

Studies on Ceratobuliminidae (Foraminifera)

By

J. C. TROELSEN

Abstract

A revision of the family Ceratobuliminidae. The subfamily Ceratobulimininae is shown to be almost exclusively dextrally coiled, while the Epistomininae are predominantly sinistral. Only the genera *Ceratobulimina*, *Lamarckina*, *Epistomina* and *Epistominoidea* are retained in the Ceratobuliminidae, while numerous others are removed from the family. Notes on the structure of *Robertinoidea*, *Allomorphina*, *Quadriformina*, *Asterigerina*, *Heminwayina*, and the four genera belonging to the Ceratobuliminidae. *Alliatina* n. gen., *Ceratolamarckina* n. subgen., *C. jullandica* n. sp., and *Epistominoidea danica* n. sp. are described. *Quadriformina* and *Ceratocancris* are redefined.

Introduction

Some years ago I noticed a strong tendency toward preferred directions of coiling in the genera *Ceratobulimina* and *Epistominoidea*, but nothing more was done until a paper by BROTZEN (1942) and two articles by HANS BOLLI (1950 and 1951) prompted an investigation of the genera which various authors assume have developed from *Epistomina* and *Lamarckina*.

Preferred directions of coiling turned out to be very common phenomena among rotaliiform foraminifera, and it soon became necessary to combine the investigations of the direction of coiling with studies of the internal structures of the tests*). Also the microstructure of the test wall was determined and recorded in as many of my species as possible, although the exact significance of ALAN WOOD's division (1948) of the hyaline tests into "perforate radiate" and "perforate granulate" types has not yet been established.

BOLLI (1951), who has mainly studied the direction of coiling in *Globorotalia* species, summarizes his conclusions in the following way:

1. Random coiling appears to be the early stage in the evolution of the direction of coiling.
2. Once a species has chosen preference for either sinistral or dextral coiling in its later stage, it does not revert to random coiling in its further evolution.

These tenets evidently rest upon the assumptions (1) that the direction of coiling is an hereditary character, dependent upon the presence of at least one gene difference, and (2) that the elimination of one or the other

*) The dissections were carried out according to the method indicated by BROTZEN (1950).

of the genes may be accomplished by some sort of evolutionary process. When using the direction of coiling in tracing lines of evolution it may, however, be necessary to consider the possibility of a reversal of the process. A case in point appears to be that of the Middle Eocene *Cerobertina kakahoica* FINLAY, which is said to be exclusively dextrally coiled, while the apparently closely related Miocene species *C. mahoenuica* FINLAY is stated to be sinistral (FINLAY, 1939, p. 120). It is difficult to understand how natural selection operates in a case like this, the direction of coiling being of no apparent importance to the individual, but it should be remembered that the survival value or disvalue of a gene may be altogether separate from the value of the visible character produced by the gene.

The problem of the significance of the direction of coiling has become somewhat more complicated by BJØRN FØYN's findings. FØYN (1936, p. 20) discovered that in Recent specimens of *Discorbina vilardeboana* D'ORB. from Herdla in Norway, about 49% of the microspheric individuals were dextrally coiled while the corresponding percentage in the megalospheric generation was about 83. Similar conditions may possibly exist in other species, and so far as they are statistically significant, the small variations in the preference of coiling, found in different lots of some of my species, may have been caused by variations in the relative abundance of the two generations. For several reasons it is difficult to solve this problem, however. In the case of small foraminifera, thanatocoenose is not easily distinguished from biocoenose, and as, furthermore, the samples from which the foraminifera were picked represent unknown lengths of time I may not have been dealing with populations in the biological sense of that word. Another difficulty lies in the fact that few fossil rotaliiform foraminifera can be made sufficiently transparent to make possible direct measurements of the prolocula, and the rather formidable task of preparing the many hundreds of oriented thin sections that are needed for the examination of only a few species has not yet been undertaken.

In any case, the taxonomic usefulness of the direction of coiling should not be overestimated. It goes without saying that while species or genera in some cases may be phylogenetically separated on the basis of a difference in the direction of coiling, agreement in this respect is no proof of the existence of a close relationship.

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The family Ceratobuliminidae

As defined by GLAESSNER (1935, p. 154), the family includes genera characterized by "chambers . . . divided internally by partitions which are inconspicuous in earlier forms, larger in advanced forms and finally completely separating the part of the chamber containing the proximal primary foramen (aperture of the preceding chamber) from the main part of the new chamber with its new aperture; a secondary foramen in each septum, above the partition*); wall thick, usually smooth, finely perforate*); sutures usually partly limbate; aperture a low slit in the apertural face of the chamber . . .". GLAESSNER (1945) included in the family the genera *Lamarckina*, *Epistomina*, *Epistominoides*, *Ceratobulimina*, *Robertina*, *Cerobertina* and *Pseudobulimina*.

BROTZEN (1942, pp. 36-39) showed the existence of two evolutionary lines, one starting with *Epistomina*, the other with *Lamarckina*. In 1948, he erected the subfamilies Epistomininae and Ceratobulimininae for these lines. In 1942 and 1948 he referred to the family a large number of genera, most of which GLAESSNER had not included in the Ceratobuliminidae. It seems that BROTZEN's arguments for including these genera were that they had either some sort of internal partition or a combination of areal, lateral and interiomarginal apertures. BROTZEN apparently regarded the septal foramen as being homologous with one of the openings in the apertural face in some unknown prototype. No description was given of the perforations of the test wall.

SIGAL (1952, pp. 230-235) elevates BROTZEN's two subfamilies to the rank of families. Under Ceratobuliminidae he mentions the secondary nature of the septal foramen. A footnote (on p. 232) suggests that he regards fine perforations as being characteristic of at least the Epistominidae. In most other respects SIGAL seems to agree with BROTZEN.

In the following I shall attempt to show

1) that a septal foramen of secondary origin is characteristic of the true Ceratobuliminidae. When a new chamber is added, the old aperture is closed and a septal foramen is formed by resorption above the internal partition. A line connecting the septal foramina would lie completely above (outside) the internal partitions (fig. 2 in the text). Some of these characters have already been correctly interpreted by PLUMMER (1934 and 1936);

*) Spaced out by me.

2) that genera with coarse perforations or with "perforate granulate" microstructure of the test wall are unrelated to the Ceratobuliminidae;

3) that while members of the subfamily Ceratobulimininae are almost exclusively dextrally coiled, the Epistomininae are either predominantly sinistrally coiled or, in a few species, coiled at random;

4) that BROTZEN's subfamilies Ceratobulimininae and Epistomininae are natural units which probably stem from the same root; and

5) that among the genera examined by me, only *Lamarckina*, *Ceratobulimina* (sensu latu), *Epistomina* (sensu latu), and *Epistominoides* can be referred to the Ceratobuliminidae, while *Robertina*, *Robertinoides*, *Alliatina*, *Allomorphina*, *Quadriformina*, *Anomalinella*, *Eponidella*, *Asterigerina* (sensu latu), *Heminwayina*, *Pulsiphonina*, *Siphonina*, *Osangularia* and *Alabamina* should not be included in the family.

The genera *Lamarckina*, *Berthelin*, and *Ceratobulimina*, *Toula*

The genera, mentioned above, are so closely related that it is convenient to deal with them in the same section. *Lamarckina* is distinguished from early species of *Ceratobulimina* chiefly through the pronounced flattening of its ventral side. As in the primitive *Ceratobulimina*, its aperture lies in the umbilicus, at the base of the apertural face (pl. X, fig. 1, a), while the septal foramen (pl. X, fig. 1, b; fig. 2) is placed in the middle of the septum. That the two openings cannot be homologous is perhaps less clear in *Lamarckina* than in *Ceratobulimina*, sensu strictu. It is easily observed, however, that when a new chamber is added, a thin plate (pl. X, fig. 2, a) closes the aperture and replaces part of the septum (the former apertural face) up to the base of the septal foramen. Later, when still another chamber is added, the small vestibule under the short internal partition is sealed by a thin plate (pl. X, fig. 2, b).

According to BROTZEN (1948, p. 122), "the division of the final chamber in *Lamarckina* is more complete than in *Ceratobulimina*: its partition is fixed on the umbilical, frontal and spiral walls . . .". This is not in agreement with my own observations, according to which *Lamarckina* has a rather small internal partition (cfr. pl. X, figs. 1-2. A specimen of *L. lamplughi* (SHERLOCK) from the Gault of Folkestone, England, possesses a similar structure).

The description, given above, is mainly based on observations on *L. wilcoxensis* CUSHMAN, the only species found in any abundance in my collection. Distinctive features of all *Lamarckina* species examined by me are, further, the very fine perforations and the occurrence of enamel-like secondary deposits on the surface of the test.

