
chassyana	cossmanni	degrangei
chastelii	costae	dekayi
chauveli	costaeimbricatus	delaignei
chickasaensis	costata	delettrei
chipolana	costellata	delphinodonta
chrysocoma	costulata	delta
ciae	cottaldi	deltoides
cillebergensis	crassa	denudata
cingulata	crassicostata	depressa
ciplyensis	crassicula	deshayesiana
circe	crebrilineata	destefanii
circularis	crenifera	desvauxi
circuliformis	crenistriata	dewalquei
claibornensis	crenulata	diaphana
	crepida	

diffidens	excisa	gottschei
dilatatae	exigua	gouldi
dilecta	exilis	gracilis
dimidiata	eximia	grandaeva
dispar	exodonta	grangei
distincta	expansa	granulata
distinguenda	extensa	grandulosa
distorta	extrema	grayi
divaricata	eymari	gregaria
divaricosta	ezquerrae	greppini
diversoides		groenlandica
dixoni	faba	guadalupae
dolabella	fabula	guineensis
domina	falcata	gurgitis
donaciformis	falklandica	gutta
doncieuxi	felipponei (= ? felp- ponei)	haeringensis
dowlingi		haesendonckii
drevermanni	fernandinae	halli
dubia	feronia	hamiltonensis
duchastelii	fluviatilis	hammeri
dunedinensis	foersteri	hanleyi
duvaliana	formosa	hannibali
dynastes	fornicata	hanoverensis
	fraasi	hanseata
eborea	fragilis	hartvigiana
eburnea	fritschi	hausmanni
ehrlichi	fultoni	hawaiensis
eightsii		hawelkai
electra	gabbi	haydeni
elegans	gabbiana	headonensis
elegantula	gabrielis	hedleyi
elenensis	gahardana	hellica
elliptica	galeottiana	henoni
elongans	gallinacea	hercynica
elongata	gaultina	hermanni
emarginata	georgiana	hians
endora	gettysburgensis	hilli
equalis	gibba	hircina
equilateralis	gibbosa	hizenensis
erato	gibbosula	hokkaidoensis
ermani	gigantea	hopensacki
erosa	glaberrima	hornbyensis
erratica	glabra	houghtoni
erycinoides	glacialis	hualpensis
eschwegeii	glanstriticea	hubbardi
eudorae	glendonensis	humphreysiana
eufalensis	glenparkensis	ignota
eurita	globosa	illinoisensis
evansi	globularis	impatiens
excavata	goldfussi	

