RECLASSIFICATION, STRUCTURE AND EVOLUTION OF THE FAMILY NUMMULITIDAE

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ABSTRACT.—On the basis of structure of the test, the Family Nummulitidae is reclassified into four subfamilies: subfamily Nummulitinae includes forms in which the test is involute and the spiral laminae are not in direct contact, like *Nummulites* Lamarck, *Operculinoides* Hanzawa, *Miscellanea* Pfender and *Sulcoperculina* Thalmann; subfamily Assilininae, subfam. nov., includes genera in which the test is either involute or evolute and the spiral laminae are in direct contact, like *Assilina* d'Orbigny and *Operculina* d'Orbigny; subfamily Heterostegininae includes genera which have either involute or evolute test with chamberlets, like *Heterostegina* d'Orbigny, *Spiroclypeus* Douvillé, *Cycloclypeus* Carpenter and *Heteroclypeus* Schubert; and subfamily Pellatispirinae, in which spiral laminae are not in direct contact but have chambers separated with canaliferous clear shell material, as *Pellatispira* Boussac and *Biplanispira* Umbgrove.

The detailed structure of the test in nummulitid genera is discussed and illustrated by stereograms. Genetic relationships and stratigraphic distribution of the family is given. The family is traced to the appearance of *Sulcoperculina* during the Upper Cretaceous times. Structurally weak *Miscellanea* is an offshoot from the *Sulcoperculina* stock early in the Paleocene times. The development of *Nummulites* is toward a structurally stronger test. *Operculinoides* is thought to have developed from ancestral *Sulcoperculina* stock. Development of *Operculina* from *Operculinoides* was accomplished by the spiral sheet coming in contact. Development of *Assilina* from *Sulcoperculina* was an attempt toward a direct contact of the spiral laminae. *Pellatispira* is derived from *Assilina* by addition of the clear shell material and *Biplanispira* from *Pellatispira* by the addition of chamberlets. The development of secondary chambers in the *Operculina* gave rise to *Heterostegina*. The acceleration of the *Heterostegina* test gave birth to *Cycloclypeus*. *Spiroclypeus* is considered to be an advance development of the *Heterostegina* by the addition of lateral chambers and stolons.

INTRODUCTION

BOTH ecologically and geologically the Nummulitidae are perhaps the most important larger foraminiferal family since

their fossil remains contributed greatly to the formation of limestones throughout the Tertiary period. World-wide significance of the family was recognized by pioneer geologists who classified *Nummulites*-bearing rocks as "nummulitique"—a term still in general use. The significance of nummulitids has been proved in zonation since most of the Tertiary faunizones were based on the diagnostic species of a certain genus within a rock unit or on the association of certain nummulitid genera or their species (Vredenburg, 1906; Cotter, 1914; Nuttall, 1926a, 1926b; Van der Vlerk and Umbgrove, 1927; Gravell and Hanna, 1938; Puri, 1953). Complex internal structure of the family has been recognized (Douvillé, 1919; Hofker, 1927; Tan Sin Hok, 1932; Hanzawa, 1937; Barker, 1939; Vaughan and Cole, 1941; Vaughan, 1945; Cole, 1947, 1953, 1956; Smout, 1954, 1955) and several attempts have been made to work out evolution of Nummulitidae (Chapman, 1902; Douvillé, 1919; Tan Sin Hok, 1932; Galloway, 1933; Glaessner, 1948; Cushman, 1948). But, in spite of the long history of the family and even a longer bibliography, there remains a universal disagreement on the nomenclature and taxonomy of its varied genera and species. There is virtually no agreement on the validity or invalidity of the various genera assigned to this family, or as to what constitutes a certain genus and how it differs from its related genera. Several generic and subgeneric names have been proposed, which

have been time and again suppressed and revived. Certain species have been assigned to as many as seven different genera by various authors and sometimes the same species has been referred to at least three different genera by the same author.

An excellent example of the lack of agreement on the nomenclature and taxonomy of a *single* species is a nummulitid originally called *Operculina bermudezi* D. K. Palmer (1934, pp. 238-240). Hanzawa (1937, p. 116) described it as a new genus and a new species, *Pellatispirella antillea* ; Barker (1939, p. 325) described it as a new species, *Camerina pellatispiroides* ; Vaughan and Cole (1941, pp. 33-35) placed part of this species under *Miscellanea antillea* and described part of it as a new species, *Miscellanea tobleri* (*op. cit.*, pp. 35-36); Caudri (1944, p. 22) placed it under *Nummulites* (*Nummulites*) and gave it a new name, *caraibensis*, because of *Nummulites antillea* Cushman ; Cole (1947, pl. 3, fig. 11) called it *Miscellanea bermudezi* and later (1953, p. 25) called it *Operculinoides bermudezi* and correctly placed all the above references in its synonymy. Another instance is ? *Camerina dickersoni* D. K. Palmer (1934, p. 243). Thalmann (1939, p. 330) made this species the type of a new subgenus, *Sulcoperculina*. Cole (1942, pp. 640, 641) placed part of it under *Miscellanea catenula* ; Applin and Jordan (1945, pp. 140, 141) described it as a new species, *Operculina* (*Sulcoperculina*) *cosdeni* ; Cole (1947, p. 14) placed it under *Miscellanea dickersoni* and later (1953, p. 7) stated that "no American species (of *Miscellanea*) are known." Yet another example is *Miscellanea nassauensis* Applin and Jordan (1945, p. 139). Cole (1947, pl. 4, figs. 1-2, 4-8, 12) placed it under *Nonion* and later (1953, p. 4) placed it under *Pellatispirella*.

Several other instances could be quoted since the literature is so full of them. These inconsistencies could be attributed in part to the complex structure of the nummulitids which is subject to a variety of interpretations and in part to the lack of our knowledge regarding the gradational dimorphic (or polymorphic) suites which are distinct as end members. Various stages in the life history of the same species from widely scattered areas have been given new names and assigned to one or another allied genus. Such a procedure has led to the disagreement as to what constitutes *Operculina*, *Operculinoides*, *Sulcoperculina*, *Pellatispirella*, *Miscellanea*, "*Camerina*", *Ranikothalia*, and even *Nonion*. All this confusion caused by a multitude of specific names and the lack of agreement as to the correct generic assignment of the various species has contributed to a decline in the use of nummulitids in biostratigraphic studies. It would appear that a clearer understanding of the internal structure of the various genera referred to this family will be necessary before any agreement on the taxonomy and nomenclature is reached. Such an agreement will not only help to clarify the evolution of the family but will also encourage the use of this important group of fossils.

A reclassification of the family is presented here. It sums up the evidence from several suites of Tertiary assemblages from Australia, East Indies, India, Pakistan, Egypt, Europe and North America. The problem is not simple since gradations between the allied genera exist in the megalospheric forms but the microspheric forms are distinct and are most helpful in tracing the evolutionary history of the nummulitid genera. In the past, too much importance has been given to such variable features as size, the number of whorls and chambers. Frequently these factors vary too considerably in the megalospheric form to be of any generic value. The importance of complex canal systems is far too much stressed. They may be useful in tracing the phylogeny but should not be taken to be generic characteristics since their function is unknown. A morphologic classification is artificial enough without the complications introduced by features that are not well understood and that have unknown functions.

Most of the Nummulitidae are strongly dimorphic. The dimorphism is reflected in the size of the tests, which in the microspheric forms frequently attain five to six times the diameter of the megalospheric forms. All gradations exist in the megalospheric individuals but the microspheric forms are fairly uniform in size. This change in size, and consequently the greater number of whorls and chambers, is largely responsible for the dual specific nomenclature. The micro- and megalospheric forms have been assigned to two different species even where polymorphic relationship is known to exist.

Such a procedure is highly confusing and it is here suggested that the law of priority be rigidly applied and all later names be rejected as synonyms (International Commission on Zoological Nomenclature, Art. 27).

ACKNOWLEDGMENTS

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CLASSIFICATION

Family NUMMULITIDAE

Type genus : NUMMULITES Lamarck, 1801, p. 101.

