

# THE CLASSIFICATION AND STRATIGRAPHICAL DISTRIBUTION OF THE GLOBIGERINACEAE

## PART I

by F. T. BANNER and W. H. BLOW

ABSTRACT. In this paper, the first of a series on the superfamily Globigerinaceae (Carpenter, emended), a new classification is given, comprising three families and eleven subfamilies. Two new subfamilies (Globorotaloidinae and Sphaeroidinellinae), two new genera (*Pseudohastigerina* and *Sphaeroidinellopsis*), two new subgenera (*Praeglobotruncana* (*Clavhedbergella*) and *Hastigerina* (*Bolliella*)), and one new species (*Hastigerina* (*Bolliella*) *adamsi*) are proposed. Particular attention is given to problems resulting from iterative evolution, and the broad aspects of the phylogeny of the superfamily are discussed.

### INTRODUCTION

THE history of previous attempts satisfactorily to classify the planktonic foraminifera, grouped in this paper as members of the Globigerinaceae, has been given adequately by Bolli, Loeblich, and Tappan (1957, pp. 17-21), and little could be added to it here. The recent work of Reiss (1957, pp. 127-43; 1958, pp. 68-69) on the fundamental wall-structure of the smaller foraminifera follows from that of Smout (1954) and shows great promise of providing a firm basis for general classification; it is, however, too general in scope to enable finer subdivisions within superfamilies to be made.

Bolli, Loeblich, and Tappan's work is the most comprehensive and important recent study, and appeared while our own work was in progress. Although agreeing to some extent with the results of their studies, especially with regard to the principles of generic distinctions, we disagree with them over the fundamental basis of classification. They appear to over-emphasize the importance of the precise position of the interiomarginal aperture relative to the extent of the umbilicus, and attach little value to the presence or absence of a keel. As a result, it is often difficult for these authors to distinguish satisfactorily between superficially similar but actually unrelated genera. The generic diagnoses given by them for *Praeglobotruncana* (op. cit., p. 39) and for *Globorotalia* (op. cit., p. 41) are virtually indistinguishable, even though the genera are clearly different and have quite distinct stratigraphical ranges. Their system of classification has resulted, for example, in no clear distinctions being made between their interpretations of the families 'Orbulinidae' and 'Globorotaliidae'. In both these 'families', the coiling may be trochospiral, the chambers ovate or spherical, the primary aperture may be umbilical-extraumbilical ('spiro-umbilical' in *Hastigerinella*, 'extraumbilical' in *Pulleniatina*, both referred to the Orbulinidae), and secondary sutural apertures may be present (op. cit., pp. 31, 39). The range of both families, consequently, is given as Cretaceous to Recent, the range of the superfamily.

Sigal (1958) expressed a view almost completely opposed to that of Bolli, Loeblich, and Tappan (1957); he attached little importance at family level to the position of the

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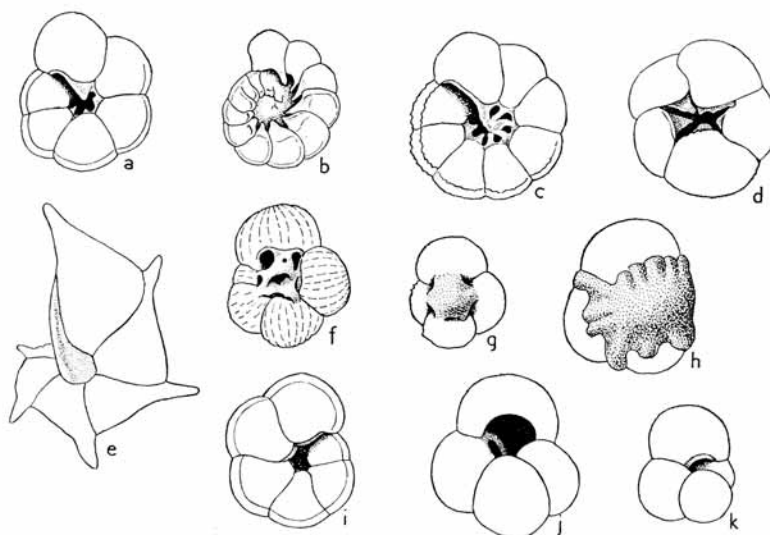
interiomarginal primary aperture relative to the umbilicus, but used the presence of carinae, mode of coiling and the shape of the adult chambers. These latter characters are believed by us to occur iteratively throughout the range of the superfamily, and we consider them to be of no more than generic or subgeneric importance.