<i>impressa</i>	<i>kessleriana</i>	<i>lingulata</i>
<i>improcera</i>	<i>keuperina</i>	<i>linki</i>
<i>inaequalis</i>	<i>konincki</i>	<i>lirata</i>
<i>incerta</i>	<i>kowalewkensis</i>	<i>lissa</i>
<i>incisa</i>	<i>krachtae</i>	<i>lobata</i>
<i>incola</i>	<i>krotonis</i>	<i>lodanensis</i>
<i>incompta (=incompta)</i>	<i>krugeri</i>	<i>lola</i>
<i>incongruens</i>	<i>kutsingensis</i>	<i>longirostra (? longi-</i>
<i>inconspicua</i>		<i>rostris)</i>
<i>inconstans</i>	<i>lacryma = lachryma</i>	<i>lorioli</i>
<i>incrassata</i>	<i>lacrymaeformis</i>	<i>lucida</i>
<i>indefinita</i>	<i>lacunosa</i>	<i>lucinformis</i>
<i>indica</i>	<i>laekensis</i>	<i>lunularis</i>
<i>infausta</i>	<i>laevigata</i>	<i>lunulata</i>
<i>inflata</i>	<i>laevirostre (? laevi-</i>	<i>lunulicrenata</i>
<i>inflexa</i>	<i>rostris and laevi-</i>	<i>lyalli</i>
<i>insignis</i>	<i>rostrum</i>	<i>lyelliana</i>
<i>insularis</i>	<i>laevis</i>	<i>lyrata</i>
<i>intermedia</i>	<i>laigneli</i>	
<i>interrupta</i>	<i>lamellata</i>	<i>macandrei (? macen-</i>
<i>iowensis</i>	<i>lamirostris</i>	<i>drei)</i>
<i>iphigenia</i>	<i>lamplughi</i>	<i>machaeraeformis (=</i>
<i>irregularis</i>	<i>lanceolata</i>	<i>machaeriformis</i>
<i>isfjordica</i>	<i>largillierti</i>	<i>macrorhyncha</i>
<i>ishidoensis</i>	<i>larimerensis</i>	<i>maetraeformis</i>
<i>isthmica</i>	<i>lata</i>	<i>(? mactriformis)</i>
<i>italica</i>	<i>latens</i>	<i>maestri</i>
	<i>lateralis</i>	<i>maga</i>
<i>jaccardi</i>	<i>laternaria</i>	<i>magdalenensis</i>
<i>jacksoni</i>	<i>latissima</i>	<i>magna</i>
<i>japonica</i>	<i>layardii</i>	<i>magnifica</i>
<i>jaworskii</i>	<i>leia</i>	<i>major</i>
<i>jeffreysi</i>	<i>leiorhynchus</i>	<i>malabarica</i>
<i>jemtlandica</i>	<i>lelofuiensis</i>	<i>mancorensis</i>
<i>joannis</i>	<i>lenticula</i>	<i>mantelli</i>
<i>Joannis Wanneri</i>	<i>leufuensis</i>	<i>margaritacea</i>
<i>johanseni</i>	<i>levata</i>	<i>margaritana</i>
<i>jucunda</i>	<i>levatiformis</i>	<i>margaritifera</i>
<i>jugleri</i>	<i>levesquei</i>	<i>mariae</i>
<i>jurassii</i>	<i>librans</i>	<i>mariana</i>
	<i>liciata</i>	<i>marmorea</i>
<i>kaffraria</i>	<i>lieseri</i>	<i>matanii</i>
<i>kahlebergensis</i>	<i>limatula</i>	<i>mauricensis</i>
<i>kalimnae</i>	<i>limonensis</i>	<i>mauritanica</i>
<i>karatsuensis</i>	<i>limosa</i>	<i>mauritiana</i>
<i>karsteni</i>	<i>limulata</i>	<i>maxima</i>
<i>kasanensis</i>	<i>linearis</i>	<i>mayeri</i>
<i>kayseri</i>	<i>lineata</i>	<i>media</i>
<i>kazanensis</i>	<i>lineolata</i>	<i>mediavia</i>
<i>kerguelensis</i>	<i>lingualis</i>	<i>medinae</i>

medio-jurensis	nina	paboensis
menkei	niotica	packardi
mercerensis	nipponica (= nipo-	packeri
meridionalis	nica)	palaestina
meyeri	nitida	palmae
micans	nitidosa	palmaeformis
michalskii	nitidula	panamina
microconcentrica	njalindungensis	panda
microdonta	nodifera	papillifera
microstriata	nogalis	paraguanana
miliaris	nokonis	parallela
milnei	nordenskioldi	parilis
minima	notabilis	parisiensis
minor	notobenthalis	partialis
minuscula	nova	parunculus
minuta	nuclea	parva
minutissima	nucleata	parvula
mirabilis	nuclens	patagonica
mirifica	nucleus	paulula
misolensis	nuda	paytensis (= ? peyten-
mitralis	nudata	sis)
mixta	nux	pectinata
moenensis	nystana	pectuncularis
monmouthensis		pella
monroensis	obesa	pellucida
montagui	obliqua	pelmensis
montenotensis	obliquata	pencana
montensis	obliterata	penita
montpelierensis	oblonga	peraequalis
moorei	oblongoides	percrassa
morantensis	obolina	perdentata
morreni	obsoleta	peredita
mucronalis	obsoletastriata	peregrina
mucronata	obtusa	perequalis
multidentata	oelica	pergibbosa
münsteri	oligodonta	perplectens
murchisoni	omaliusi	perminima
musculosa	opima (= opina)	pernambucensis
myalis	opulenta	perobliqua
myroidea (= myoi-	orbicella	peronaica
dea)	ornata	perovata
	ornatissima	peruana
nana	otamaringaensis	perumbonata
narica	ouachensis	petriola (? = petri-
nasuta	ovalis	cola)
navicularis	ovallei	phalanta
neckeriana	ovata	phaseolina
neda	ovula (= ovulum)	philippiana
neglecta	ovum	phillipsi
nelsoni	ox	picturata
nicobarica	oxfordiana	pigafettae
nimbosa		piligera