All *Lamarckina* specimens in my collection are dextrally coiled. In the literature I have found a few figures of sinistral specimens. Some of these have, however, been misidentified. Thus, topotype specimens of "*L.*" *stormi* BROTZEN lack all internal structures characteristic of the true *Lamarckina*.

Among the numerous descriptions of *Ceratobulimina*, the one given by

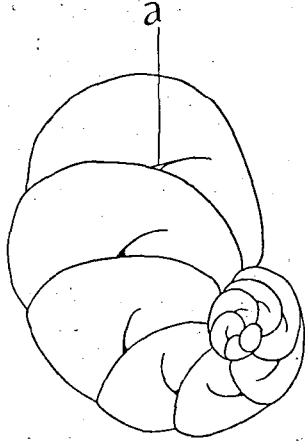


Fig. 1. *Ceratobulimina* (*Ceratobulimina*) *contraria* (REUSS). Faarup brickwork, Faarup St., Denmark (Middle Olig.). Dorsal view of clarified specimen showing dorsal attachments of internal partitions. *a* is a small pit (accessory aperture?), which is closed by secondary shell material in earlier chambers. Length of specimen: .52 mm.

PLUMMER (1936) is undoubtedly the best. The account, given below, agrees rather closely with PLUMMER'S.

Nearly 100% of my specimens are dextrally coiled (see the remarks on the different species). The perforations of the test wall are always very fine. The wall is commonly layered, with a smooth and glistening surface. The microstructure is perforate radiate (cfr. WOOD, 1948).

The aperture is typically at the base of the apertural face. CUSHMAN (1946) a. o. describe the aperture as being elongate or slit-like, extending into the apertural face and in perfect specimens covered by a thin plate which forms a bulge over the aperture. Actually, no aperture is concealed beneath the bulge (the elongate aperture found in *Ceratobulimina*, sensu strictu, constitutes a special case).

Three different types of apertures can be distinguished in *Ceratobulimina*. In *C. woodi* KHAN, *C. cretacea* CUSHMAN & HARRIS, *C. perplexa* (PLUMMER), *C. tuberculata* BROTZEN, and *C. jullandica* n. sp., i. e., in Cretaceous and Paleocene species, the aperture is a rather wide slit which lies exclusively in the umbilicus, at the base of the bulge. The

aperture is bounded on one side by the point of attachment of the ultimate chamber to the previous whorl and on the other by a notch, which marks the lower end of the internal partition (cfr. PLUMMER, 1936, p. 460; and BROTZEN, 1948, pl. 19, figs. 2-3). In this group of species, the internal partition just reaches the dorsal chamber wall without being attached to it. The free edge of the partition is commonly serrate and usually curved gently downward toward the aperture (in the Epistomininae, the partition is bent in a similar way). The septal foramen lies above (distally to) the partition and is evidently of secondary origin. When a new chamber is added, the umbilical aperture is closed and the bulge of the apertural face is replaced by a thin tongue-like plate, which extends from the umbilicus to the base of the septal foramen but separated from it by the partition. For the group of species, described above and partly figured by PLUMMER (1936, figs. 1-5) and BROTZEN (1948, pl. 19, figs. 1-3), I propose the subgeneric name of *Ceratolamarckina*. The type species is to be *C. tuberculata* BROTZEN, 1948, and the subgenus is characterized by having a rather short and wide, exclusively umbilical aperture; a very small notch at the posterior (distal) end of the aperture; and an internal partition which is not attached to the dorsal chamber wall.

Another type of aperture is found in the species which are grouped around the genotype, *C. contraria* (REUSS). The name of the subgenus

must then be *Ceratobulimina*, sensu strictu (cfr. FINLAY, 1939). In members of this group, the umbilical aperture sends a long slit-like extension into the apertural face. PLUMMER (1936, p. 463) assumed that the extension was a very deep notch rather than a real aperture. FINLAY (1939) did not consider the slit the complete homologue of the notch but compared it to the aperture which he assumed existed beneath the apertural bulge. Studies of large suites of *C. contraria* have shown, however, that the long slit in the apertural face of *Ceratobulimina*, sensu strictu, is a real opening formed by an extension of the umbilical aperture along the very deep notch at the posterior end of the bulge. Abnormal specimens of *C. tuberculata* have been found in which the notch is deepened so much that a transition is formed to the aperture found in *Ceratobulimina*, sensu strictu. In *C. contraria*, the strongly curved internal partition is attached to the posterior (right-hand) side of the apertural extension (pl. X, fig. 13). It is, further, attached for a fair distance to the dorsal chamber wall (fig. 1 in the text). A small pit on the external side, at the junction between the septum and the partition (a in fig. 1), may be the orifice of a canal or an accessory aperture, but I have been unable to trace its course. The pit is closed when a new chamber is added. (See *postscript 1*).

Because the internal partition is comparatively complete in *C. contraria*, a particularly clear picture is obtained of the relationship between the aperture, the partition and the septal foramen. Figs. 5 and 13 in pl. X show that the bend of the partition completely surrounds the aperture, while a line connecting the septal foramina would lie on the outside (distal side) of the partitions (cfr. also fig. 2 in the text). The septal foramen can, therefore, not be homologous with any part of the aperture but must be of secondary origin. I regard this relationship, repeatedly referred to in this paper, as one of the most important characteristics of the Ceratobuliminidae.

A third type of aperture is found in the subgenus *Ceratocancris* FINLAY, which includes *C. cliffdenensis* FINLAY (the type species), *C. haueri* (D'ORB.), *C. eximia* (RZEHAČ), a. o. According to FINLAY, the characteristic feature of *Ceratocancris* is the presence of a plate which completely covers the aperture which he assumes extends into the apertural face. PLUMMER (1936, p. 460) has more aptly described the aperture in *C. eximia* in the following words: "the aperture is a very narrow slit along the base of the face (at base of bulging area). The slit lies over part of the ventral side of the previous whorl and over part of the umbilicus, and it extends from a notch near the periphery . . . to another notch on the edge of the umbilicus . . .". The latter notch is identical with the one referred to under *Ceratolamarckina* and *Ceratobulimina*, sensu strictu. The aperture is of the type called interiomarginal and umbilical by BROTZEN (1942). A very interesting feature was disclosed by the dissection of *C. aff. haueri* (pl. X, fig. 4, e), viz., the presence of a low, accessory internal partition, which is attached to the surface of the previous whorl, and which extends obliquely downward and inward from the upper end of the aperture. It is interesting that PLUMMER (1936, fig. 8) figures a similar structure in *C. eximia* without, however, referring to it in the text. Whether the accessory internal

partition is present in the type species, *C. clifdenensis*, is not known, and it would therefore be premature to mention it in the diagnosis of the subgenus. For the time being, *Ceratocancris* must be defined as a group of *Ceratobulimina* species in which the aperture is umbilical and basal (interiomarginal); the notch at the posterior (distal) end of the aperture a very small one; and the internal partition not attached to the dorsal chamber wall. (See *postscript 2*).

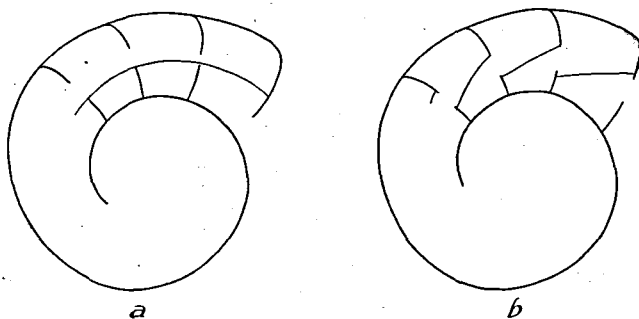


Fig. 2. Highly diagrammatical sections through last chambers of (a) *Lamarckina* and *Ceratobulimina* and (b) *Robertinoides* and *Alliatina*, showing mutual position of apertures, septa, internal partitions and septal foramina (both primary (in b) and secondary (in a)).

Lamarckina wilcoxensis, Cushman

Pl. X, fig. 2.

L. wilcoxensis, CUSHMAN, Contrib. Cushman Labor. Foram. Res., vol. 2 (1), 1926, p. 9, pl. 1, figs. 3 a-c.

Material: Railroad cut 1 mile north of Ozark, Alabama (Wilcox form.; Eocene?; G. M. PONTON leg.); 76 dextral specimens; microstructure: perforate radiate.

Ceratobulimina (Ceratolamarckina) woodi, Khan

Pl. X, figs. 3, 10-12.

Pulvinulina haueri, CHAPMAN, (non D'ORBIGNY), Jour. Roy. Micr. Soc., vol. 18, 1898, pp. 5-6, pl. 1, figs. 7 a-b.

Ceratobulimina woodi, KHAN, Jour. Roy. Micr. Soc., ser. 3, vol. 70 (3), 1950, p. 276, pl. 2, figs. 15-16, 20-21.