We have tried to base our classification at family level on the fewest possible common morphological characters, which, in our interpretation, are of kind rather than of degree. We also consider that the least subjective means of determining the significance of any morphological character, in these very simply constructed but highly variable foraminifera, is its range in geological time. It is well known that members of the Globigerinaceae with spherical, ovate, clavate, or spinose chambers, with trochospirally or planispirally coiled adult tests, with apertures confined to the umbilicus or extending outside it or even reaching the periphery in an equatorial position, have occurred in the Cretaceous, Palaeogene, and Neogene. But it is clearly noticeable that external structural modifications of the apertures are comparatively restricted, and it is on these we have based our classification. Imperforate, distinctly asymmetrical flaps (portici) occur from the Cretaceous to Eocene (and possibly in the Oligocene—see p. 20) only; the complex imperforate umbilical coverplates (tegilla) which reached their maximum development in the younger species of *Globotruncana* are confined to the Upper Cretaceous; thin, narrow, practically symmetrical, perforate lips are often present on post-Cretaceous forms, except where they broaden to form equally symmetrical 'umbilical teeth' (e.g. *Globoquadrina*) or where they are replaced in the adult by perforate inflated bullae, which are again unknown before the Tertiary. These structures (see text-fig. 1) have been taken, therefore, to define the three families of the Globigerinaceae. Modifications of the primary apertures themselves, their shape and position, have been used to define the subfamilies; these characters can, of course, grade, and we hope that intra-family relationships will then emerge. The presence or absence of true supplementary apertures, accessory apertures, relict apertures (see Glossary), together with the development of elongate, clavate, or tubulospinose chambers and the presence or absence of imperforate peripheral keels (carinae) have been used to define the genera and subgenera. We distinguish between the true carina, which is imperforate and probably a primary structure, and which is believed to be of subgeneric value, and the pseudocarina, which is merely a peripheral thickening of the test wall, perforate uniformly with the remainder of the test, and which we consider to be of no more than specific importance.

In order to make this classification as unambiguous as possible, it has been partly set out in tabular form, the comment reduced to a minimum. It has been found necessary to erect two new genera and two new subgenera. The known ranges of the taxonomic groups are inserted in parentheses. This paper is an introduction to an exhaustive and fully illustrated study of all published species of the Globigerinaceae, which is now in preparation. In this, and in all succeeding parts, the authors' names are alphabetically arranged, and the arrangement implies no seniority of authorship whatsoever.

Throughout our work we have adhered strictly to the Rules of the International Commission on Zoological Nomenclature; failure to do so has often caused confusion in terminology, and we are strongly of the opinion that excessive invocation of exceptions is highly undesirable since they tend to make the rules themselves ineffective. We greatly regret the opinion rendered by the I.C.Z.N. (opinion 552), which rejected the prior family name *Orbulinidae* Schultze in favour of *Globigerinidae* Carpenter on the grounds of

usage, since the change seems to us to be quite unnecessary, and some of the facts given in the proposal (Dusenbury 1957, *Bull. Zool. Nomencl.* **13**, part 6) can be shown to be incorrect—for example, the range of the genus *Globigerina* is not so great as that claimed by Dusenbury (op. cit., p. 194) and the apparent abundance of the genus *Globigerina* in Recent deposits is reduced when the interpretation of that genus is restricted.