pinguis	puelchana	ripae
pireti	puellata	ristorii
pisum	pueyrrydonensis	roemeri
placentina	pugetensis	rossiana
plana	pulchella	rosthorni
planata	pulcherrima	rostralis
planimarginata (? planomarginata)	pulchra	rostrata
platynotus	pullastriformis	rotunda
plicata	pulvellus	rotundata
plicatella	pumila	rozieri
podolica	punctata	ruatakiensis
polii	punica	rugifera
polita	puschi	rugosa
pollux	pusilla	rugulosa
polydonta	pusio	ryckholtiana
polyodonta	pygmaea	
ponderata		sacyi
poposiensis	quadrata	sagittata
poronaica	quirica	salamensis
porrecta	quiriquinae	sana
portlandica	quisquilia	sandbergeri
postangulata		sansibarensis
poststriata	rabaniana	sapotilla
potens	radiata	savatieri
potomacensis	radiatocostata	scalaris
praecox	ramondi	scapha
praecuta	randalli	schlotheimiana
praelonga	randolphensis	schomburgki
praelongata	raulinana	scitula
praemissa	recta	sculpturata
praetenta	rectangula	sectoralis
pragensis	rectangularis	securicula
predazzensis	recurva	securiformis
primaeva	redempta	sedanensis
primigenius	reflexa	sedgewickii (= sedge- wichi)
prisca	regnum	sejugata
proava	rembangensis	semen
producta	renauxiana	semicostata
productoides	rescuensis	semilunaris
profundorum	reticularis	semiornata
prolata	reticulata	semiramisensis
propinqua	retusa	semirostrata
protei	reussi	semistriata
protensa	rhamphodes	seranensis
protracta	rhombodea	sericea
proxima	rhomboides	serotina
prunicola	rhotomagensis	serrata
pseudomenkii	ribeiroi	shaleri
puelcha	richardsonii	shumardana
	rigaccii	

shumardi	subaequalis	sundaica
shumardiana	subaequilatera	superba
siberutensis	subaequilateralis	superstes
signata	subarqualis	suprastriata
silens	subcancellata	symetrica
siliqua	subcarinata	
similaris	subclaviformis	taeniolata
similis	subcompressa	taliabutica
simplex	subcordata	taliabuticum
simplicior	subcornuta	tampae
simsii	subcostata	tamulica
sinaria	subcuneata	tanneri
sindensis	subcylindrica	taphria
sinuatella	subdeltoidea	tatei (? tateiana)
sinuosa	subdilecta	telleri
slackiana	subelliptica	tellinaeformis
smithi	subglobosa	tellinella
snyderensis	subhammeri	tellinoides
solea	subimpressa	tellinula
solenoides	sublaevigata	tenella
solitaria (? solitaria)	sublaevis	tenera
somaliensis	sublata	tenerrima
sorianoi	submargaritacea	tenisoni
sowerbyi	subnasuta	tenui-arata
spathulata	subnuda	tenuilineata
speciosa	subobliqua	tenuirostris
speetonensis	suboblonga	tenuis
speluncaria	subobtusa	tenuisculpta
spheniopsis	subovalis	tenuistriata
sphenoides	subovata	tenuisulcata
stachei	subplana	terminalis
stahli	subradiata	tersior
stantoni	subrecurva	texata
stationis	subredempta	thanatiana
stella (? stilla)	subrotunda	thieryi
stillwaterensis	subrotundata	thraciaeformis
storrsi	subscritula	timorensis
stotteri	subserradensis	timotheana
strangei (? = stran- gii)	subspirata	tinguiriricana
striata	substriata	tokyoensis
striatissima	subtransversa	torresi
striatula	subtriangula	towsendi
strigillata (= strigi- lata)	subtrigona	traskana
striolata	subzelima	tremolate-striata
studerii	sulcata	triangula
suahelica	sulcellata	triangularis
subacuminata	sulcifera	triangularia
subacuta	sulcosa	tricesima
	sultana	trigona
	sumatrana	trigonale