Test planispiral, lenticular or complanate; generally bilaterally symmetrical; finely perforate ; with or without chamberlets ; involute in early stages, later stages often evolute or even annular ; secondary skeleton of pillars, pustules and marginal cord present; with a septal, marginal and vertical canal system.

The following four subfamilies are recognized in the family :

Nummulitinae, Assilininae, Heterostegininae, and Pellatispirinae.

Subfamily NUMMULITINAE

Type genus : NUMMULITES Lamarck, 1801, p. 101.

Test involute, chambers numerous ; spiral laminae not in direct contact ; marginal cord present, but degenerated in some species.

The following genera are retained in the subfamily :

Genus *Nummulites* Lamarck, 1801 (synonyms *Nummulita* Fleming, 1828 ; *Nummulina* d'Orbigny, 1826 ; *Nummularia* Sowerby and Sowerby, 1826 ;*Nummulitella* Dorreen, 1948). Type species (by monotypy) : *Camerina laevigata* Bruguièri, 1792, pp. xvi, 395.

Genus *Operculinoides* Hanzawa, 1935 (synonyms *Operculinella* Yabe, 1918 ; *Ranikothalia* Caudri, 1944). Type species : *Operculina willcoxi* Heilprin, 1802, pp. 321-322, figs. 1, 2.

Genus *Miscellanea* Pfender, 1934. Type species : *Nummulites miscella* d'Archiac and Haime, 1853, p. 345, pl. 35, figs. 4, 4a-c.

Genus *Sulcoperculina* Thalmann, 1939 (as subgenus of *Operculina*), p. 330. Type species: *? Camerina dickersoni* D. K. Palmer, 1934, 11 p. 243, pl. 14, figs. 1, 2, 4, 6, 8 ; pl. 14, fig. 1, text figs. 4, 5.

Structurally both *Miscellanea* Pfender (1934) and *Pellatispirella* Hanzawa (1937) are similar. The aperture in *Pellatispirella* is a series of pores similar to those of *Elphidium*. This has led Cole (1947, 1953) to place correctly *Pellatispirella* with the nonionids. I have followed Cole in excluding *Pellatispirella* from Nummulitidae since the wall structure of *Pellatispirella* is very similar to that of *Elphidium* and it develops pectinations (see Hofker, 1927, p. 18) but *Miscellanea* has definite pillars in the walls. Cole (1956) has published further photographs showing the aperture and the wall structure of *Pellatispirella*.

Operculinella Yabe (1918), type species *Amphistegina cumingi* Carpenter (1860), represents one of the stages in the development of *Operculinoides*. The flare and the curvature in the final whorl is no greater than that developed in certain American species of *Operculinoides*. (Compare, for example, Vaughan and Cole, 1941, pl. 9, figs. 3, 4, with Hanzawa, 1936, pl. 16, fig. 2). Dr. Cole (personal communication, May 1954) is in agreement with this view.

Subfamily ASSILININAE, Subfam. nov.

Type genus : ASSILINA d'Orbigy, 1839, pp. vii-xlviii, 48.

Test involute or evolute, chambers numerous ; spiral laminae in direct contact.

The following genera are assigned to the subfamily :

Genus *Assilina* d'Orbigny, 1826 (as a subgenus of *Nummulina* d'Orbigny, 1826). Types species : (subsequent designation by d'Archiac and Haime, 1853) *Assilina depressa* d'Orbigny, 1850. Cushman (1927) designated *Assilina discoidalis* (d'Orbigny), originally described as *Nummulina* (*Assilina*)

discoidalis, as the type species. Glaessner (1948) and Bermudez (1952) have followed Cushman's choice. This designation is invalid because of prior designation by d'Archiac and Haime (*op. cit.*).

Genus *Operculina* d'Orbigny, 1826, p. 281. Type species : (subsequent designation by Cushman, 1914) *Lenticulites complanata* Defrance, 1822, p. 453.

The following genera are assigned to the subfamily :

Genus *Heterostegina* d'Orbigny, 1826, pp. 304-305. Type species : (subsequent designation by Parker, Jones and Brady, 1865) *Heterostegina depressa* d'Orbigny, 1826, p. 305, pl. 17, figs. 5-7, mod. no. 99.

Genus *Spiroclypeus* Douvillé, 1905, p. 458. Type species : *Spiroclypeus orbitoides* Douvillé, 1905, p. 460, pl. 14, figs. 1–6.

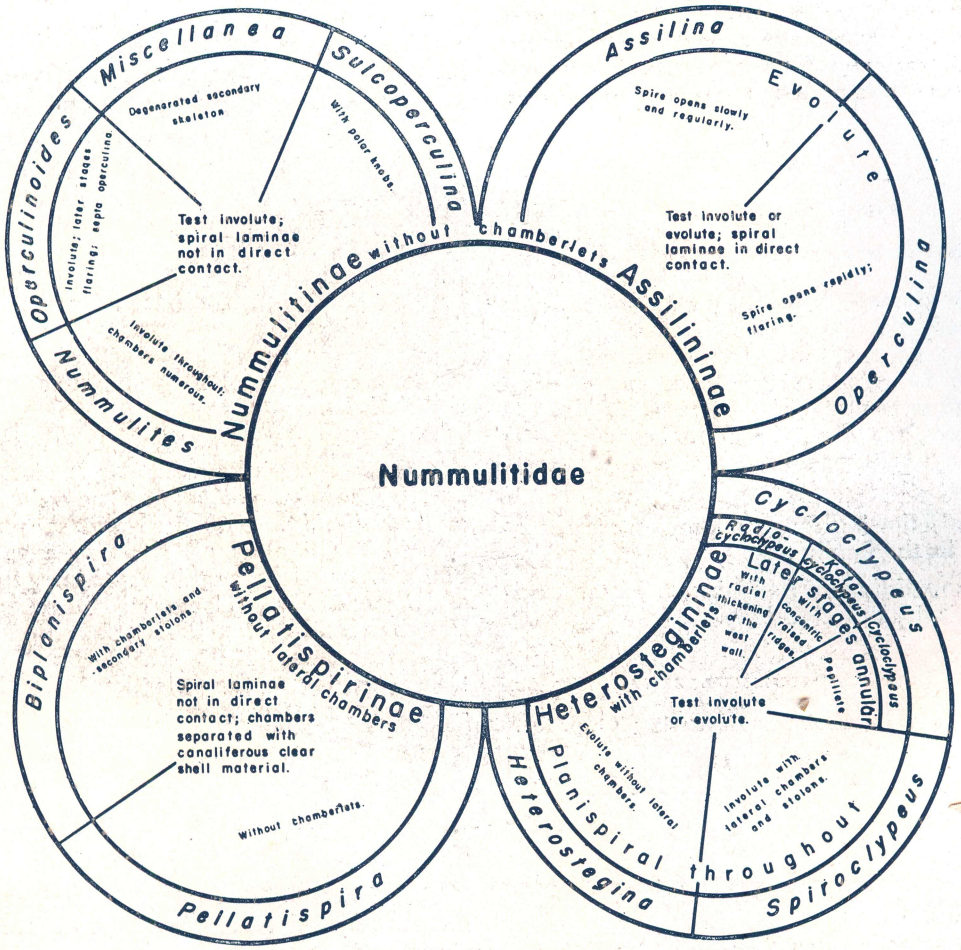


FIG. 1 Diagram showing the relationship of the Nummulitid genera, their classification and distinguishing characters.

Subfamily HETEROSTEGININAE

Type genus : HETEROSTEGINA d'Orbigny, 1826.

Test evolute or involute ; without lateral chambers ; with chamberlets.

Genus *Cycloclypeus* Carpenter, 1856, p 555, pl. 29, figs. 10–12; pl. 30, figs. 1, 3, 4; pl. 31, figs. 2–6, 8-10. Type species : (monotypic, Carter's specimens, originally called *Cycloclypeus* sp.) *Cycloclypeus carpenteri* H. B. Brady, 1881, pp. 66-67.