TEXT-FIG. 1. Diagrams illustrating the apertural accessory structures of the Globigerinaceae. *a*, *Praeglobotruncana* (*Praeglobotruncana*) *stephani* (Gandolfi); after Reichel (1949) 1950,  $\times 50$ ; showing umbilical-extraumbilical primary aperture furnished with an asymmetric imperforate porticus. *b*, *Planomalina* (*Planomalina*) *chenioursensis* (Sigal); after Sigal 1952,  $\times 37.5$ ; showing asymmetric imperforate portici covering the primary and the relict parts of the previous apertures. *c*, *Ticinella alpha* (Reichel); after Reichel (1949) 1950,  $\times 50$  (*Globotruncana* (*Thalmaninella*) *ticinensis* var. *alpha* Gandolfi of Reichel, first valid transliteration of '*Globotruncana ticinensis* var.  $\alpha$ ' Gandolfi 1942); showing distal fusion of the portici, and formation of accessory apertures. *d*, *Globoquadrina altispira* (Cushman and Jarvis); after Bolli, Loeblich, and Tappan 1957,  $\times 35$ ; showing essentially perforate, practically symmetrical 'umbilical teeth'. *e*, *Hantkenina* (*Hantkenina*) *alabamensis* Cushman; after Brönnimann 1950,  $\times c. 50$ ; showing the accentuated asymmetry of the porticus by its distal elongation and extension over the umbilicus. *f*, *Rugoglobigerina* (*Rugoglobigerina*) *rugosa* (Plummer); after Bolli, Loeblich, and Tappan 1957,  $\times c. 50$ ; showing imperforate complex tegillum covering the umbilicus. *g*, *Catapsydrax dissimilis* (Cushman and Bermúdez); after Bolli, Loeblich, and Tappan 1957,  $\times 30$ ; showing perforate, convex bulla covering the umbilicus, and its marginal accessory apertures. *h*, *Tinophodella ambitacrena* Loeblich and Tappan; after Loeblich and Tappan 1957,  $\times 72.5$ ; showing the morphologically advanced form of the single, perforate, inflated bulla which covers the umbilicus. *i*, *Globorotalia* (*Globorotalia*) *menardii* (d'Orbigny); after Phleger, Parker, and Peirson 1953,  $\times 17$ ; showing the perforate, symmetrical lip and umbilical-extraumbilical aperture. *j*, *Globigerina bulloides* d'Orbigny; after Bolli, Loeblich, and Tappan 1957,  $\times 57.5$ ; showing the intraumbilical aperture, and the loss of the apertural lip in morphologically advanced forms of the Globigerininae. *k*, *Globigerina triloculinoides* Plummer; after Loeblich and Tappan 1957,  $\times 72.5$ ; showing the intraumbilical aperture, with the symmetrical perforate lip of the morphologically more primitive forms of the Globigerininae.

## CLASSIFICATION

## Order FORAMINIFERA

Superfamily GLOBIGERINACEAE Carpenter 1862, emended; nom. transl.

(Synonyms Globigerinidea Schwager 1876, Globigerinidea Morozova 1957)

*Diagnosis.* Coiled, multilocular Foraminifera with hyaline, perforate, calcareous walls which are radial in structure and characteristically more or less spinose or hispid superficially, although this hispidity is reduced in advanced forms and is often lost in the later chambers of adult individuals. Usually trochospirally coiled, at least in the young of the microspheric form; sometimes becoming involute and turgid; or planispiral, evolute and laterally compressed in the adult or in advanced forms; very occasionally becoming enrolled biserial, never rectilinear. Septa simple, lacking canal systems. Imperforate peripheral carinae (which may tend to become occluded internally but which never form discrete canals) may be present, but no tectoria or associated infundibulae occur. No umbilical plugs, pillars, or canal systems are present. No internal tubes, toothplates, tongues, or other structures internally modifying the apertures occur; apertural accessory structures are always external. Habitat believed to be always planktonic in normal marine environments, at least in the juvenile stage.

Family GLOBIGERINIDAE Carpenter 1862, nom. correct.

(Synonym Orbulinida Schultze 1854; suppressed by I.C.Z.N. Op. 552)

*Diagnosis.* Globigerinaceae which possess apertures unmodified by tegilla or portici, but which may possess narrow, perforate, symmetrical lips, or, in advanced forms, perforate bullae or umbilical teeth, or in which the primary aperture may be concealed in the adult and is replaced by multiple small apertures or large pores. Tests trochoid, adults dorsally evolute, ventrally involute, or completely involute, or evolute both ventrally and dorsally [Range: Danian to Recent].