Non *Ceratobulimina gaultina*, TEN DAM, 1946, p. 11, figs. 1 a-b.

KHAN (op. cit.) says about the aperture of *C. woodi* that it is "umbilical, extending into the apertural face with a protecting plate". Observations on specimens in my own collection lead me to make the following amendments to KHAN's diagnosis "External aperture under long, slightly curved lip, which forms one side of umbilicus. At distal end (i. e., farthest from junction with previous whorl) of apertural lip a small but distinct notch,

from which a very faint dent or furrow continues for a short distance across septal face. Septal foramen relatively large, oval, placed in center of septum. Narrow granulate band connects umbilicus with septal foramen. Internal partition well developed, strongly curved. Its line of attachment runs from notch in apertural lip in almost straight line upwards to upper (dorsal) end of septal foramen and continues from there in a slightly curved line across septal face to upper, inner corner of septum, at junction with previous whorl. Microstructure of test wall perforate radiate. Direction of coiling wholly or at least predominantly dextral”.

The identity with CHAPMAN's species (op. cit.) seems complete. TEN DAM (op. cit.) considers his *C. gaultina* from the Albien of the Netherlands identical with CHAPMAN's species, but *C. gaultina* is much shorter, and, judged by TEN DAM's figures, the internal partition seems to have a shape that is different from that of the partition in *C. woodi*. In TEN DAM's species, the attachment of the partition seems to run obliquely upwards and outwards from the upper end of the septal foramen.

Together with *C. gaultina*, *C. woodi* is the oldest known representative of its genus. It is interesting to note the similarity to the Paleocene species of the subgenus. The umbilical aperture is relatively longer; the thin, clear plate which in the septa of the geologically younger species connects the umbilicus with the base of the septal foramen is here represented by a granulate area; and the portion of the partition dorsal to the septal foramen is much longer; but in all essential respects there is very good agreement with such species as *C. tuberculata* or *C. jullandica*.

Material: Folkestone, England (Gault clay; exact horizon not known); 14 dextral specimens; microstructure: perforate radiate.

***Ceratobulimina* (*Ceratolamarckina*) *tuberculata*, Brotzen**

C. tuberculata, BROTZEN, 1948, pp. 124-125, pl. 19, figs. 2-3.

C. perplexa, BROTZEN (non PLUMMER), 1948, pp. 123-124, pl. 19, fig. 1.

BROTZEN (op. cit.) divided his material of *Ceratobulimina* from the Danish-Swedish Paleocene into two species, both of which are strongly inflated. One of them, having narrow, depressed sutures, he called *C. tuberculata*, while the other, which had strongly limbate sutures, he referred to *C. perplexa* (PLUMMER), with the remark that his specimens “do not differ from the topotypes available . . . from the Midway formation”. PLUMMER (1926, p. 156, pl. 12, fig. 2) says, however, about this species that it is “considerably compressed”, and her figures (op. cit. and 1936, fig. 1-4) show a test which is much more depressed than BROTZEN's *C. perplexa*. It thus seems doubtful whether the real *C. perplexa* is present in the Scandinavian Paleocene. On the other hand, I have found all gradations between typical *C. tuberculata* and such which show the strongly limbate sutures typical of BROTZEN's *C. perplexa*. I have therefore found it advisable to unite BROTZEN's two species under the name of *C. tuberculata*.

All the specimens, mentioned below, have come from the Paleocene deposits of Denmark:

1. Kongedybet, near Copenhagen; 19 dextral specimens.
2. Hvalløse (light-colored, soft marl); 59 dextral specimens.
3. Hvalløse (hard, glauconitic marl); 64 dextral, 1 sinistral specimen.
4. Lellinge (black clay); 7 dextral specimens.
5. Kerteminde (gray marl); 4 dextral specimens.
6. Sundkrogen, Copenhagen (black clay); 10 dextral specimens.
7. Vestre Gasværk, Copenhagen (gray clay); 15 dextral specimens; microstructure: perforate radiate.
8. Rugaard (yellow marl); 79 dextral specimens; microstructure: perforate radiate.

Ceratobulimina (Ceratolamarckina) jutlandica, n. sp.

Pl. X, figs. 7-9.

Diagnosis: Test flattened; outline an oblong hexagon with strongly rounded corners; peripheral margin rather narrowly rounded, very slightly lobate. Total number of chambers about eight besides proloculum; about six chambers in final whorl on dorsal side; on ventral side only five visible; rapidly increasing in size; outline of ultimate chamber a rounded triangle. Sutures on ventral side straight; narrow; hardly depressed; radiating from umbilicus. On dorsal side sutures narrow; not depressed; straight except near periphery where they are curved slightly backwards; pointed backwards without being tangential to spiral suture. Apertural face nearly flat; its dorsal margin straight; slightly convex bulge above aperture bounded on posterior side by short and indistinct furrow. Umbilicus large and open; its sides covered by granules. Internal structure as in subgenotype and *C. perplexa*. Length of holotype: .25 mm; width: .18 mm; thickness: .13 mm.

Remarks: This species is characterized by its rounded hexagonal outline and its large pointed ultimate chamber having one straight side (the dorsal margin of the apertural face). It is easily distinguished from small specimens of *C. tuberculata* by being flatter and having sutures which are hardly depressed.

Material:

1. Rugaard, Denmark (type locality; yellow marl; Paleocene); 79 dextral specimens; microstructure: perforate radiate.
2. Hvalløse, Denmark (light-colored, soft marl; Paleocene); 4 dextral specimens.

Ceratobulimina (Ceratobulimina) contraria (Reuss)

Pl. X, figs. 5 and 13.

C. contraria, TEN DAM & REINHOLD, 1942, p. 92, pl. 6, fig. 9.

C. contraria, CUSHMAN, 1946, p. 110, pl. 17, figs. 10-11.

General remarks on this species may be found in the paragraph on *Ceratobulimina*, sensu strictu (p. 453).

Material: Faarup brickwork, Faarup St., Denmark (Middle Olig.); 202 dextral, 4 sinistral specimens; microstructure: perforate radiate.

Ceratobulimina (Ceratocancris) aff. haueri (d'Orbigny)

Pl. X, figs. 4 and 6.

For description of the typical species, see MARKS (1951, pp. 67-68), where further references may be found. My specimens differ from the Miocene species figured by D'ORBIGNY by being somewhat more inflated, thereby approaching *C. eximia* (RZEHAČ) from the Eocene.

Material:

1. Baden near Vienna, Austria (Late Mediterr. stage; Miocene); 19 dextral specimens; microstructure: perforate radiate.
2. Lapugy, Hungary (Miocene); 7 dextral specimens.

The accessory internal partition, mentioned in the paragraph on *Ceratocancris*, has been observed in specimens from both localities.

The genera *Epistomina*, *Terquem*, and *Epistominoides*, Plummer

Excellent descriptions and figures of typical representatives of *Epistomina* and *Epistominoides* have been published by PLUMMER (1934, pp. 602-605) and BROTZEN (1948, pp. 92-97).

BROTZEN (op. cit.) divided the genus *Epistomina* into two: *Epistomina*, sensu strictu, having a lateral aperture (i. e., the aperture lies in the middle of the ventral wall of the chamber) and an areal septal foramen (i. e., in the middle of the septum); and *Höglundina*, with a lateromarginal (marginal) aperture and an interiomarginal (basal) septal foramen. TEN DAM (1948 a; 1949), citing MACFADYEN, points out that TERQUEM's figures, on which BROTZEN based his definition of *Epistomina*, sensu strictu, appear to be misleading and that a subdivision of the genus *Epistomina* is therefore hazardous or at least premature. In the following, I, too, shall consider *Höglundina* a synonym of *Epistomina* as even my Jurassic specimens show all the essential characters of the Cenozoic and Recent species.

Although my material of *Epistomina* has not as yet been completely studied, the following results (not all new, of course) may be set forth:

- 1) All of my species, which range in age from the Late Jurassic to Recent, have one, and only one, external aperture. This aperture is always lateromarginal.
- 2) An internal partition is always present, at least in the ultimate chamber. (In *E. spinulifera* the partition is developed (and preserved) in all chambers except the one following the proloculum). The partition is joined to the dorsal lip of the aperture.

- 3) When a new chamber is added, the primary aperture is sealed, and a secondary septal foramen is formed by resorption above the internal partition. There seems to be no essential difference between areal and interiomarginal (basal) foramina.

Epistomininae differ from Ceratobulimininae in two respects only:

- 1) The external aperture has moved from the base of the apertural face to the peripheral margin of the chamber. In spite of this migration of the aperture, the mutual position of aperture, septal foramen and partition is exactly the same in the two subfamilies.
- 2) With the exception of two species which are coiled at random, *Epistomina* is predominantly sinistral, while nearly all Ceratobulimininae are dextral.