trigonalis	uruguayensis	waipaoa
trigonella		waltoni
trigonula	variabilis	wanneri
triquetra	varicosa	washingtonensis
trivialis	ventricosa	weldensis
truncata	venusta	wenoensis
truncula	verillii	westendorpii
tswayensis	vestigia	wetherelli
tuberculata	vibrayeana	wewokana
tumescens	vicentina	whitfieldi
tumida	vicksburgensis	wymmensis (? wimmensis)
tumidula	victa	
turgida	vieta	yakatagensis
tutamoensis	vinti	yuani
ulysses	virletiana (? = virletina)	zahirae
umbonata	vitis	zelima
umbra	volgensis	zicteni (= zieteni)
undata	vox	zinkeiseni
undulata		zollikoferi
unilateralis		zululandensis
unioniformis	waikouraensis	

### What is a family ?

The word « family » is here employed as a technical taxonomic term to include a number of allied genera of organisms which have a certain assemblage of morphologic features in common, or occasionally it may include only one genus. The family is the unit most generally selected by theorists interested in drawing up phylogenetic charts. One frequently encounters statements in the literature to the effect that such and such a morphologic feature « does not possess family value ». Surely there is ample reason to ask investigators to consider the question : What is a family ?

The question is probably futile. Just as there are more than a hundred definitions of a species, so it is likely that there will be just as wide a range of opinion as regards a family. The evaluation of the taxonomic value of various homologous structures depends not only upon the experience and ability of the individual scientist but also upon his point of view, and it is therefore doubtful if even the most idealistic dreamer will admit that there can ever be agreement on the subject of the proper arrangement of organisms. Nevertheless there may be certain broad, vague, and perhaps not universally satisfactory grounds for general accord.

One basic principle is that a family should be monophyletic.

There is no phylogeny, however, of either fossil or Recent organisms that is not based in part upon assumptions. What may be a « natural » classification to one investigator is « artificial » to another. It is no more logical to claim that the gills of bivalve mollusks prove blood relationship and descent from a common ancestor than to claim that the hinge characters permit of sound deductions, for the same type of reasoning enters into each assertion. Moreover, the exponents of one method of classification rarely have a thorough knowledge of the other method to which they object. Schemes of phylogeny are subjective, not objective, whether they be as determined by zoologists or by paleontologists.

A *single* morphologic feature common to the constituent elements of a family is not sufficient. In the case of the nuculids, not only must all the species and genera have a chondrophore, but they must all have also taxodont dentition, et cetera.

This second principle — an assemblage of morphologic features — must govern a definition of a family. When a certain combination of homologous structures is taken as defining a family, a change in this combination demands the recognition of another family. Suppose, for example, that characters 1, 3, 4, 7 and 9 are shared by all the genera of Family A; another group of genera shares characters 1, 3, 5, 6, and 8. This would justify the recognition of Family B, despite the fact that characters 1 and 3 are present in both families. That certain characters have greater systematic value than others is, of course, obvious. In defining the family Nuculidae, the adductor muscle scars are not to be ranked with the chondrophore; the position of the ligament is more important than sculpture (43); and a

(43) Dr. Ed. Lamy, discussing classification with me in Paris (February 5, 1934) emphasized the points brought out in his paper on resemblances in the case of mollusks (Journ. Conchy., vol. LXXVI, pp. 142-181, 1932). He believes that sculpture has little taxonomic value because sculpture is so often an ecologic response, frequently due to convergence. I do not here question the principle of convergence, though I am of the opinion that many of the « facts » presented in its favor are not convincing, especially when single morphologic features are selected. As for the nuculids, I believe that there is a correlation between the mantle of the animal and the ribs of the shell and that, therefore, the sculpture in this family is not due to environmental influences. This opinion is supported by the fact that there are numerous species of *Acila* ranging in age from Cretaceous to Recent, and to-day living in various habitats.

nacreous shell means more than size. Not one of these characters can be taken as the sole criterion in establishing the boundaries of the family.