Subfamily ORBULININAE Schultze 1854, emended, nom. transl.

(Synonym Candeininae Cushman 1927 in part)

Globigerinidae with no distinct primary aperture visible externally in the adult; adult apertures sutural and/or areal, a series of slit-like or pore-like openings, with no specialized accessory structures [Eocene; L. Miocene to Recent].

1. Apertures a series of discontinuous pores, some at least areal in position:

- (a) Last chamber embracing all or nearly all of earlier test:  
genus *Orbulina* d'Orbigny 1839 (L. Miocene to Recent), type species *O. universa* d'Orbigny, 1839.  
(Synonym *Candorbulina* Jedlitschka 1934, type species *C. universa* Jedlitschka 1934.)
- (b) Penultimate chamber embracing all or nearly all of earlier test:  
genus *Biorbulina* Blow 1956 (L. Miocene to Recent), type species *Globigerina bilobata* d'Orbigny 1846.

## 2. Apertures confined to sutures:

- (a) Last chamber embracing much of earlier test:
- (i) Apertures small, slit-like or pore-like, present between earlier as well as later chambers:  
genus *Porticulasphaera* Bolli, Loeblich, and Tappan 1957 (M. Eocene and L. Miocene),  
type species *Globigerina mexicana* Cushman 1925.
- (ii) Apertures arched, in suture of last chamber only:  
genus *Globigerapsis* Bolli, Loeblich, and Tappan 1957 (M. to U. Eocene), type species  
*G. kugleri* Bolli, Loeblich, and Tappan 1957.
- (b) Last chamber not embracing earlier test; chambers in relatively high trochoid spire, few in  
number in last whorl; apertures a series of small arched openings:  
genus *Candeina* d'Orbigny 1839 (L. Miocene to Recent), type species *C. nitida* d'Orbigny  
1839.

## Subfamily GLOBIGERININAE Carpenter 1862, emended, nom. transl.

Globigerinidae, in which the adult test is clearly trochoid, and possesses a distinct primary interiomarginal intraumbilical aperture in the adult. Wall structure simple [Danian to Recent].

## 1. Without supplementary apertures:

- (a) Aperture intraumbilical throughout ontogeny:  
genus *Globigerina* d'Orbigny 1826 (Danian to Recent), type species *G. bulloides* d'Orbigny  
1826.
- (b) Aperture initially extraumbilical in part, but becoming solely intraumbilical in ontogeny;  
typically with exceptionally strong lips (umbilical teeth):  
genus *Globoquadrina* Finlay 1947 (Aquitanian to Pliocene), type species *Globorotalia dehiscens*  
Chapman, Parr, and Collins 1935.

## 2. With supplementary sutural dorsal apertures:

- genus *Globigerinoides* Cushman 1927 (Danian to Recent), type species *Globigerina rubra*  
d'Orbigny 1839.

## Subfamily SPHAERODINELLINAE, new subfamily

Globigerinidae, in which the adult test is clearly trochoid, and possesses a distinct primary interiomarginal umbilical aperture throughout life. Wall structure complex, consisting, at least in part, of more than one layer of shell material; primary wall covered by a secondary cortex, superficially smooth and shiny, in which the perforations of the primary wall may be much reduced or absent. Lips thickened to become flange-like, often crenulate, but still fundamentally symmetrical [L. Miocene to Recent].

## 1. Without supplementary sutural apertures in the adult:

- genus *Sphaeroidinellopsis* gen. nov. (L. to U. Miocene), type species *S. subdehiscens* (Blow)  
= *Sphaeroidinella dehiscens subdehiscens* Blow 1959.

## 2. With supplementary sutural apertures in the adult:

- genus *Sphaeroidinella* Cushman 1927 (U. Miocene? to Pliocene to Recent), type species *Sphaeroidinella bulloides* (d'Orbigny) var. *dehiscens* Parker and Jones 1865.

## Subfamily CATAPSYDRACINAE Bolli, Loeblich, and Tappan 1957

Globigerinidae, in which the test is clearly trochoid, and possesses a primary interiomarginal intraumbilical aperture which is covered in the adult by a swollen perforate plate

(bulla) or by a bulla-like extension of the last chamber, and which opens to the exterior by accessory apertures at the margins of, or within the area of, the bulla [Eocene to Recent].