As for the genus *Epistominoides*, it is evidently a specialized branch of *Epistomina*. The specialization seems to have caused a complete elimination of dextral coiling.

The genera *Epistomina* and *Epistominoides* are the only ones among the forms studied by me which I find it possible to retain in BROTZEN's subfamily Epistomininae. With this restriction, I consider the subfamily a natural unit.

Epistomina sp. 1

A sample of Upper Jurassic sand from Glos in France contains at least three species of *Epistomina*, of which only one, as yet undescribed, occurs in any abundance. This is an almost smooth species with all the essential characters of the genus.

Material: "Sablière de Glos près de Lisieux", 50 kilometres east of Caen, France (Séquanien, Upper Jurassic); 216 specimens; about 85% sinistral; microstructure: perforate radiate.

Epistomina sp. 2

A small, undescribed species, which is characterized by strongly limbate, somewhat elevated sutures. In a sample of dark, fossiliferous clay from Ringstead Bay, Dorset, England (Kimmeridge, Upper Jurassic), 15 sinistral and 3 dextral specimens were found. Microstructure: perforate radiate.

Epistomina sp. 3

A highly ornate species, which seems to be related to *E. mosquensis* UHLIG from the *ornatus*-clay of Russia, occurs together with *E. sp. 2*. Species 3 is represented by 32 sinistral and 1 dextral specimen. Microstructure: perforate radiate.

Epistomina caracolla (Roemer)

Gyroldina caracolla, ROEMER, Die Verstein. d. norddeutsch. Kreidegeb., 1841.
Epistomina caracolla, TEN DAM, 1948c; here further references.

Besides *E. carpenteri* (see below), this is the only *Epistomina* species in which random coiling has been recorded.

Material: Speeton, England (Speeton clay with *Belem. jaculus* PHIL.; Hauterivien); 142 specimens; about 55% sinistral; microstructure: perforate radiate.

Epistomina spinulifera (Reuss)

Rotalia spinulifera, REUSS, Sitz. Ber. Akad. Wiss. Wien, vol. 46, 1862, pp. 93-94, pl. 13, figs. 3-5.

Epistomina spinulifera, TEN DAM, 1948c (here further references and synonymy).

This species is represented in my collection by three lots of specimens from the Gault clay of Folkestone, England. No information is available as to the exact horizons from which the samples were collected.

Lot 1. 494 specimens; about 93% sinistral.

Lot 2. 330 specimens; about 97% sinistral; microstructure: perforate radiate.

Lot 3. 45 specimens; about 96% sinistral.

Epistomina carpenteri (Reuss)

Rotalia carpenteri, REUSS, Sitz. Ber. Akad. Wiss. Wien, vol. 46, 1862, p. 94, pl. 13, fig. 6.

Epistomina carpenteri, TEN DAM, 1948c (here further references).

The specimens before me came from the same sample of Gault clay as Lot 2 mentioned above under *E. spinulifera*. Among 269 specimens of *E. carpenteri*, about 55% were sinistral (see above under *E. caracolla*). Microstructure: perforate radiate.

Epistomina chapmani, ten Dam

Rotalia elegans, JONES & PARKER (non D'ORBIGNY), Quart. Jour. Geol. Soc., vol. 16, 1860, pl. 20, fig. 46.

Epistomina chapmani, TEN DAM, 1948c (here further references).

My specimens came from the same sample of Gault clay as Lot 2 mentioned above under *E. spinulifera*. Of 120 specimens, about 77% were sinistral. Microstructure: perforate radiate.

Epistomina scalaris, Franke

Höglundina scalaris, BROTZEN, 1948, p. 94, pl. 15, figs. 2-3 (here further references).

As pointed out by BROTZEN (op. cit.), *E. scalaris* is almost identical with *E. elegans*.

Material:

1. Rugaard, Denmark (Paleocene); 63 sinistral, 3 dextral specimens; microstructure: perforate radiate.
2. Lellingø, Denmark (Paleocene); 4 sinistral specimens.
3. Hvalløse, Denmark (hard, glauconitic marl; Paleocene); 5 sinistral, 1 dextral specimen.
4. Hvalløse, Denmark (light-colored, soft marl; Paleocene); 26 sinistral, 4 dextral specimens.
5. Sundkrogen, Copenhagen (Paleocene); 11 sinistral, 2 dextral specimens.
6. Vestre Gasværk, Copenhagen (Paleocene); 4 sinistral specimens.

Epistomina elegans (d'Orbigny)

Rotalia elegans, D'ORBIGNY, Ann, Sci. Nat., Paris, ser. 1, t. 7, 1826, p. 276.

In most samples this species occurs very sparsely. In the following list I have omitted localities from which only one or two specimens are known.

Material:

1. Faarup brickwork, Faarup St., Denmark (Middle Olig.); 22 sinistral, 1 dextral specimen.
2. Sooss-bei-Baden, near Vienna, Austria (Tortonian; Miocene); 6 sinistral, 1 dextral specimen.
3. Coast of northwest Africa (cores taken by Swedish Deepsea Exped.; Pleistocene); 9 sinistral, 2 dextral specimens.

Epistominoides midwayensis, Plummer

E. midwayensis, PLUMMER, 1934, p. 605, pl. 24, fig. 4.

E. midwayensis, BROTZEN, 1948, p. 96, pl. 17, fig. 5.

Three (sinistral) specimens from Hvalløse, Denmark (light-colored, soft marl; Paleocene), agree perfectly with PLUMMER's species.

Epistominoides wilcoxensis (Cushman & Ponton)

E. wilcoxensis, PLUMMER, 1934, p. 604, pl. 24, figs. 1-3 (here further references).

This species has not previously been recorded from Europe. As in PLUMMER's material, the suites from Denmark exhibit considerable variation in the sharpness of the carination and in the relative breadth of the septal face. There is no doubt, however, of the identity with CUSHMAN & PONTON's species.

Material:

1. Hvalløse, Denmark (light-colored, soft marl; Paleocene); 7 sinistral specimens.

2. Vestre Gasværk, Copenhagen (Paleocene); 2 sinistral specimens; microstructure: perforate radiate.
3. Kongedybet, near Copenhagen (Paleocene); 1 sinistral specimen.

It is worth mentioning that a "suite of about sixty Wills Point specimens" in PLUMMER's collection were "consistently left-handed" (PLUMMER, 1934, p. 604).

***Epistominoides danica*, n. sp.**

Pl. XI, figs. 1-3.

Diagnosis: Test oval, bilaterally unsymmetrical, very narrowly umbilicate. Ratio length/breadth varies between 1.25 and 1.38. Periphery with thin, broad flange. Dorsal face gently convex, ventral face somewhat more convex. Chambers about six in the mature whorl, increasing successively at the rate of about 1.3, subdivided internally by a thin partition that extends from the short, slit-like aperture into each chamber across its ventro-anterior angle making by its junction with the ventral wall a supplementary ventral suture close to the anterior edge of the chamber and nearly parallel to it. Septal face triangular, width about three-quarters the height and marked externally by the junction of the inner partition from the anterior end of the apertural slit part way across the apertural face and parallel to its ventral edge. Ventral sutures nearly straight and marked by a distinct bulge of the ventral wall between each true suture and the parallel supplementary suture to form well-defined ridges that radiate from a narrow umbilical depression, the ridges being sharp and narrow near the center, broader and blunter toward the periphery and finally tapering because of the slight overlap of the chambers. Dorsal sutures limbate, slightly elevated, radiating from a broad central boss and sharply curved backward near the periphery. Older chambers obscured by a secondary enamel-like deposit. Aperture a short, elongate slit located at the peripheral end of the apertural face and bounded by protruding ventral and dorsal lips. When a new chamber is added, the old aperture is sealed and partly covered by the new chamber, and a secondary septal foramen is formed close to the center of the ventral edge of the septum.

Length of holotype: .83 mm; breadth: .61 mm.

Remarks: The description, given above, follows PLUMMER's diagnosis of *E. midwayensis* rather closely. *E. danica* is distinctly different from *E. midwayensis* in having a broad, thin peripheral flange, a relatively broader test, and very distinct ventral sutural bulges that are sharply prominent near the center.

Material:

1. Rugaard, Denmark (type locality; Paleocene); 17 sinistral specimens; microstructure: perforate radiate.
2. Hvalløse, Denmark (Paleocene); 8 sinistral specimens.

The genera *Robertina*, *d'Orbigny*, and *Robertinoides*, Höglund

(Figures 2-5 in the text).

GLAESSNER (1937 and 1945) places *Robertina* in the Ceratobuliminidae, and BROTZEN (1942) even derives it directly from *Ceratobulimina*. SIGAL (1952, p. 220), citing HÖGLUND, doubts the relationship to the Ceratobuliminidae and erects the subfamily Robertininae within the Buliminidae. HÖGLUND himself, however, declares that the placing of *Robertina* in the Ceratobuliminidae seems plausible (1947, p. 23, footnote).