Also governing the definition of a family are utility and practicality. Taxonomists may draw lines where none exist in nature, and the result has been what many regard as an appalling multiplication of names. Yet in the spirit of justice one may enquire whether it is not actually scientifically unsound to have too few names just as it is to have too many. One science generally depends — in an uncritical fashion — upon the *words* produced by another science. The proof of the principle of the longevity of generalized types of organisms, for instance, is sometimes based upon *names*. Thus, in order to prove the antiquity of modern deep sea organisms scholars have cited, as a case in point, *Nucula* — a form that they suppose has endured from the early Paleozoic to the present. But what is meant by the word « *Nucula* »? As proof of the biogenetic « law » (44) one often reads the statement that other bivalves recapitulate the characters of *Nucula* and that the Nuculidae are the stock from which sprang all other pelecypods. It is easy to prove any theory, and thus to establish any law, when the terms are conveniently defined. It is simple to make the Nuculidae a radicle for a phylogeny when by definition it is a family comprising all bivalve mollusks with taxodont dentition, whether they have little else in common with the type species of *Nucula* or not.

The classification of genera into families will vary with the worker and with time. A grouping that may seem practical at one time for one investigator may be totally impractical for him and for others at a later date when more specimens are at hand and the technique of investigation has improved. It is a simple task to synchronize widely separated geologic formations and to show the wanderings of animals during past epochs when the species are broadly defined but it is next to impossible to do so when they are so minutely discriminated that only the original author can identify the species — if he knows the locality and

(44) Perhaps no theory adopted by paleontologists is so generally misunderstood and misapplied as the biogenetic « law », but it is beside the point to enlarge upon this theme here. Those who insist on referring to the « conclusive proof » offered by the ammonites may well refer to a review by Spath published recently in the *Palaeontologisches Zentralblatt* (Ab. B, Bd. 3, pp. 345-347, 1 November, 1933); also his « The evolution of the Cephalopoda » in *Biol. Rev.*, vol. VIII, N° 4, pp. 418-462, Cambridge, 1933.

age. A practical classification, it seems to me, is one that is based upon careful, non-provincial morphologic and nomenclatural studies, and one that other experienced taxonomists can understand and apply.

The definition of a family is unfortunately rendered difficult by many obstacles. To determine whether a « new » genus is based upon an immature representative of a previously named genus is an illustration of one difficulty. Sometimes it is necessary to examine a score or more Recent shells to find one individual that has the hinge well enough preserved so that one can gain an exact idea of the character and number of teeth. This difficulty is greatly magnified in the case of fossil forms. Does it not seem strange that while many writers have many times announced their conviction that the hinge is the most important part of the shell for the discrimination of the various systematic units yet those same writers have erected new genera and subgenera without having seen the hinge of the type species?

As a corollary of a definition of the family is the matter of nomenclature. For the Foraminifera Galloway (45) recently applied the « international » rules of zoological nomenclature to families and subfamilies as rigidly as to genera and species. Was Galloway correct in applying the law of priority to families? This question, I think, needs to be discussed by systematists in general before following in Galloway's footsteps. The most logical system (46) to follow in family nomenclature appears to be as follows: The family name is derived from the name of the type genus and changed with it. The type genus is the genus taken as type by the author who first separates the family (and not the oldest described genus included in the family). If two genera which have been made family types are brought together into the same family, the latter takes its name from the one first made a family type.

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(45) GALLOWAY, J. J., (1933), A Manual of Foraminifera, 483 pp., 1933. See especially pp. 2-3.

(46) According to L. R. Cox, 23 March, 1934, in reviewing the typescript of this paper.

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## ADDENDUM

- LAMY, Ed., 1926, *Sur le prétendu genre Diabolica Jousseau*. (Comptes rendus du Congrès des Sociétés savantes en 1925. Sciences, p. 1-3, 1 fig., Paris, 1926.)