The genus *Heterosteginella* Silvestri (1937, p. 117) created for forms intermediate between *Operculinella* and *Spiroclypeus* is invalid according to International Commission on Zoological Nomenclature (Art. 25) since no species were named.

The genera *Heteroclypeus* Schubert, 1906, and *Paraspiroclypeus* Hanzawa, 1937, are not completely understood. *Paraspiroclypeus* should perhaps be abandoned as a synonym of *Operculinoides*. It shows some aborted chambers which led Hanzawa to believe that it represented an "advanced type of *Operculinoides*."

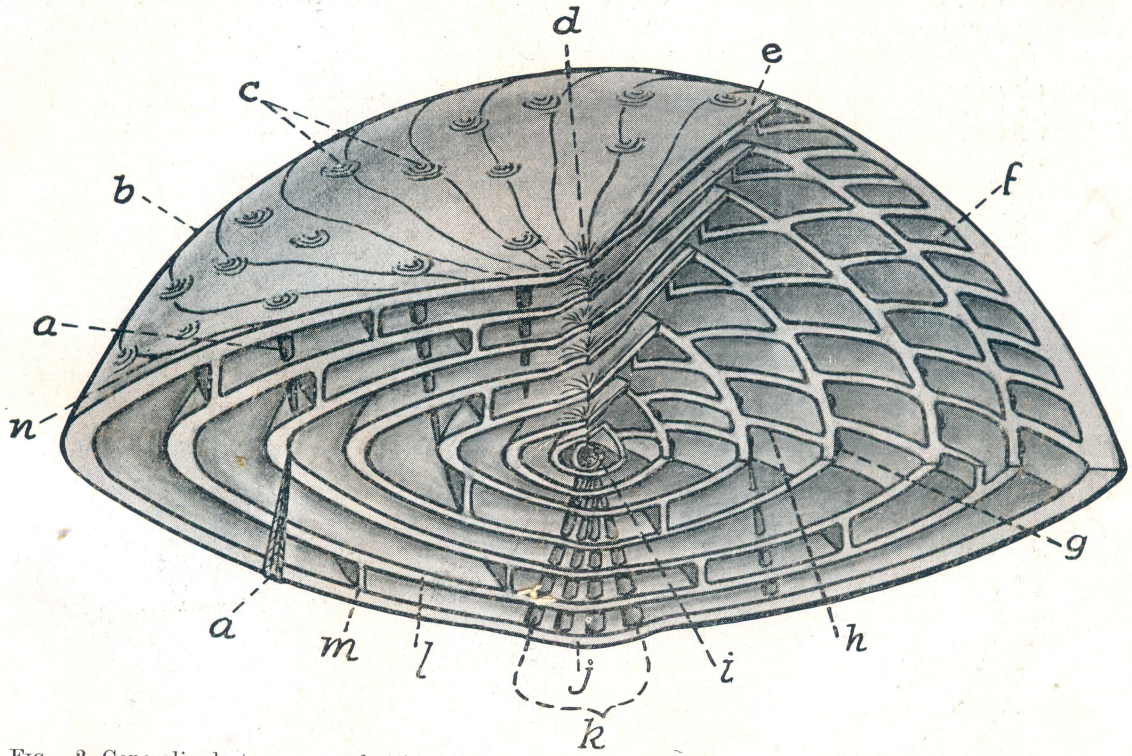


FIG. 2 Generalized stereogram showing structure of the test in *Nummulites* Lamarck (modified after Carpenter, de La Harpe and H. E. Wheeler). a, pillar or column; b, periphery; c, surface prolongation of the pillar or column commonly appears as a granule or papilus; d, medium pustule or boss; e, l, spiral lamina; f, chamber; g, interlocular orifice; h, septum; i, proloculum or initial chamber; j, marginal cord; k, medium pustule; m, septum; and n, septal filament.

Subfamily PELLATISPIRINAE

Type genus : PELLATISPIRA Boussac, 1906, p. 91.
Type species P. DOUVILLÉI Boussac, 1906, p. 91, pl. 2, figs. 10–13.

Test evolute ; spiral lamina not in direct contact; without lateral chambers ; early chambers closely coiled; later chambers separated with canaliferous clear shell material.

Pellatispira shows well-developed canal system consisting of radial, marginal and interseptal canals. The development of secondary shell material in the later stages led Cushman (1948, p. 306) to place the genus *Pellatispira* in Calcarinidae. Until functions of the canals are known, it is thought best to retain *Pellatispira* in Nummulitidae where it morphologically belongs.

Genus *Biplanispira* Umbgrove, 1937, p. 309 (n. name for *Heterospira* Umbgrove, 1936, p. 156). Type species : *Heterospira mirabilis* Umbgrove, 1936, p. 157, plate figs. 1–11.

This genus bears the same relationship to *Pellatispira* as *Heterostegina* does to *Operculina*.

Hanzawa (1937, pp. 113, 114) included two genera in his new family Pellatispiridae : *Pellatispira* Boussac (1906) and *Pellatispirella* Hanzawa (1937). Hanzawa (*op. cit.*, p.115) regarding the peculiar apertures in *Pellatispirella* says :

"While *Camerina* and *Operculina* usually have a single slit-like aperture at the median part of the base of the septa, *Pellatispirella* has small multiple apertures along the base of the septa."

The multiple apertures exhibited by the various species at the base of the septa would associate *Pellatispirella* with the nonionids rather than nummulitids.

Smout (1955, p. 205) includes *Pellatispira* and *Biplanispira* in the family Miscellaneidae.

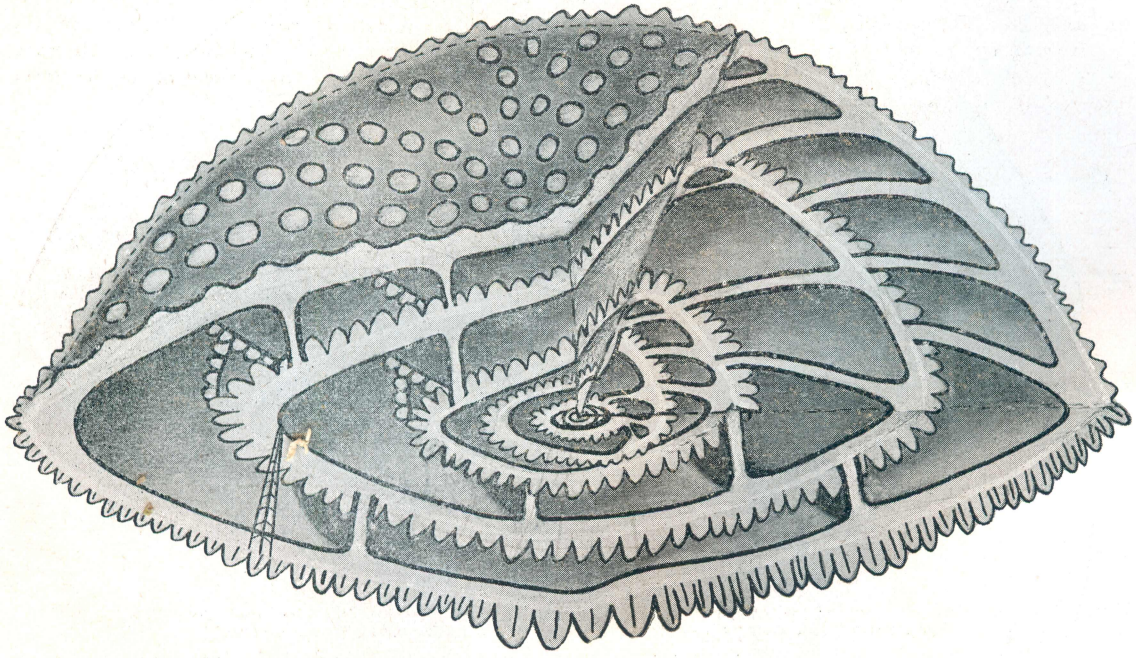


FIG. ? Generalized stereogram showing structure of the test in *Miscellanea* Pfender.