The genus *Robertinoides* was erected by HÖGLUND (1947, p. 222) for *Robertina*-like forms having a double main aperture, one branch of which lies at the suture between the two chamber-halves, the other in the apertural face of the distal chamber-half, and possessing a labyrinthic inner structure much more complicated than that of *Robertina*. Whether *Robertinoides* should be considered "primitive" or "advanced" in relation to *Robertina* is as yet an open question. Personally I am inclined to consider it a "primitive" form.

Among the species so excellently described and figured by HÖGLUND, *Robertinoides normani* (Goës) is the one that most nearly resembles *R. declivis* (RÆUSS), of which a fairly large suite has been available to me. Certain differences deserve mention, however. The saddle-shaped opening which in *R. normani* connects the two chamber-halves corresponds to the thin plate (g in fig. 5 in the text) which spans the septal foramen in *R. declivis* and which is really part of the floor of the "arch", as HÖGLUND has dubbed the internal structure. According to HÖGLUND (op. cit., pp. 221 and 223; pl. 19, figs. 2 b and 3), the accessory aperture at the back of the chamber constitutes the external orifice of a canal which is bounded on two sides by the laminae of the diaphragm and which has an internal orifice on the distal side of the diaphragm. In spite of careful examinations of the distal chamber-halves of well-preserved specimens of *R. declivis* I have been unable to detect any internal opening of this canal. Instead, I have observed that the canal opens into the cavity of the "arch" (fig. 5 in the text). This is in agreement with my view that the two main apertures, the accessory aperture, and the internal structure (diaphragm, "arch", lip tube, and bridge across septal foramen) are parts of one single fold of the outer test wall.

A very important point is the discovery that the septal foramen is homologous with part of the aperture (fig. 5 in the text). Although the two genera, like the Ceratobulimininae, are predominantly dextrally coiled, *Robertinoides* and *Robertina* can, therefore, not be placed in the Ceratobuliminidae, in which the septal foramen is a secondary feature (cfr. fig. 2 in the text).

Robertina arctica d'Orbigny

R. arctica, HÖGLUND, 1947, p. 219; pl. 18, fig. 2; pl. 19, fig. 1.

Material:

Bottom sample, near Spitzbergen (Recent); 5 dextral specimens.

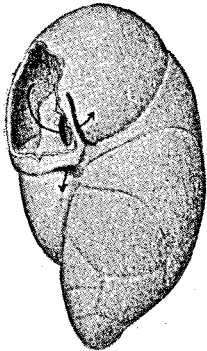


Fig. 3.

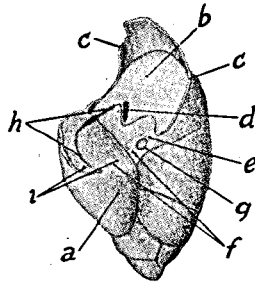


Fig. 4.

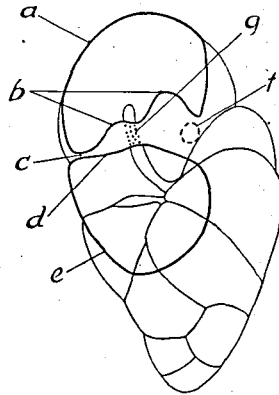


Fig. 5.

Fig. 3. *Robertinoides declivis* (REUSS). Faarup brickwork, Faarup St., Denmark (Middle Olig.). Distal chamber-half and frontal wall of lip tube of ultimate chamber opened to show passage through lip tube window leading to main apertures. Length of test: .47 mm.

Fig. 4. *Robertinoides declivis* (REUSS). Faarup brickwork, Faarup St., Denmark (Middle Olig.). Distal half and "arch" of ultimate chamber removed. *a*: proximal half of ultimate chamber. *b*: apertural face of distal half of penultimate chamber. *c*: remains of wall of distal half of ultimate chamber. *d*: septal foramen. *e*: site of distal branch of main aperture. *f*: site of proximal branch of main aperture. *g*: line of attachment of lip tube. *h*: line of attachment of "arch". *i*: diaphragm between two halves of ultimate chamber. Length of test as shown: .37 mm.

Fig. 5. *Robertinoides declivis* (REUSS). Faarup brickwork, Faarup St., Denmark. (Middle Olig.). Outline drawing of specimen in which ultimate chamber has been removed. Heavy lines indicate attachment of structures belonging to ultimate chamber. *a*: line of attachment of distal half of ultimate chamber. *b*: line of attachment of "arch". *c*: accessorial aperture and its connection with cavity under "arch". *d*: attachment of diaphragm separating two halves of ultimate chamber. *e*: line of attachment of proximal half of ultimate chamber. *f*: attachment of lip tube (not clearly visible in this specimen). *g*: thin plate bridging distal branch of main aperture of penultimate chamber. Length of specimen: .30 mm.

Robertinoides declivis (Reuss)

Figures 3-5 in the text.

Bulimina declivis, REUSS, Sitz. Ber. Akad. Wiss. Wien, vol. 48 (1), 1863, p. 55, pl. 6, figs. 70 a, b; idem vol. 62, pt. 1, p. 484.
Robertina declivis, CUSHMAN & PARKER, 1947, p. 73, pl. 18, fig. 7.

The species figured by CUSHMAN & PARKER shows but little resemblance to REUSS's type figure, but as my specimens agree perfectly with CUSHMAN & PARKER's figure and description, I prefer to use the name of *R. declivis*.

Material:

1. Faarup brickwork, Faarup St., Denmark (Middle Olig.); 44 dextral specimens; microstructure: perforate radiate.

2. Faarup brickwork, Faarup St., Denmark (Upper? Olig.); 11 dextral, 1 sinistral specimen.
3. Cilleborg, south of Mariager Fjord, Denmark (Upper Olig.); 2 dextral, 1 sinistral specimen.

The diameter of the prolocula of all my specimens varies between 30 and 60 microns. Undoubtedly all the specimens are megalospheric.

The genus *Alliatina*, n. gen.

Genotype: *Cushmanella excentrica* DI NAPOLI ALLIATA.

Diagnosis: Test free, lenticular, involute, nearly planispiral, at least in the adult stages. Test wall calcareous, of the perforate radiate type. Perforations very fine, Chambers of two kinds: large, conspicuous chambers; and small, accessory chambers in one to three series at the umbilical margins on both sides of the test. Apertures of two kinds: one a simple slit at the base of the apertural face; the other an oblique oval near the center of the apertural face. When a new chamber is added, the basal aperture is closed, while the areal aperture is enlarged somewhat and serves as the septal foramen. Within the last main chamber an asymmetrical internal partition, V-shaped in cross-section, extends across the chamber. Anteriorly, the ventral (umbilical) margin of the partition is attached to the inside of the apertural face, while the dorsal (spiral) margin is partly free. The areal aperture is enclosed within the bend of the partition. Posteriorly, the diverging wings of the partition both are attached to the preceding septal face below the septal foramen and extend to the lateral walls of the test. In the preceding chambers the partitions are partly resorbed, and only their ventral wings are preserved.

Remarks: PALMER & BERMUDEZ's figures (1936) of *Cushmanella browni* (D'ORB.), the genotype of *Cushmanella*, are not particularly clear, but in their diagnosis they expressly state that the test is bilaterally symmetrical. HOFKER (1951, fig. 11, a) represents the internal tube in *C. browni* as being bilaterally symmetrical and entirely different in its construction from the internal partition of *ALLIATINA*. Although I have not had access to material of *C. browni*, I therefore feel justified in maintaining that there is no relationship between *CUSHMANELLA* and *ALLIATINA*. That DI NAPOLI ALLIATA referred his species to *Cushmanella* is understandable in view of the similarity to *C. primitiva* CUSHMAN & McCULLOCH. The latter may, in fact, belong to *Alliatina*. (See *postscript 3*).

At first glance, the internal partition of *Alliatina* would appear to be homologous with that of *Ceratobulimina*. The impression of a close relationship is strengthened by the glistening surface of the test and the tendency toward dextral coiling in *Alliatina*. The conclusion must be, however, that *Alliatina* cannot be very closely related to *Ceratobulimina*. In *Alliatina* the septal foramen is homologous with the areal (septal) aperture, while in *Ceratobulimina* the septal foramen is formed by secondary resorption. Another important difference lies in the position of the

septal foramen with respect to the internal partition. In *Alliatina* the foramen lies within the V that is formed by the bend of the partition (i. e., on the proximal side of the partition), while in *Ceratobulimina* a line connecting the septal foramina would lie entirely outside (distally to) the internal partition (fig. 2 in the text; pl. XI).