1. Without supplementary apertures in the primary chambers:
  - (a) Umbilicus and primary aperture covered by a discrete bulla:
    - (i) Primary chamber wall and bulla similar in structure; accessory apertures few and unrestricted:
 

genus *Catapsydrax* Bolli, Loeblich, and Tappan 1957 (L. Eocene to L. Miocene), type species *Globigerina dissimilis* Cushman and Bermúdez 1937.
    - (ii) Primary wall thicker and more coarsely perforate than bulla; accessory apertures small, numerous, often restricted by lips:
 

genus *Tinophodella* Loeblich and Tappan 1957 (L. Miocene to Recent), type species *T. ambitacrena* Loeblich and Tappan 1957.
  - (b) No discrete bulla; umbilicus covered by perforate, bulla-like extension of last chamber wall:
 

genus *Globigerinita* Brönnimann 1952 (L. Miocene to Recent), type species *G. naparimaensis* Brönnimann 1952.
2. With supplementary sutural apertures in primary chambers, covered by bullae:
  - (a) With an early *Globigerinoides*-stage; supplementary apertures present in sutures of last chamber and some at least of earlier chambers:
 

genus *Globigerinoita* Brönnimann 1952 (M. Miocene), type species *G. morugaensis* Brönnimann 1952.
  - (b) With an early *Globigerapsis*-stage; supplementary apertures present only in the suture of the last chamber:
 

genus *Globigerinatheka* Brönnimann 1952 (M. to U. Eocene), type species *G. barri* Brönnimann 1952.
3. Supplementary apertures sutural and areal; bullae formed in at least two series, with secondary bullae covering accessory apertures in primary bullae:
 

genus *Globigerinatella* Cushman and Stainforth 1945 (L. Miocene), type species, *G. insueta* Cushman and Stainforth 1945.

Subfamily GLOBOROTALIINAE Cushman 1927 emended, nom. transl.

(Synonym, in part, Pulleniatininae Cushman 1927)

Globigerinidae, in which the test is clearly trochoid, possessing a primary aperture which is umbilical–extraumbilical and ventral in ontogeny, and in the adult [Danian to Recent].

- I. Test uniformly trochospiral throughout life:
  - (1) No dorsal supplementary apertures:
 

genus *Globorotalia* Cushman 1927 (Danian to Recent), type species *Pulvinulina menardii* (d'Orbigny) var. *tumida* Brady 1877.

(Synonyms *Truncorotalia* Cushman and Bermúdez 1949, type species *Rotalina truncatulinoides* d'Orbigny 1839; ? *Pseudogloborotalia* Haque 1956, type species *P. ranikotensis* Haque 1956; *Planorotalites* Morozova 1957, type species *Globorotalia pseudoscitula* Glaessner 1937.)
  - (a) Test with an imperforate peripheral carina, at least in part:
 

Subgenus *Globorotalia* (U. Palaeocene to Recent).
  - (b) Test without imperforate peripheral carina:
    - (i) Chambers not radially elongate:
 

Subgenus *Turborotalia* Cushman and Bermúdez 1949 (Danian to Recent), type species *Globorotalia centralis* Cushman and Bermúdez 1937.

(Synonyms *Acarinina* Subbotina 1953, type species *A. acarinata* Subbotina 1953; *Globanomalina* Haque 1956, type species *G. ovalis* Haque 1956.)

(ii) Adult chambers radially elongate:

Subgenus *Hastigerinella* Cushman 1927 (L. Miocene to Recent), type species *Hastigerina digitata* Rhumbler 1911 (not *Globigerina digitata* Brady 1879) = *Hastigerinella rhumbleri* Galloway 1933.

(2) With dorsal sutural supplementary apertures:

genus *Truncorotaloides* Brönnimann and Bermúdez 1953 (L. to U. Eocene), type species *T. rohri* Brönnimann and Bermúdez 1953.