EXPLANATION OF PLATE III.

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<p>FIGURE 1.</p>	
<p>Lateral aspect (X 2) of <i>Nucula (Pectinucula) pectinata</i> Sowerby, from the Gault (Cretaceous) of Folkestone, England. Hypotype N° 25, Cat. Types Invert. ter. Musée royal d'Histoire naturelle de Belgique. The specimen is 27 mm. long. Note the strong radial ribs. (Original drawing.) ... ..</p>	23
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## FIGURE 5a.

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FIGURE 5b.

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EXPLANATION OF PLATE IV.

FIGURE 1.

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## FIGURE 3b.

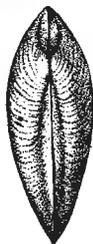
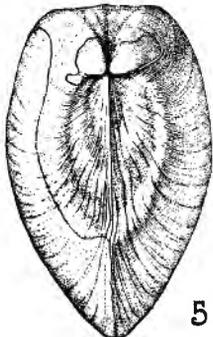
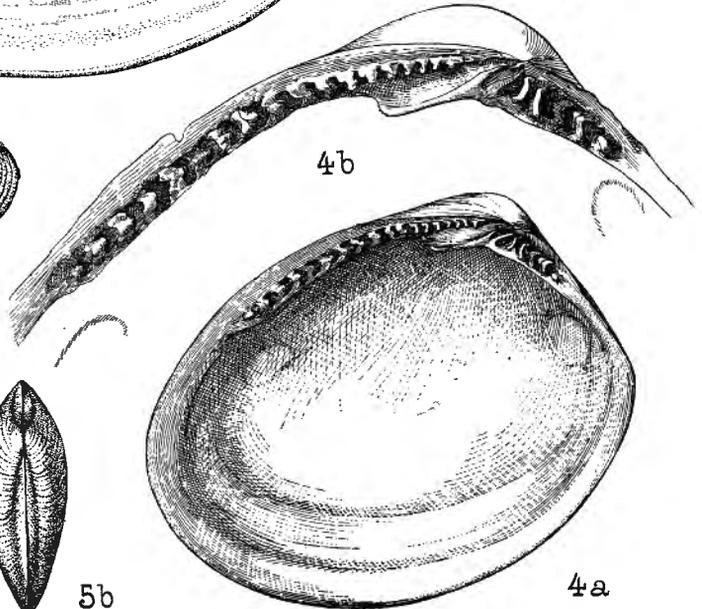
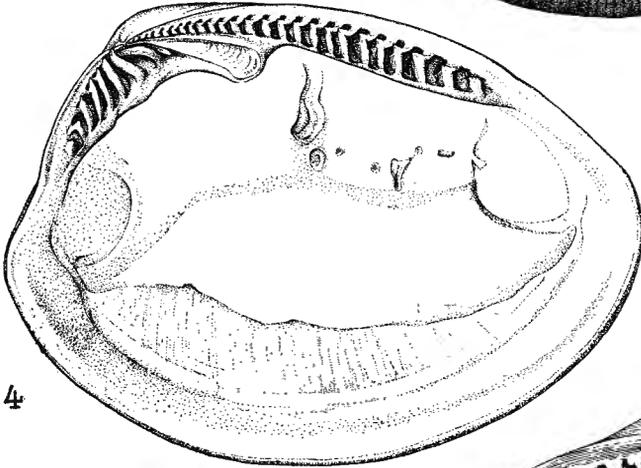
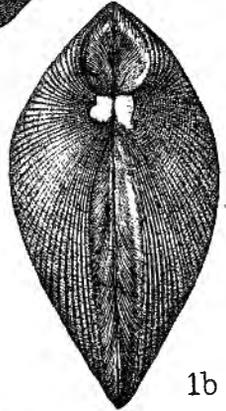
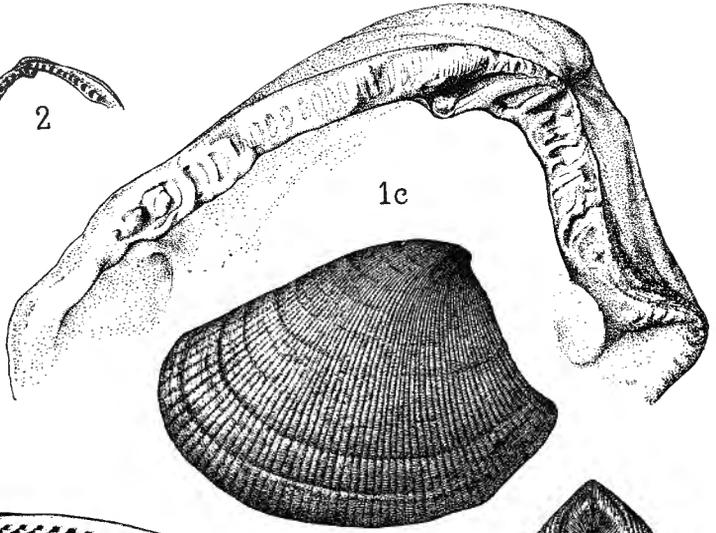
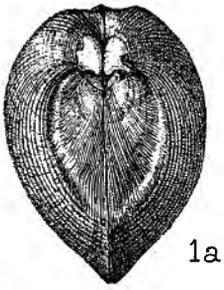
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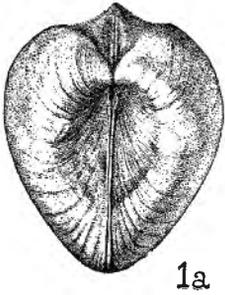
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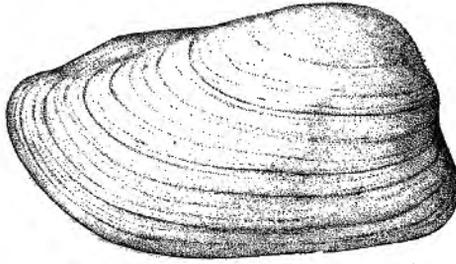
5a