STRUCTURE

The test in the family Nummulitidae exhibits its highest structural development. The typical member of the family is the genus *Nummulites* Lamarck, 1801, which appears early in the Paleocene. Earlier records of it are not reliable. The name *Camerina Bruguièri*, 1792, has priority over *Nummulites* Lamarck, 1801, but the former has been rejected by the International Commission of Zoological Nomenclature (1945, Opinion 192) because of the wider use of the latter. Since the basic structure of the test in the genus *Nummulites* is reflected in all other nummulitid genera, a clearer understanding of it is necessary. Figure 2 shows the structure of the test.

The test is planispiral. The spiral lamina (e, l) is an inner, completely involute, continuous skeleton which forms the basic structure of the test. The successive laminae are not in direct contact with one another and there are empty spaces between them. The initial portion of the spiral lamina is the proloculus which is single and is rounded in the microspheric form ; in the megalospheric form it is often double and the intial chambers are subrounded. All the successive chambers (f) are formed by a double fold of the spiral lamina, which descend into the preceding whorl and extend to the roof of the succeeding whorl. This double fold of the spiral lamina is called the septum (h). There are as many layers of test deposition as there are septa. Therefore, the number of septa primarily control the

thickness of the test. There is a crescent-shaped opening between the chambers, which may or may not represent a former aperture. Septal filaments (n) are the continuation of the septal fold after it bifurcates to pass over on the opposite side of the underlying spiral lamina. They are either clearly visible from the outside or can be observed by slight polishing of the test. The septal filaments are an important feature of the test as they afford a means of grouping various species of the genus on external morphology alone. D'Archiac and Haime (1857) recognized four groups on the nature of the septal filaments : the laevis group (*N. gizenhensis* and *N. distans*); the subreticulata group (*N. laevigatus*) ; the reticulate group (*N. fichteli*) and the punctulate group (*N. ramondi*, *N. murchisoni*, *N. planulatus* and *N. variolaria*). This feature has also been used in the tracing of the evolution of the genus *Nummulites* (A. M. Davies, 1935 ; Glaessner, 1948).

shows no pillars at all. The marginal cord (b) is best developed around the periphery in complanate forms but its existence is doubted in the globose forms where the periphery is more rounded (Davies, 1937). A complex canal system has been noticed in the marginal cord (Hofker, 1927; Vaughan and Cole, 1941; Vaughan, 1945) and the variations of this canal system have been considered to be of generic rank. Our knowledge as to its function is lacking and hence this feature is not considered to be of any diagnostic value within the family.

Pillars (a) are columns of clear calcite which originate where the spiral laminae bend sharply and transverse from their point of origin toward the surface of the test. Where pillars intersect the surface of the test they often form granules (c). In most globose species, pillars anastomose to form a polar pustule (k).

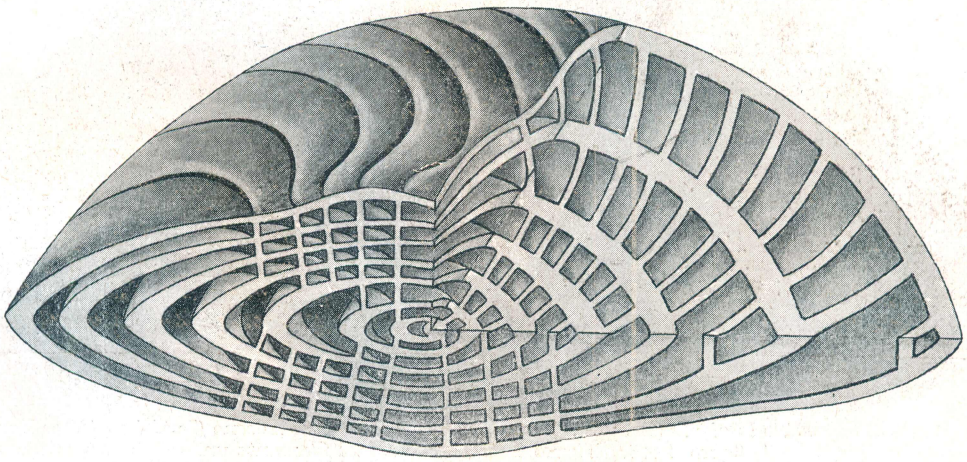


FIG. 4 Generalized stereogram showing the structure of the test in *Operculinoides* Hanzawa.

Besides the basis and primary skeleton, there exists in the *Nummulites* a supplementary skeleton. It consists of two main features : the marginal cord (b) and the pillars (a), which anastomose near the poles to form polar pustules (k). The function of both these features is perhaps strengthening of the test but it also could be ecological as the same species (*N. obtusus*) in the dominantly calcareous environment (Sind) shows well-developed pillars but in lesser calcareous but contemporaneous environment (Assam)

The genus *Miscellanea* Pfender, 1934, is essentially a *Nummulites* since their basic skeletal structure is the same (see text-fig. 2). The main difference between the two genera is that in *Miscellanea* the secondary skeleton decimates all around the spiral laminae to form small granules ; hence the marginal cord as such does not exist. These granules show up on the surface of the test as well as in lateral and equatorial sections. The type species is *Nummulites miscella* d'Archiac and Haime.

The genus *Operculinoides* Hanzawa, 1935, has the same basic structure of the test as *Nummulites* except that it is loosely coiled and the chambers are considerably higher in the last whorl (fig. 3). The septa normally are strongly curved. This genus represents a gradation between *Nummulites* and *Operculina* inasmuch as it shows the typical *Nummulites* feature in the early portion of the test but later portions resemble the flaring nature of *Operculina*. Nevertheless, it is morphologically distinct and could be readily recognized.

Sulcoperculina Thalmann, 1939 (pl. 2, fig. 5), is shaped like an *Operculina* but is involute. There is a knob of clear shell material at the poles and the last chambers tend to uncoil The type species shows a marginal sulcus and a peripheral canal. Internally, as seen in transverse sections, it is similar to *Operculinoides*.

The genera *Assilina* and *Operculina* represent a natural unit in which the spiral laminae are in direct contact. The genus *Assilina* d'Orbigny, 1826, is discoid in typical

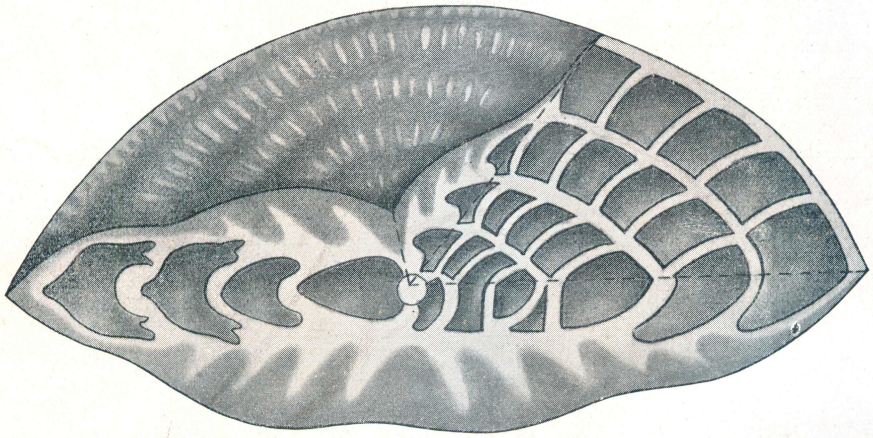


FIG. 5 Generalized stereogram showing structure of the test in *Assilina* d'Orbigny.

Operculinella Yabe, 1918 (type species *Amphistegina cumingi* Carpenter, 1860, p. 32) represents an early stage in the development of the *Operculinoides*.

forms like *A. granulosa* but is lenticular in *A. dandotica* group. *A. pustulosa* Doncieux group shows a polar depression. The test is typically planispiral and is loosely coiled

EXPLANATION OF PLATE 10

FIGS. 1, 2—*Nummulites laevigata* (Bruguière) var. *aquitanica* Benoist. Eocene (Lutétien) (after Benoist). Figure 1×4; figure 2×6. Figure 1 illustrates septal filaments under the last spiral lamina which has been eroded.