II. Test becoming streptospiral in adult:

genus *Pulleniatina* Cushman 1927 (M. Miocene? to U. Miocene to Recent), type species *Pullenia sphaeroides* d'Orbigny var. *obliquiloculata* Parker and Jones 1869.

#### Subfamily GLOBOROTALOIDINAE new subfamily

Globigerinidae, in which the test is clearly trochoid, possessing a primary aperture which is interiomarginal umbilical–extraumbilical during ontogeny, but which is covered in the adult by a bulla [Eocene to Miocene].

genus *Globorotaloides* Bolli 1957 (M. Eocene to M. Miocene), type species *G. variabilis* Bolli 1957.

#### Subfamily HASTIGERININAE Bolli, Loeblich, and Tappan 1957, emended

Globigerinidae, in which the test is initially distinctly trochospiral, but becomes nearly, but imperfectly, planispiral in the adult; juvenile interiomarginal umbilical–extraumbilical aperture becomes extraumbilical–peripheral (equatorial) in the adult [L. Miocene to Recent].

genus *Hastigerina* Thomson 1876 (L. Miocene to Recent), type species *H. murrayi* Thomson 1876 = *Nonionina pelagica* d'Orbigny 1839.

(Synonym *Globigerinella* Cushman 1927, type species *Globigerina aequilateralis* Brady 1879.)

1. Chambers not radially elongate in adult:

Subgenus *Hastigerina* (L. Miocene to Recent).

2. Chambers radially elongate in adult:

Subgenus *Bolliella* subgen. nov. (Recent), type species *Hastigerina (Bolliella) adamsi* sp. nov.

#### Subfamily CASSIGERINELLINAE Bolli, Loeblich, and Tappan 1957

Globigerinidae with an initial trochoid stage followed by enrolled biserial ('cassidulini-form') coiling in the adult [Oligocene to Lower Miocene].

1. Aperture interiomarginal, simple:

genus *Cassigerinella* Pokorný 1955 (Oligocene to Lower Miocene), type species *C. boudecensis* Pokorný 1955.

(Synonym *Globalternina* Ivanova, in Subbotina, Glushko, and Pishvanova 1955, type species (by monotypy) *G. globolocolata* Ivanova 1955 MS. (nom. nud.) = *Cassigerinella globolocolata* Ivanova 1958.)

#### Family HANTKENINIDAE Cushman 1927, emended

*Diagnosis.* Globigerinaceae with tests which are primitively or initially trochospiral (at least in the microspheric form), advanced forms often becoming planispiral. The test is

characterized by a primary aperture which is modified by an imperforate porticus, which is essentially an asymmetric, imperforate flap-like projection from the chamber wall into the umbilicus, more or less covering the primary aperture. The portici may, in primitive forms, be so strongly developed over the relict apertures in all chambers of the last whorl that they fuse to form accessory apertures (Rotaliporinae, in part); in advanced forms they may be visible on the later chambers or last chamber only. No bullae, tegilla, true lips, or umbilical teeth are present [Range: Lower Cretaceous to Palaeogene].

Subfamily ROTALIPORINAE Sigal 1958, emended, nom. transl.

Hantkeninidae which are trochospirally coiled throughout life, and which possess an umbilicus and apertures on the ventral side only. Primary aperture interiomarginal, umbilical–extraumbilical, not extending beyond the periphery on to the dorsal side. Portici strong on all chambers of the last whorl [Aptian to Maestrichtian].

1. Portici fuse distally:

- (a) No supplementary apertures; relict parts of primary apertures open to exterior through accessory apertures between unfused proximal parts of portici:
  - genus *Ticinella* Reichel 1950 (Aptian? to Albian to Turonian to L. Coniacian?), type species *Anomalina roberti* Gandolfi 1942.
  - (Synonym *Helvetoglobotruncana* Reiss 1957, type species *Globotruncana helvetica* Bolli 1945.)
- (b) With true supplementary ventral sutural apertures, opening to exterior beyond the portici:
  - genus *Rotalipora* Brotzen 1942 (U. Albian? to L. Turonian), type species *R. turonica* Brotzen 1942 = *Globorotalia cushmani* Morrow 1934.
  - (Synonym *Thalminella* Sigal 1948, type species *T. brotzeni* Sigal 1948.)