The shape and position of the internal partition in *Alliatina* reminds one of the "arch" in *Robertinoides* (fig. 3 in the text). The partial resorption of the internal partitions in both genera is a further point of similarity. Transitional forms must be found, however, before one can seriously consider the possibility of a relationship between the two genera. At the moment, the taxonomic position of *Alliatina* must be said to be unknown.

It is possible that "*Bulimina*" *convoluta* MILLETT (non WILLIAMSON) and "*B.*" *nitida* MILLETT should be referred to *Alliatina*.

The genus is named in honor of E. DI NAPOLI ALLIATA, who first described the genotype species.

***Alliatina excentrica* (di Napoli Alliata)**

Pl. XI, figs. 4-6, 8-9, 12.

Cushmanella excentrica, DI NAPOLI ALLIATA, 1952, pp. 11-13, pl. 5, figs. 1, 1 a, 1 b.

Material:

1. "Castell'Arquato, sabbie gialle a nord del paese (Piacenza)", northern Italy (Upper Pliocene (Astiano)); 10 dextral, 1 sinistral (?) specimen (metatypes); microstructure: perforate radiate.
2. Valle Andona, northern Italy (Upper Pliocene); 8 dextral, 1 doubtful specimen; microstructure: perforate radiate.

The genera *Asterigerina*, d'Orbigny, and *Heminwayina*, Bermudez

For the genus *Asterigerina*, various descriptions of the connections between the dorsal (also called ordinary or peripheral) chamberlets and the ventral (or secondary, supplementary or stellar) chamberlets have been given by TEN DAM (1947), BROTZEN (1948) and HOFKER (1948 and 1951). As we shall see, our species vary a little in the position of the septal foramina, enough to explain the disagreements between the descriptions, just mentioned.

BROTZEN, HOFKER, and SIGAL (1952) place *Asterigerina* in (or close to) the family Ceratobuliminidae because of the supposed similarity between the internal partition in *Lamarckina* and *Ceratobulimina* and the wall between the dorsal and ventral chamberlets in *Asterigerina*.

The oldest of the species examined by me, *A. norvangi*, is in some respects a generalized type. The apertural granules, though not always present, place the species in *Asterigerina*. On the other hand, the occasional flattening of the umbilical side and, above all, the shape of the aperture

point toward *Heminwayina*. In *A. nørvangi* and the very closely related *A. primaria* PLUMMER from the Texas Midway, the aperture is nearly circular and bounded on its anterior side by a very narrow extension of the last dorsal chamberlet, while in geologically later species of *Asterigerina* the aperture is a slit of varying width along the edge of the last dorsal chamberlet. Further evidence that *A. nørvangi* belongs to an ancestral group may be found in the direction of coiling. In the small material at hand there is a tendency toward sinistral coiling. The true *Heminwayina* seems to be almost exclusively sinistrally coiled while the typical *Asterigerina* species in my material are predominantly dextral.

In *A. nørvangi* BROTZEN, *Heminwayina hemisphaerica* (CUSHMAN) and *H. mamilla* (WILLIAMSON), the aperture of the penultimate dorsal chamberlet is entirely covered by the succeeding (ultimate) ventral chamberlet. The connection between the ventral and dorsal chamberlets is effected by a rounded opening at the base of the internal partition. Similar constructions are present in *A. (?) planorbis* D'ORB. The opening can obviously not be homologous with the septal foramen in the Ceratobuliminidae where the septal foramen is placed in the main septum.

The structure of *A. gürichi* (FRANKE) appears at first glance to be somewhat different from that of the species mentioned above. Studies of large suites of specimens from the Middle and Upper Oligocene of Denmark show that in this species the connection between successive chambers is not quite as described by BROTZEN (1948, p. 125) and TEN DAM (1947). The partition between the dorsal and ventral chamberlets forms a bridge across the aperture of the preceding dorsal chamberlet in such a way that the larger portion of the aperture opens into the succeeding ventral chamberlet while a smaller opening connects with the succeeding dorsal chamberlet. In *A. gürichi* there is thus a direct connection between successive dorsal chamberlets while the ventral chamberlets only connects with the preceding dorsal chamberlet. This type of structure can easily be derived from that found in *A. nørvangi* if one imagines the internal partition moved backwards a little. It is at any rate quite evident that the septal foramina are entirely homologous with the final aperture and that there are no secondary septal foramina of the kind found in the true Ceratobuliminidae. Also the relatively coarse perforations found in *Asterigerina* and *Heminwayina* would seem to remove this group from the Ceratobuliminidae.

***Asterigerina nørvangi*, Brotzen**

A. nørvangi, BROTZEN, 1948, p. 126, pl. 18, fig. 4.

The apertural characters have been described above. According to BROTZEN, this species is biconvex in contrast to the more nearly planoconvex but otherwise closely related *A. primaria* PLUMMER of the Texas Midway formation. Specimens from the Danish Paleocene show transitions from one type to the other, and the two species may have to be united.

Material: Rugaard, Denmark (Paleocene); 6 dextral, 16 sinistral specimens; microstructure of test wall: perforate radiate.

Asterigerina gürichi (Franke)

Discorbina gürichi, FRANKE, Mitteil. Mineral. Geol. Inst. Hamburg, h. 1, 1922, pp. 29-31, fig. 1.

A. gürichi, TEN DAM & REINHOLD, 1942, pp. 90-91, pl. 7, fig. 1.

A. frankei, TEN DAM & REINHOLD, 1942, p. 91, pl. 7, fig. 3.

In the large material at hand, specimens which agree with *A. frankei* are connected through transitional stages with apparently typical *A. gürichi*, and the features which are said to be characteristic of the two species may be seen in all possible combinations. I, therefore, agree with HOFKER (1948) that the two species can hardly be kept separate.

Material:

1. Gammelgaard brickwork, Skive, Denmark (Middle Olig.); 143 specimens; about 91 % dextral; microstructure: perforate radiate.
2. Branden brickwork, Salling, Denmark (Middle Olig.); 288 specimens; about 95 % dextral; microstructure: perforate radiate.
3. Faarup brickwork, Faarup St., Denmark (Middle Olig.); 198 specimens; about 85 % dextral; microstructure: perforate radiate.
4. Cilleborg, south of Mariager Fjord, Denmark (Upper Olig.); 99 specimens; about 90 % dextral; microstructure: perforate radiate.

Asterigerina (?) planorbis, d'Orbigny

A. planorbis, MARKS, 1951, p. 66, pl. 8, figs. 1 a-c (here further references).

This species lacks the granules around the aperture typical of most *Asterigerina* species. The center of the umbilical side is either smooth or adorned by a few short, irregular wrinkles or low costae. The species may, therefore, be related to *Asterigerinata* BERMUDEZ, 1949. The nature of the septal foramina has been described on p. 466.

Material:

1. Valle Andona, Asti, northern Italy (Upper Pliocene); 114 specimens; about 98 % dextral; microstructure: perforate radiate.
2. Castell 'Arquato, northern Italy (Upper Pliocene); 12 dextral specimens; microstructure: perforate radiate.
3. Asti (exact locality not stated), northern Italy (Pliocene-Pleistocene); 23 dextral, 2 sinistral specimens; microstructure: perforate radiate.
4. Vicinity of Vienna, Austria (sand with *Strombus bonelli*; Miocene); 50 specimens; about 98 % dextral.

Heminwayina hemisphaerica (Cushman)

Discorbis hemisphaerica, CUSHMAN, Contrib. Cushman. Labor. Foram. Res., vol. 7 (3), 1931, p. 59.

H. hemisphaerica, BERMUDEZ, Soc. Cien. Nat. La Salle; Mem.; 1951, vol. 11, no. 30 (Caracas, Venezuela).

In a sample of Moody's Branch marl (Upper Eocene) from north of Jackson, Mississippi, 93 sinistral and 1 dextral specimen were found. Microstructure of test wall: perforate radiate.

Heminwayina mamilla (Williamson)

Rotalina mamilla, WILLIAMSON, Rec. Foram. Gt. Britain; Ray Soc. (London), 1858, p. 54, pl. 4, figs. 109-111.

Asterigerina mamilla, DI NAPOLI ALLIATA, 1952, p. 1.

Material:

1. Castell 'Arquato, northern Italy (Upper Pliocene); 25 sinistral specimens (in this figure is included a variety with raised, fimbriate sutures on the spiral side); microstructure: perforate radiate.
2. Bonden, Kristineberg, Sweden (Recent); 97 sinistral, 3 dextral specimens; microstructure: perforate radiate.

The genus *Eponidella*, Cushman and Hedberg

GLAESSNER (1937), BROTZEN (1942, p. 38) and SIGAL (1952, p. 234) refer *Eponidella* to the Ceratobuliminidae, undoubtedly because of its internal partition.