3—*Miscellanea miscella* (d'Archiac and Haime). Paleocene, India (after Davies). ×3. Note the supplementary skeleton degenerating into pillars that show up as granules on the surface.

4–6—*Operculinoides floridensis* (Heilprin). 4, Upper Eocene, Crystal River formation, Kendrick pit, external view; 5, Buda pit, median section; 6, Kendrick pit, median section. ×15.

7—*Operculinoides ocalanus* (Cushman). Upper Eocene, Crystal River formation, Newberry corporation pit. ×15.

8—*Operculinoides willcoxi* (Heilprin). Upper Eocene, Crystal River formation, Newberry Corporation pit. ×15. Note the last spiral lamina enveloping the entire test.

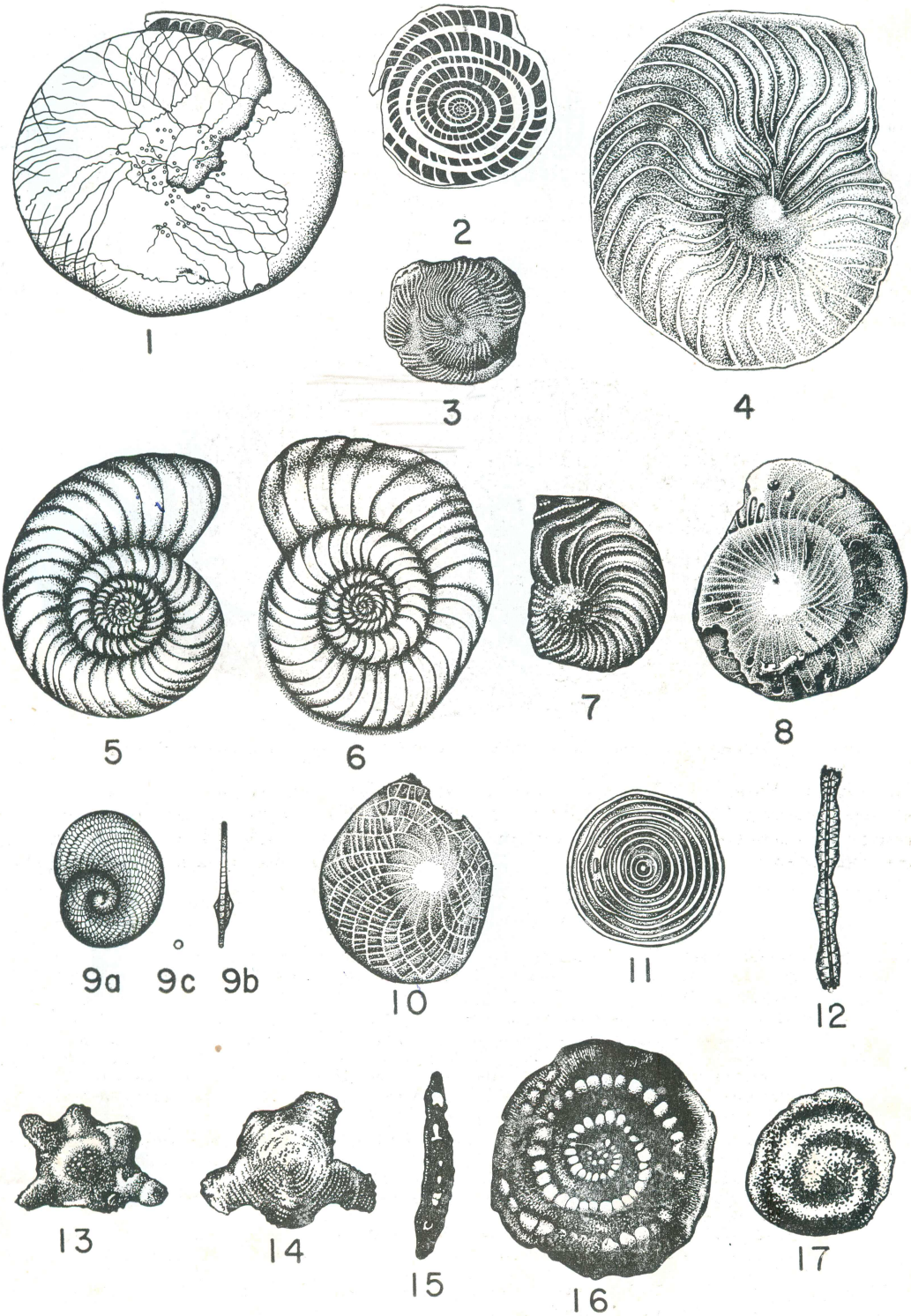
9—*Heterostegina depressa* d'Orbigny. Recent, Adriatic Sea (after d'Orbigny). ×20.

10—*Heterostegina ocalana* Cushman. Upper Eocene, Crystal River formation, Crystal River quarry. ×15.

11, 12—*Cycloclypeus* (*Kataclypeus*) *annulatus* Martin. Miocene, Java. ×2/3 (after Martin).

13, 14—*Cycloclypeus* (*Radioclypeus*) *neglectus* Martin var. *stellatus* Tan. "Tertiary f", Java (after Tan). ×6.

15–17—*Pellatispira douvillei* Boussac. Upper Eocene, Italy (after Boussac). 15, axial section; 16, median section; 17, external view. ×5.



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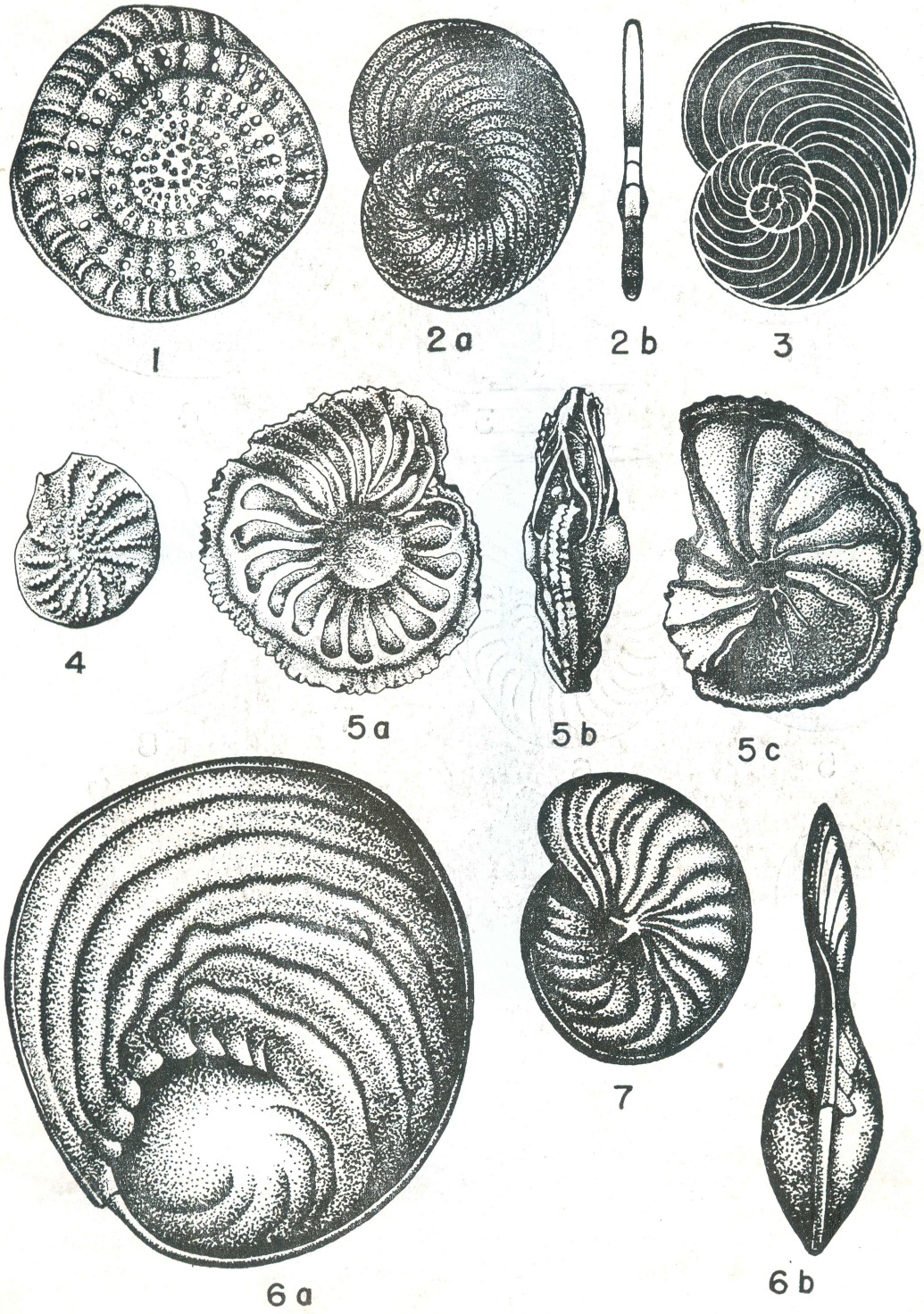