5b

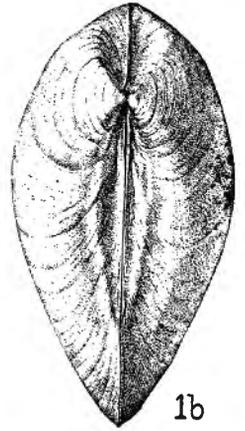
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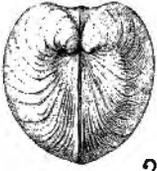
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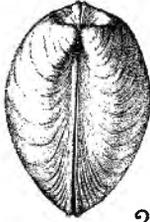
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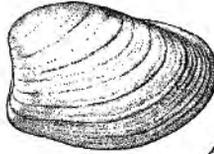
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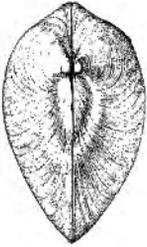
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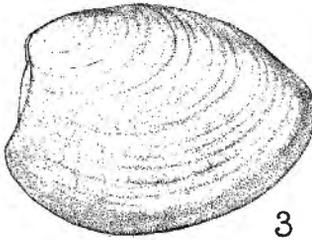
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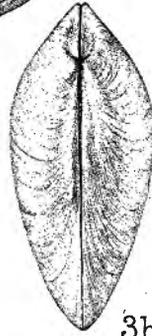
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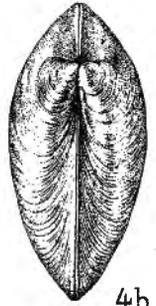
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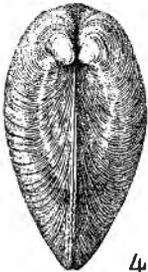
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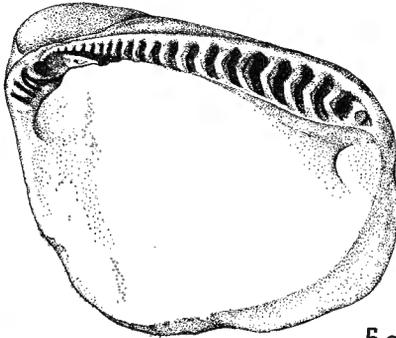
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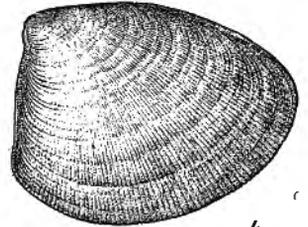
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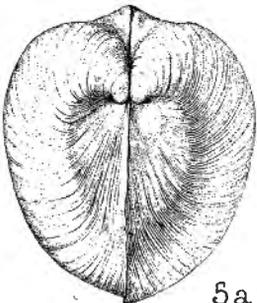
4a