Four species have been described: *E. libertadensis* CUSHMAN & HEDBERG, *E. cushmani* STEPHENSON, *E. palmerae* BERMUDEZ, and *E. gardenislandensis* AKERS. At least two of the holotype specimens are sinistral, a character which makes a descendance from *Ceratobulimina* doubtful, for as we have seen that genus is almost entirely dextrally coiled. All four of the *Eponidella* species are described as being coarsely (or conspicuously) perforate, while in the true Ceratobuliminidae the wall is very finely perforate. In my opinion the taxonomic position of *Eponidella* will have to be reconsidered.

The genus *Anomalinella*, Cushman

BROTZEN (1942) derives this form from *Epistomina* because of its lateromarginal aperture. I agree with SIGAL (1952, p. 229) that *Anomalinella* should be placed among the Anomalinidae. SIGAL's argument would seem to be the coarse perforations found in that genus. I, myself, wish to point out that of the two apertures, a lateromarginal and an interiomarginal one, only the former is sealed when a new chamber is added, while the interiomarginal aperture remains open and serves as the septal foramen, a character which removes the genus from the Ceratobuliminidae. There is, further, no trace of an internal partition, and as first shown by ALAN WOOD (1948), the microstructure of the test wall is perforate granulate.

In my collection I have 10 specimens of *A. rostrata* (BRADY) from a bottom sample (depth: 20 meters), taken near Waling in the Kei Islands

in the East Indies. If the position of the lateromarginal aperture is taken to indicate the ventral side of the test, 7 of my specimens are sinistral. The species is probably coiled at random.

The genera *Alabamina*, *Toulmin*, *Osangularia*, *Brotzen*, *Pulsiphonina*, *Brotzen* and *Siphonina*, *Cushman*

BROTZEN (1942 and 1948) (and after him SIGAL, 1952) placed these genera near the Epistominidae (Ceratobuliminidae) because of their apertural characters. The septal fold ("scrobis septalis" plus "infundibulum") in *Alabamina* he correlated with the marginal aperture and the internal partition in *Epistomina*, while the two apertures (areal and interiomarginal or basal) in *Osangularia* (= *Parella*, FINLAY, 1939) reminded him of the marginal aperture and the basal or areal septal foramen in *Epistomina*. From *Osangularia* he derived such genera as *Pulsiphonina* and *Siphonina* (1948, pp. 105-106).

After having examined a number of species of these genera from the Upper Cretaceous, the Danien and the Cenozoic I have come to the conclusion that they cannot be derived from *Epistomina* or related forms. The lack of an internal partition may not be of much importance as the partition may have been lost by reduction (TEN DAM, 1948 b, however, removes *Parella* [*Osangularia*] and *Pulvinulinella* from the Ceratobuliminidae because of their lack of an internal partition). Neither can the direction of coiling be considered conclusive evidence. Most of the early species of the four genera, mentioned above, are coiled at random while preferred directions (generally sinistral) do not occur until the Cenozoic, but we have seen that some of the early species of *Epistomina* likewise are coiled at random. It is of decisive importance, however, that the septal foramen in the four genera is homologous with the external aperture (or part of it); in other words, the septal foramen is of primary, not secondary origin.

The genera *Allomorphina*, *Reuss*, *Valvulineria*, *Cushman*, and *Quadriformina*, *Finlay*

Pl. XI, figs. 7, 10, 11, 13.

The three genera, listed, above, may seem to have very little in common with the other forms treated in this paper. I have included them in my revision of the Ceratobuliminidae because BROTZEN (1948), in his beautiful account of the internal partition in *Allomorphina halli* JENNINGS, suggests the possibility of a connection with Ceratobuliminidae.

The genus *Allomorphina* is easily dealt with. BROTZEN (1948, p. 129) declares that he has not examined the genotype, *A. trigona* REUSS, and that it may not have the same structure as "*Allomorphina*" *halli* JENNINGS. Through the courtesy of Drs. R. GRILL and C. W. DROOGER I have had occasion to examine good specimens of *A. trigona* from the Vienna Basin,

and I have found that they have no internal partitions at all. In a closely related species from the Paleocene of Denmark (pl. XI, fig. 13) I have found a similar lack of internal partition; further, that the apertural lip is a narrow band with subparallel sides while the lip in "*Allomorpha*" *halli* is triangular.

"*Allomorpha*" *halli* is, in other words, no *Allomorpha* at all, and its relatives must be sought elsewhere. BROTZEN (1948, p. 130) mentions the possibility of a connection with "Cretaceous *Valvulineria* and *Quadriformina allomorphinoides* (REUSS) and ... *Rotamorphina cushmani*", and I have therefore examined such representatives of these forms as I have been able to find in my samples.

"A." *halli* from the Vincentown formation of New Jersey turned out to have exactly the same internal structure as BROTZEN's specimens from the Paleocene of Sweden.

In *Quadriformina allomorphinoides* (REUSS) from the Lower Senonien of Eriksdal, southern Sweden, I found the structure shown in pl. XI, fig. 10. The umbilical lip of the penultimate chamber is crossed by a low internal partition (α in pl. XI, fig. 10), which divides the septal foramen into two parts. The internal partition continues on the inside of the umbilical lip of the ultimate chamber as a narrow crest running more or less parallel to the aperture. This is almost exactly what BROTZEN found in "A." *halli*. We see (1) that "*Allomorpha*" *halli* should be referred to *Quadriformina* and (2) that the septal foramen of the latter is homologous with (part of) the aperture and that a relationship to the Ceratobuliminidae can therefore be excluded.

A further search disclosed that various "*Valvulineria*" species from the Upper Danien of Sweden, the Paleocene of Denmark and the Vincentown formation of New Jersey had similar structures in their interiors. One of them is shown in pl. XI, fig. 7. The question is, then, whether a connection exists between *Quadriformina* and *Valvulineria*. I must here refer to ALAN WOOD (1948), who found that *Valvulineria californica* CUSHMAN, the genotype, belongs to the group having a perforate radiate type of test wall, while both *Allomorpha* and *Quadriformina allomorphinoides*, the genotype, show a perforate granulate microstructure of the test wall. A renewed examination of my material showed that a *Valvulineria* from the Middle Oligocene of Faarup, Denmark, had no trace of an internal partition and that its test belonged to the perforate radiate type, while, on the other hand, a specimen of *Valvulineria laevigata* PHLEGER & PARKER (Recent Globigerina-mud, Atlantic Ocean) belonged to the perforate granulate type and had faint traces of an internal partition. Also the Danien-Paleocene "*Valvulineria*'s" having internal partitions turned out to belong to the perforate granulate type and should be referred to *Quadriformina*. The genus *Valvulineria* ought probably to be revised in the light of Alan Wood's discoveries.

It is a curious fact that the largest internal partitions are found in the *Quadriformina* species having the smallest number of chambers in their final whorls.

Our conclusion must be (1) that *Allomorpha*, *Quadriformina* and

Valvulineria are not closely related, and (2) that the genus *Quadriformina*, FINLAY, 1939, must be redefined. I propose the following diagnosis:

Test flatly trochoid; three to six chambers in the final whorl; aperture umbilical, covered by a large, rounded or triangular lip; umbilical lips of earlier chambers carry low internal partitions, which run at an angle to the septal foramina, and which commonly continue on the inside of the next following umbilical lips as narrow crests. Test wall of the perforate granulate type; perforations fine.