2. Portici distinct, separate or fused proximally, but not forming accessory or supplementary apertures:

- genus *Praeglobotruncana* Bermúdez, 1952 (Aptian to Maestrichtian), type species *Globorotalia delrioensis* Plummer 1931 (non *Globigerina cretacea* var. *delrioensis* Carsey 1926 = *Praeglobotruncana* (*Hedbergella*) *delrioensis* (Carsey) = *Globotruncana stephani* Gandolfi 1942, s.l.
- (Synonyms *Rotundina* Subbotina 1953, type species *Globotruncana stephani* Gandolfi 1942; *Globotruncanella* Reiss 1956, type species *Globotruncana citae* Bolli 1951.)
- (a) With imperforate peripheral band and carina or carinae, at least in part:
  - Subgenus *Praeglobotruncana* (U. Albian? to Cenomanian to Maestrichtian).
- (b) Without imperforate peripheral band or carina:
  - (i) Chambers not radially elongate:
    - Subgenus *Hedbergella* Brönnimann and Brown 1958 (Aptian to Maestrichtian), type species *Anomalina lorneiana* (d'Orbigny) var. *trocoidea* Gandolfi 1942.
  - (ii) Chambers radially elongate in the adult:
    - Subgenus *Clavihedbergella* subgen. nov. (U. Albian to Turonian), type species *Hastigerinella subcretacea* Tappan 1943.

Subfamily PLANOMALININAE Bolli, Loeblich, and Tappan 1957 nom. transl., emended

Hantkeninidae with biumbilicate tests which become planispiral in the adult; primary aperture interiomarginal, umbilical–extraumbilical, equatorial, a low arch not elongate in the plane of coiling; adult individuals often possess paired primary apertures in the last chambers and often tend to become biserial. Portici present both ventrally and dorsally in adult [Aptian to Eocene to Oligocene?]



1. Relict parts of primary apertures open between distinct, long portici both ventrally and dorsally in all or nearly all chambers of the last whorl:
  - genus *Planomalina* Loeblich and Tappan 1946 (Aptian to Maestrichtian), type species *P. apsidostroba* Loeblich and Tappan 1946.
  - (a) With imperforate peripheral carina:
    - Subgenus *Planomalina* (Aptian to Cenomanian).
  - (b) Without imperforate peripheral carina:
    - (i) Chambers not radially elongate:
      - Subgenus *Globigerinelloides* Cushman and ten Dam 1948 June (Aptian to Maestrichtian), type species *G. algeriana* Cushman and ten Dam 1948.
      - (Synonyms *Biglobigerinella* Lalicker 1948 September, type species *B. multispina* Lalicker 1948; *Biticinella* Sigal 1956, type species *Anomalina breggiensis* Gandolfi 1942.)
    - (ii) Chambers radially elongate:
      - Subgenus *Hastigerinoides* Brönnimann 1952 (Cenomanian to Santonian), type species *Hastigerinella alexanderi* Cushman 1931.
      - (Synonym *Eohastigerinella* Morozova 1957, type species *Hastigerinella watersi* Cushman 1931.)
2. Relict apertures and umbilical parts of portici weak; visible on last few chambers only:
  - (a) Chambers radially elongate:
    - genus *Schackoina* Thalmann 1932 (Aptian? to Albian to Maestrichtian), type species *Siderolina cenomana* Schacko 1896 (1897).
    - (i) Chambers with slender extensions (which are not true tubulospines, and have unthickened walls):
      - Subgenus *Schackoina* (Cenomanian to Maestrichtian).
    - (ii) Chambers with bulb-shaped extensions:
      - Subgenus *Leupoldina* Bolli 1957 (Aptian? to Albian to Cenomanian?), type species *L. protuberans* Bolli 1957.
  - (b) Chambers not radially elongate:
    - genus *Pseudohastigerina* gen. nov. (Palaeocene? to L. Eocene to U. Eocene to Oligocene?), type species *Nonion micrus* Cole 1927.