5c



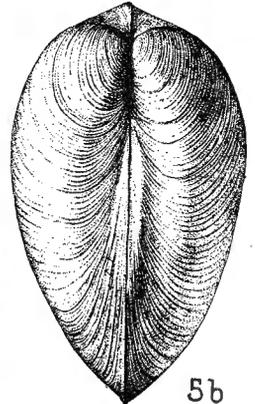
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5a

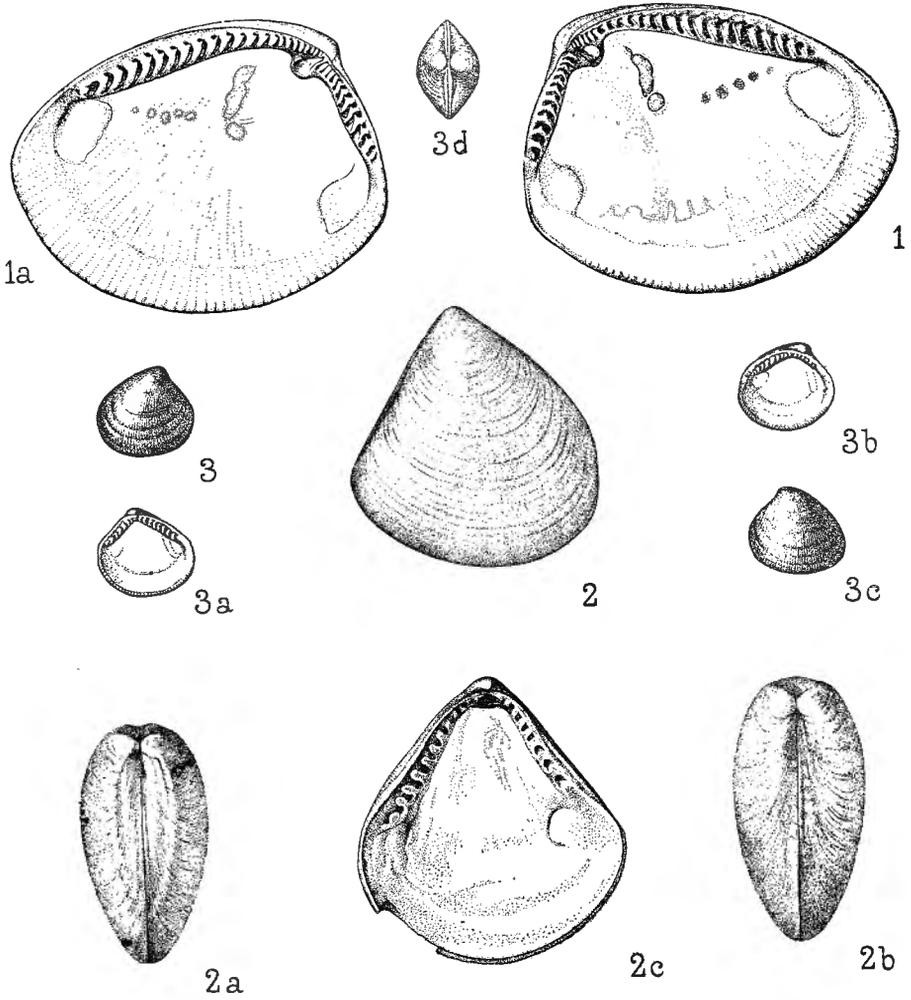


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PLATE V.



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