PURI : STRUCTURE OF THE NUMMULITIDAE

so that the rate of opening of the spire is regular (fig. 4). The septa are generally straight but they could also be slightly curved. The last whorl embraces the preceding one and the last chambers are shorter in height than the preceding ones.

Operculina d'Orbigny, 1826 (fig. 5), is basically an *Assilina* but the rate of uncoiling is rapid, so that the last whorl is far removed from the preceding whorl and the chambers are two to three times the height of the chambers in the preceding whorl. The septa are also arched in the upper half.

Heterostegina d'Orbigny, 1826 (fig. 6), is basically an *Operculina* but has supplementary chambers which are easily seen on the surface of the test.

Cycloclypeus Carpenter, 1856 (fig. 7), is

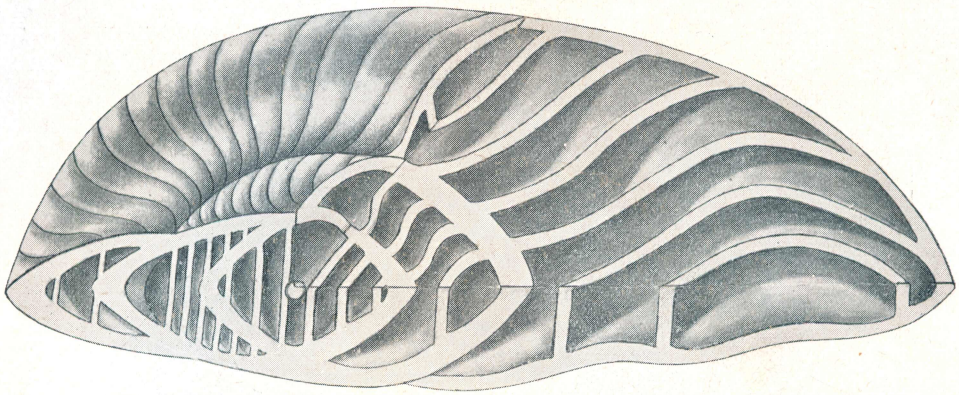


FIG. 6 Generalized stereogram showing structure of the test in *Operculina* d'Orbigny.

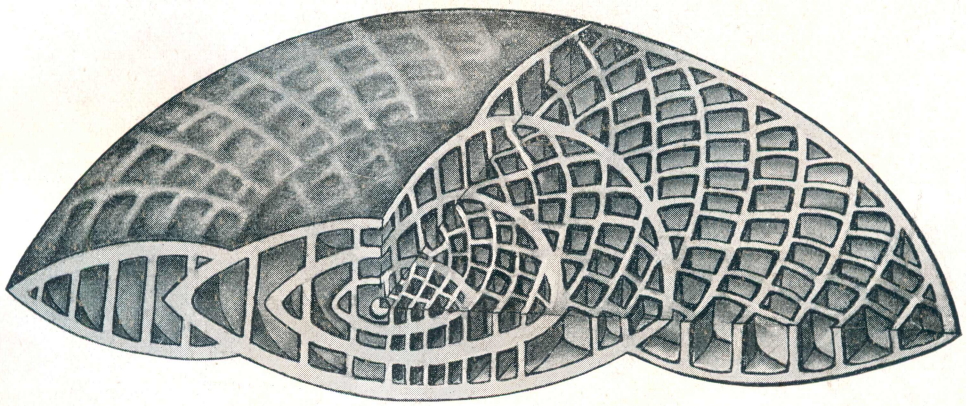


FIG. 7 Generalized stereogram showing structure of the test in *Heterostegina* d'Orbigny.

EXPLANATION OF PLATE 11

FIGS. 1—*Assilina granulosa* (d'Archiac). Eocene, Pakistan. ×10.
2, 3—*Operculina complanata* (Defrance). Recent, Adriatic Sea (after d'Orbigny). ×7.
4—*Operculina mariannensis* Vaughan. Upper Eocene, Williston formation, Newberry Pit. ×15.
5—*Sulcoperculina dickersoni* (D. K. Palmer). Upper Cretaceous, Cuba (after D. K. Palmer). ×40.
6, 7—"*Operculinella*" *cumingii* (Carpenter). Recent, Philippine Seas. Figure, 6×10 (after Carpenter). In figure 7, note striking similarity to *Operculinoides*.

an *Operculina* in the early portion of the test, some of the chambers are subdivided like *Heterostegina*; but the later portion is annular, subdivided into rectangular chamberlets. Lateral chambers are absent. The test is discoid and the periphery is circular.

Subgenus *Katacyclypeus* Tan Sin Hok, 1932, (pl. 1, figs. 11, 12) shows concentric raised rings. Subgenus *Radiocycloclypeus* Tan Sin Hok., 1932, shows radial thickenings of the test wall.

sheet, presence or absence of lateral chambers and development of chamberlets. The development is from forms without lateral chambers to forms with lateral chambers, which eventually develop chamberlets. Thus, *Heterostegina* without lateral chambers gives rise to *Spiroclypeus* with lateral chambers. Reliable records of the occurrence of the genus *Sulcoperculina* during the Upper Cretaceous is known to exist. In both time and structure it is believed to be more primitive.

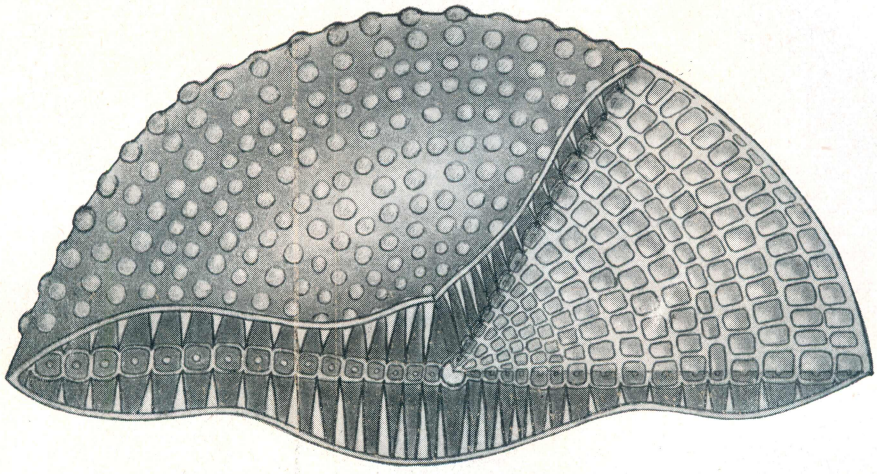


FIG. 8 Generalized stereogram showing the structure of the test in *Cycloclypeus* Carpenter.

Spiroclypeus Douvillé, 1905 (fig. 8), is a *Heterostegina* in the median layer and secondary stolons connect the chamberlets within the same chamber. The test is involute and shows well-developed lateral chambers.