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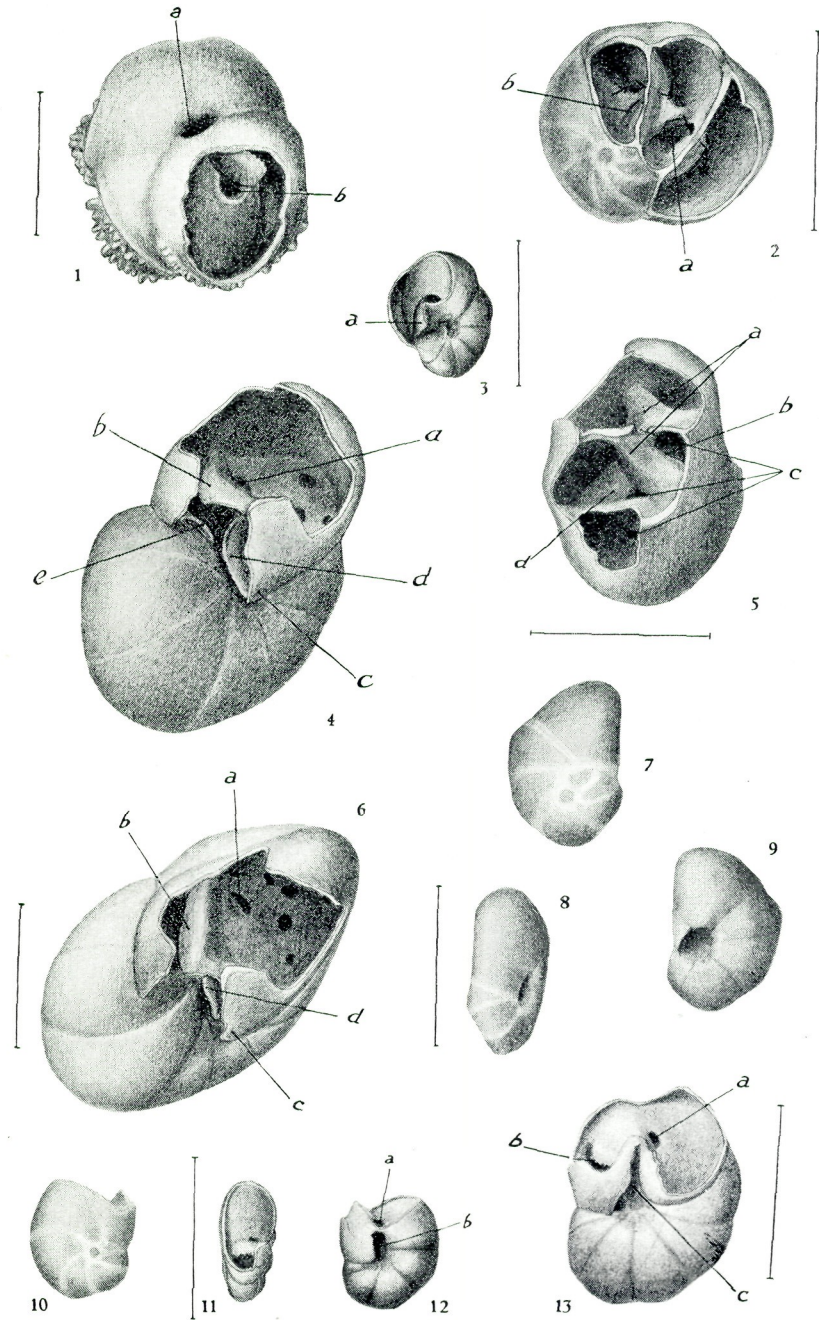
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Plate X

- Lamarckina rugulosa* PLUMMER. 2 miles N.N.W. of Mexia, Tehuacana, Texas. Wills Point form. (Paleocene). H. J. PLUMMER det.
- Fig. 1. Ventral view of specimen in which ultimate chamber has been opened. *a*: external aperture (in umbilicus). *b*: septal foramen. The short internal partition may be seen between *a* and *b*.
- Lamarckina wilcoxensis* CUSHMAN. 1 mile N. of Ozark, Alabama. Wilcox form. (Eocene?). G. M. PONTON leg.
- Fig. 2. Dorsal view of specimen in which three chambers have been opened. Arrows indicate route protoplasma must follow through septal foramina to pass out of test. *a*: thin plate closing aperture and replacing part of apertural face. Above plate may be seen free edge of internal partition. *b*: thin plate connecting edge of internal partition with floor of chamber whereby vestibule is sealed off.
- Ceratobulimina (Ceratolamarckina) woodi* KHAN. Folkestone, England (Gault).
- Fig. 3. Oblique ventral view showing (at *a*) remnants of internal partition. Below partition may be seen vestibule, which opens into umbilicus. Above partition lies septal foramen.
- Figs. 10-12. Dorsal, peripheral and ventral views of another specimen, in which ultimate chamber is incomplete. *a*: septal foramen. *b*: external aperture.
- Ceratobulimina (Ceratolamarckina) jullandica* n. subgen., n. sp. Rugaard, Denmark (Paleocene).
- Figs. 7-9. Dorsal, peripheral and ventral views of holotype.
- Ceratobulimina (Ceratocancris) aff. haueri* (D'ORB.). Baden near Vienna, Austria (Late Mediterr. stage; Miocene).
- Fig. 4. Oblique ventral view into ultimate chamber. *a*: septal foramen (the other openings in the septum are resorption phenomena not normally found in this species). *b*: edge of internal partition. *c*: umbilical lip of ultimate chamber. *d*: umbilical lip of penultimate chamber. *e*: accessory internal partition of ultimate chamber.
- Fig. 6. Another view of same specimen.
- Ceratobulimina (Ceratobulimina) contraria* (REUSS). Faarup brickwork, Faarup St., Denmark (Middle Olig.).
- Fig. 5. Oblique dorsal view showing internal partitions (*a*) of last two chambers. *b*: free edge of internal partition of penultimate chamber. *c*: septal foramina of last three chambers. *d*: septum.
- Fig. 13. Ventral view showing position of septal foramen (*a*), internal partition (its free edge is marked by *b*) and external aperture (*c*).

The scales each represent .25 mm. All figured specimens are kept in the type collection of the Mineralogisk-geologisk Museum, Copenhagen.

Paratypes of new species to be deposited in the U. S. National Museum.



Postscript 1. (page 453):

In specimens of *Ceratobulimina* (*Ceratobulimina*) *kellumi* FINLAY, generously presented by Dr. N. DE B. HORNIBROOK traces of a similar pit may be seen.

Postscript 2 (page 454):

In topotypes of *Ceratobulimina* (*Ceratocancris*) *clifdenensis* FINLAY, acquired through the courtesy of Dr. HORNIBROOK, the accessory internal partition is present, though fragile. Also in other respects, such as the shape of the main internal partition and the bulge above the aperture, *C. clifdenensis* resembles *C. haueri*. *Ceratocancris* can thus be defined as a group of *Ceratobulimina* species in which the aperture is umbilical and basal; the notch at the posterior (distal) end of the aperture a very small one; the internal partition not attached to the dorsal chamber wall; and a low accessory internal partition attached to the surface of the previous whorl just inside the external aperture.

Postscript 3 (page 464):

The assumption of a fundamental difference between *Cushmanella* and *Alliatina* is confirmed through examination of topotypes of *C. browni* (D.ORB.), generously presented by Dr. P. J. BERMUDEZ.

Plate XI

Epistominoides danica n. sp. Rugaard, Denmark (Paleocene).

Figs. 1-3. Ventral, peripheral and dorsal views of holotype.

Alliatina excentrica (DI NAPOLI ALLIATA) n. gen. Metatypes of the genotype species. "Castell'Arquato ... a nord del paese (Piacenza)" (Upper Pliocene).

Fig. 4. Oblique dorsal view, showing septal foramen (*a*), internal partition (its ridge marked *b*) and areal aperture (*c*).

Figs. 5-6. Peripheral and ventral views of complete specimen. *a*: areal aperture. *b*: suture marking ventral attachment of internal partition. *c*: basal (interiomarginal) aperture.

Fig. 8. Peripheral view of specimen in which part of apertural face (fig. 9) has been broken away. Shows internal partition and septal foramen.

Fig. 9. Inside view of apertural face of specimen shown in fig. 8. Shows attachment of internal partition to apertural face. Areal aperture lies within bend of partition.

Fig. 12. View of posterior side (inside) of septum between ultimate and penultimate chambers. Shows septal foramen and internal partition, of which only ventral wing has escaped resorption.

Quadriformina allomorphinoides (REUSS). Eriksdal, southern Sweden (Lower Senonian).

Fig. 10. Ventral view of specimen with ultimate chamber opened. *a*: internal partition. *b*: part of septal foramen. *c*: umbilical lip of ultimate chamber. *d*: crest on inside of umbilical lip.

Quadriformina sp. Kerteminde, Denmark (Paleocene).

Fig. 7. Oblique ventral view. Part of wall, including umbilical lip, has been removed from ultimate chamber. *a*: internal partition. *b*: part of septal foramen. *c*: umbilical lip of penultimate chamber. *d*: matrix filling part of chamber.

Quadriformina? sp. Bjärnum, southern Sweden (Maestrichtien).

Fig. 11. Ventral view. Greater part of ultimate chamber removed. *a*: broken edges of ultimate chamber. *b*, *c*, *d*: three preceding chambers. *e*: aperture of ultimate chamber viewed from within. *f*: part of septal foramen (aperture of penultimate chamber), the rest being concealed behind internal partition. *g*: internal partition of ultimate chamber. Note the untypical narrow apertural lip.

Allomorphina aff. *macrostoma* KARRER. Kongedybet near Copenhagen (Paleocene).

Fig. 13. Inside view of broken specimen. *a*: remnants of ultimate chamber. *b*: aperture of ultimate chamber. *c*: remnants of penultimate chamber. *d*: septal foramen (aperture of penultimate chamber). *e*: aperture of third-but-last chamber.

The scales each represent .25 mm.

All figured specimens are kept in the type collection of the Mineralogisk-geologisk Museum, Copenhagen.

Paratypoids of new species to be deposited in the U. S. National Museum.