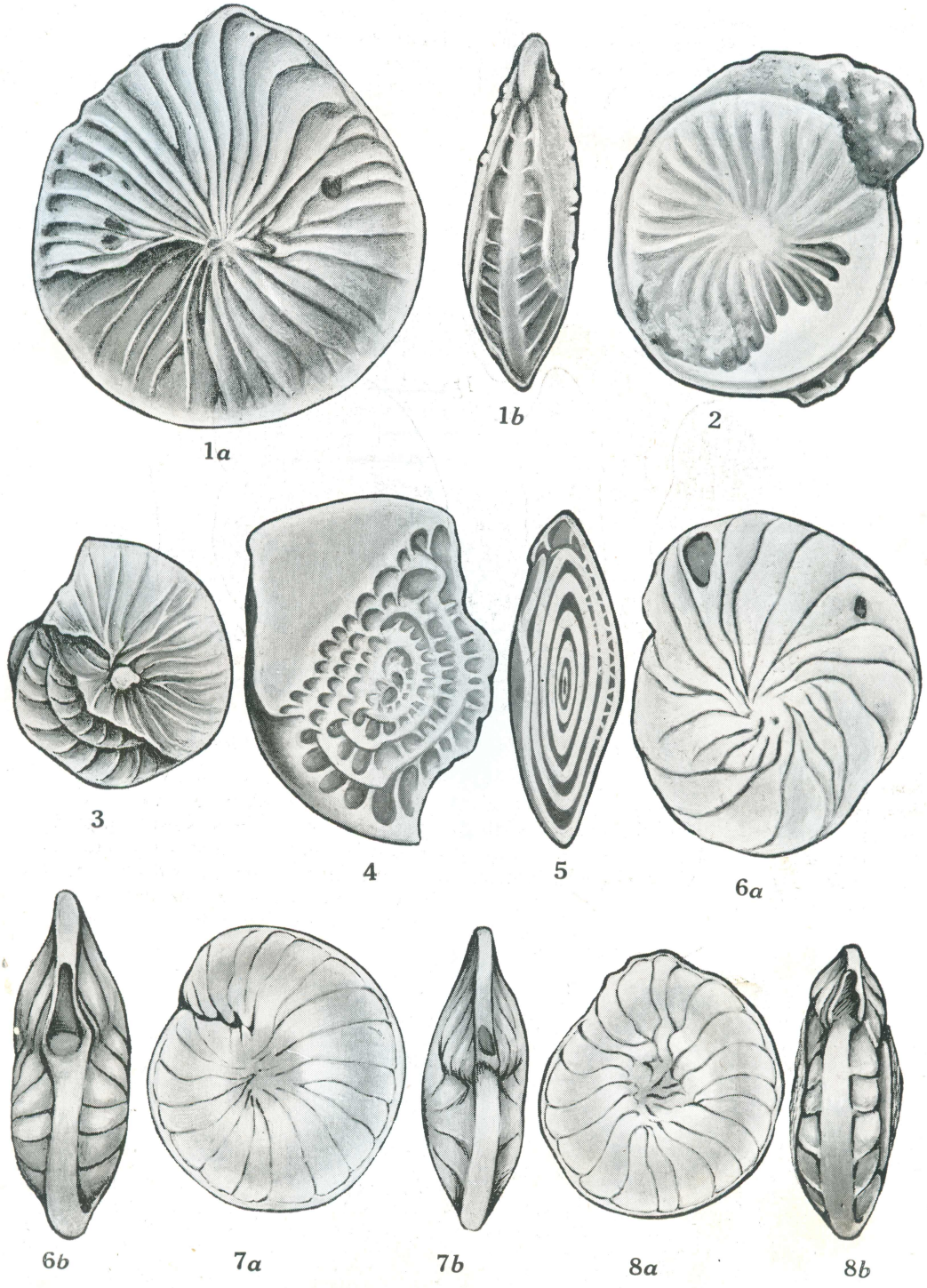
STRATIGRAPHIC DISTRIBUTION AND GENETIC RELATIONSHIPS

The diagnostic features that differentiate the nummulitid genera are the (direct or indirect) nature of the contact of the spiral *Miscellanea*, which is an offshoot of the *Sulcoperculina* stock early in the Paleocene, is planispiral with weak spiral laminae that are not in direct contact with one another, and the development is toward structurally stronger *Nummulites* by strengthening of the granular spiral laminae of *Miscellanea* by addition of calcium carbonate, and building of the peripheral cord. This tendency toward increased deposition of calcium started early in the Paleocene and continued until early Oligocene times. During this period the various species of *Nummulites*

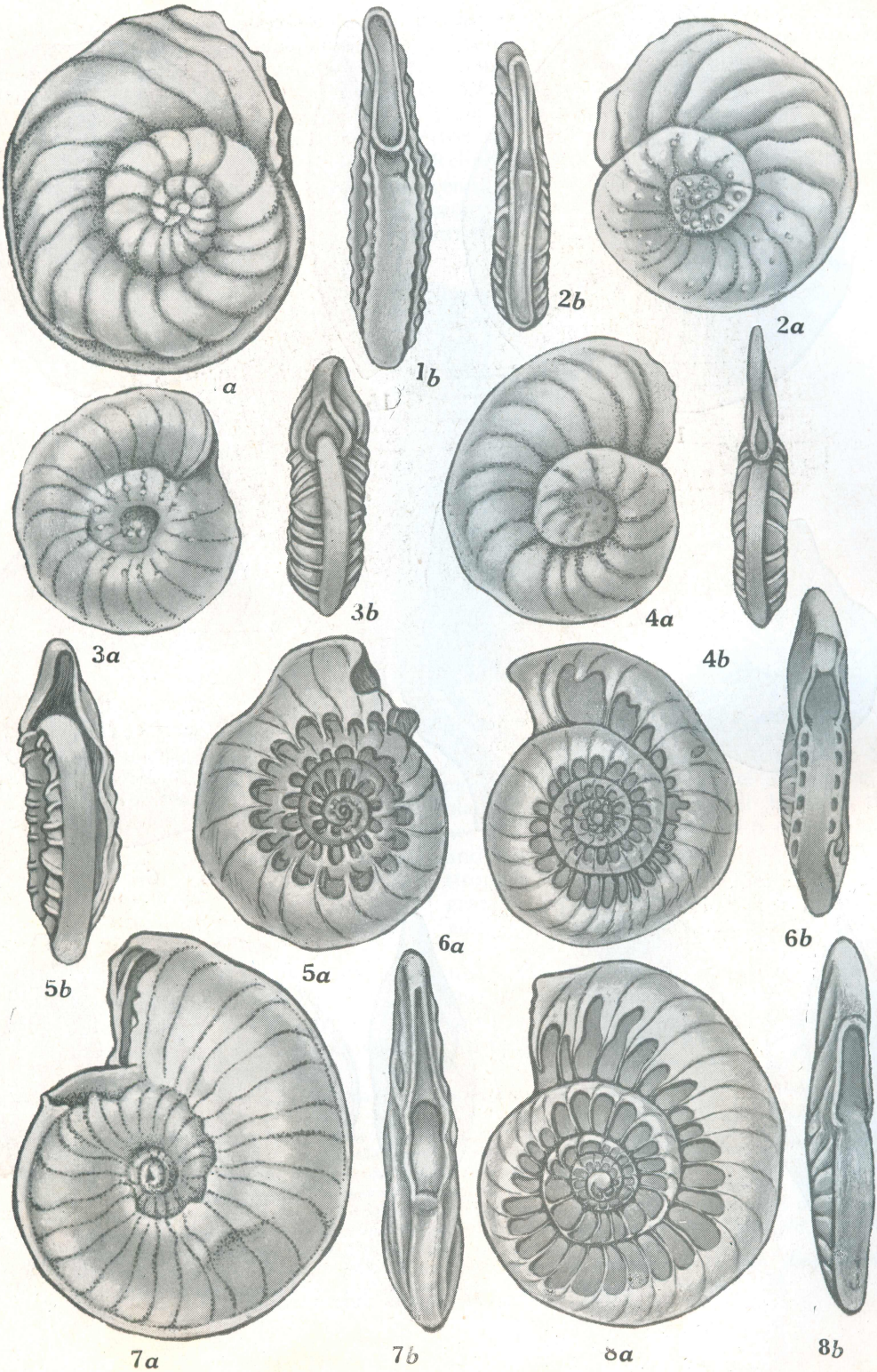
EXPLANATION OF PLATE 12

FIGS. 1–5—*Operculinoides moodybranchensis* (Gravell and Hanna). Upper Eocene, Acree Creek, 200 yards downstream, Andalusia, Alabama. Figure 1a, side view of weathered specimen showing the last two spiral laminae and septal filaments; 1b, peripheral view of the same specimen; 2, side view showing the last spiral lamina mostly removed, enveloping the spiral lamina below it; 3, specimen eroded to show the earlier spiral laminae and the whorls in a median plane; 4, specimen eroded to show the spiral laminae and the whorls. Note the successive spiral laminae enveloping the earlier ones completely. ×15.

6–8—*Operculinoides* sp. Recent, New Hebridies (Esperto Santo). Note the *Amphisteginа*-like effect of the septal filaments as they approach the center of the test. ×15.



PURI : STRUCTURE OF THE NUMMULITIDAE



PURI : STRUCTURE OF THE NUMMULITIDAE

developed gigantic tests. The importance of this factor is evidenced by the fact that structurally stronger *Nummulites* flourished during the Paleocene with a far greater abundance of both individuals and species, while *Miscellanea* disappeared in the middle Eocene. That *Nummulites* were better suited to the environment is further shown by their evolution into more complex and sturdy forms. The species of *Miscellanea* are few and very similar and they retained their primitiveness which caused their extinction.

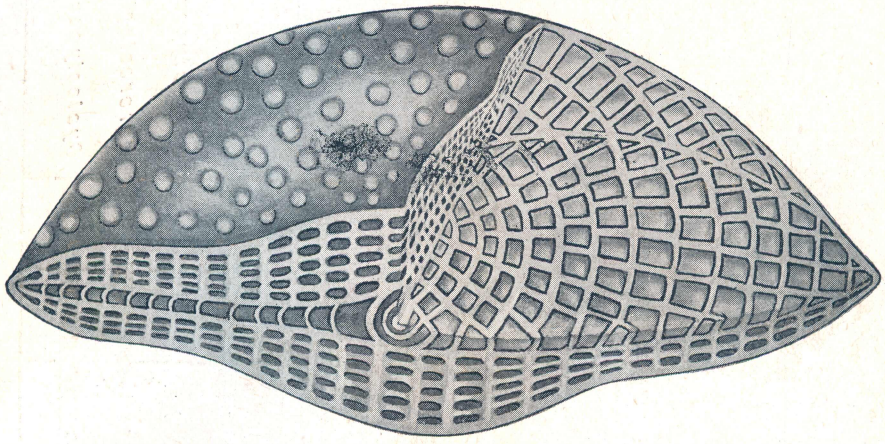


FIG. 9 Generalized stereogram showing the structure of the test in *Spiroclypeus* Douvillè.

Early during the Paleocene times *Operculinoides* developed from ancestral *Sulcoperculina* stock. The development of *Operculina* from *Operculinoides* was a simple step by spiral sheet coming in contact. The development of *Assilina* from *Sulcoperculina* was an attempt toward direct contact of the spiral laminae. *Assilina* thrived during the Paleocene and early Eocene times and then became extinct. During the Eocene, *Pellatispira* developed from *Assilina* by the addition of canaliferous clear shell material between the whorls. *Biplanispira* evolved from *Pellatispira* by the addition of chamberlets during late Eocene times. The development of secondary chambers in *Operculina* gave rise to *Heterostegina* during the Eocene. By acceleration of the *Heterostegina* test, it was an easy step toward *Cycloclypeus*. The ontogeny repeats the phylogeny in *Cycloclypeus*

EXPLANATION OF PLATE 13

FIGS. 1–4—*Operculina* sp. Recent, New Hebridies (Esperto Santo). ×15. Figure 1a, microspheric form, side view; 1b, peripheral view; 2, a variant of the same species; 3a, megalospheric form showing thickening of the test with the decrease in size and acuteness of the periphery; 3b, peripheral view; 4, another specimen showing variation. Note the successive spiral laminae are not in direct contact and all the whorls could be seen in external view.

5–8—*Operculinoides* sp. Recent, New Hebridies (Esperto Santo). ×15. Figure 5a, specimen etched with acid to show the successive laminae completely enveloping the earlier ones; 5b, peripheral view of the same specimen; 6a, b, another specimen showing slight variation in the test; 7a, external view; 7b, peripheral view; 8a, an etched microspheric form; 8b, peripheral view of the same specimen.

where the few early chambers are operculine without the chamberlets; later chambers are heterostegine. *Spiroclypeus* is an advanced development from *Heterostegina* by the addition of lateral chambers and secondary stolons. The probable origin of the family is diagrammatically shown in the accompanying chart (fig. 10).

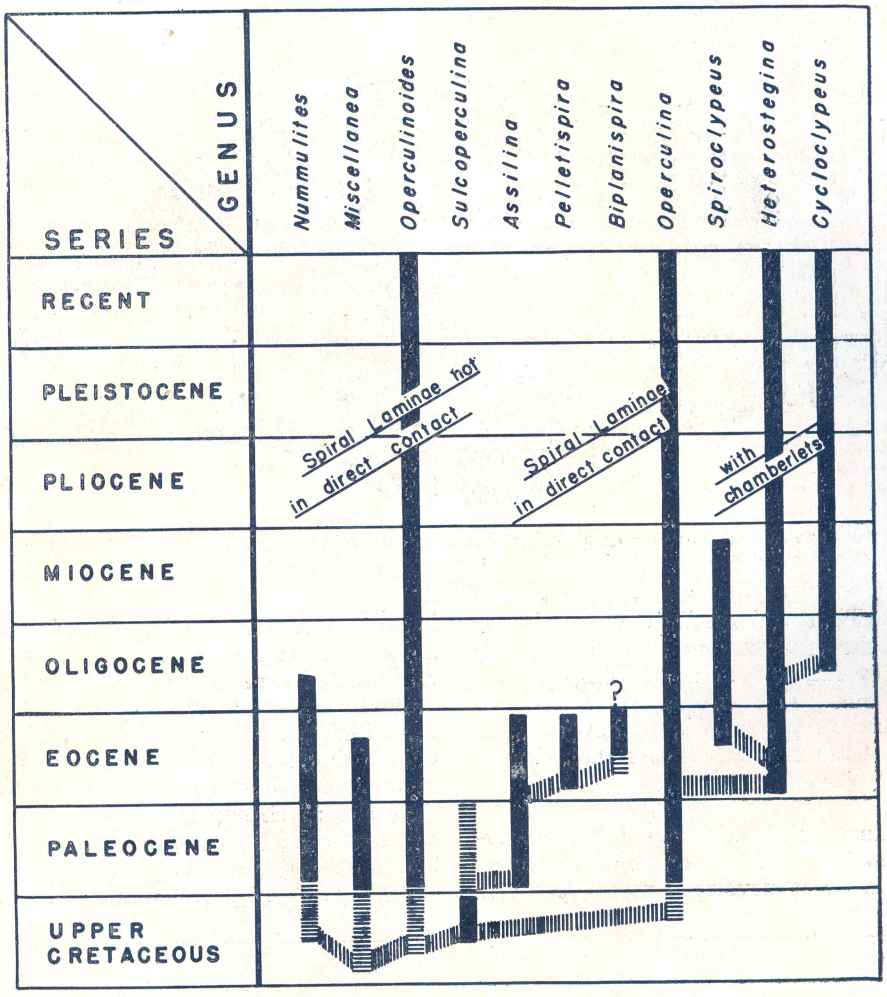


Figure 10

Probable Origin of the Nummulitid Genera

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