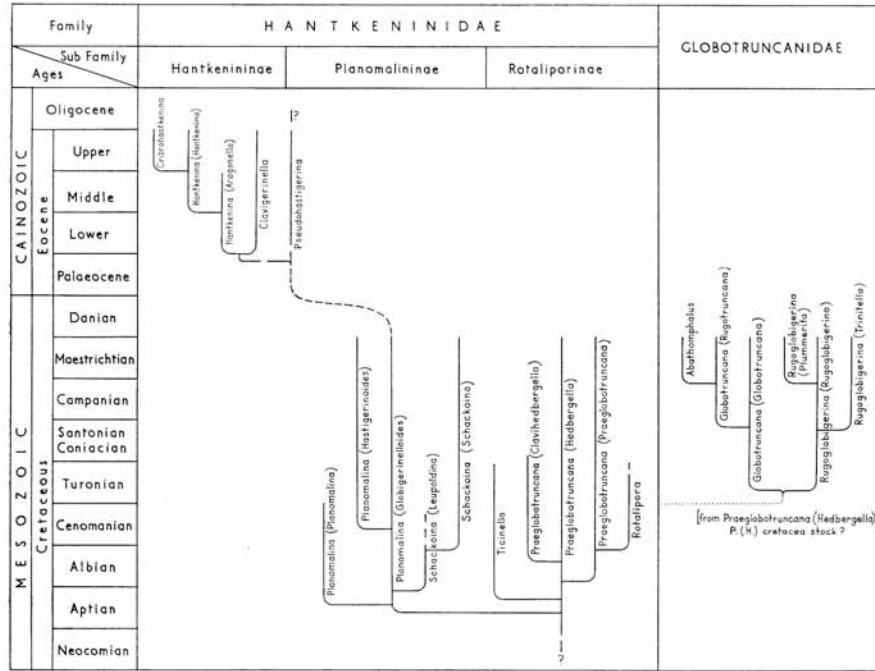
#### Subfamily HANTKENININAE Cushman 1927, emended

Hantkeninidae with biumbilicate, planispiral adult tests; the test possesses an interior-marginal, umbilical-extraumbilical equatorial primary aperture in the shape of a high arch, elongated in the apertural face in the plane of coiling, or a subdivided tripartite arch, also elongated in the plane of coiling, or areal and cribrate. No paired primary apertures known. Portici visible on the last chamber only, where they broaden strongly to form distinct lateral flanges in both ventral and dorsal umbilici [Eocene].

1. Chambers with thick-walled true tubulospines:
  - (a) No supplementary areal apertures:
    - genus *Hantkenina* Cushman 1925 (Eocene), type species *H. alabamensis* Cushman 1925.
    - (Synonyms *Sporohantkenina* Bermúdez 1937, type species *Hantkenina brevispina* Cushman 1925; *Hantkeninella* Brönnimann 1950, type species *Hantkenina mexicana* Cushman var. *primitiva* Cushman and Jarvis 1929.)
    - (i) Primary aperture tripartite, with well developed basal lobes:
      - Subgenus *Hantkenina* (M. to U. Eocene).
    - (ii) Primary aperture a simple arched opening, with insignificant basal lobes:
      - Subgenus *Aragonella* Thalmann 1942 (L. to M. Eocene), type species *Hantkenina mexicana* Cushman var. *aragonensis* Nuttall 1930.
      - (Synonym *Applinella* Thalmann 1942, type species *Hantkenina dumblei* Weinzierl and Applin 1929.)

(b) With supplementary apertures areal in apertural face:  
 genus *Cribohantkenina* Thalmann 1942 (U. Eocene), type species *Hantkenina* (*Cribohantkenina*) *bermudezi* Thalmann 1942 = *H. danvillensis* Howe and Wallace 1934.

2. Chambers elongate, with no true tubulospines, but rather clavate:  
 genus *Clavigerinella* Bolli, Loeblich, and Tappan 1957 (L. to U. Eocene), type species *C. akersi* Bolli, Loeblich, and Tappan 1957.



TEXT-FIG. 2. Suggested phylogeny of the Hantkeninidae and Globotruncanidae.

Family GLOBOTRUNCANIDAE Brotzen 1942  
 (Synonym Globotruncanidae Morozova 1957)

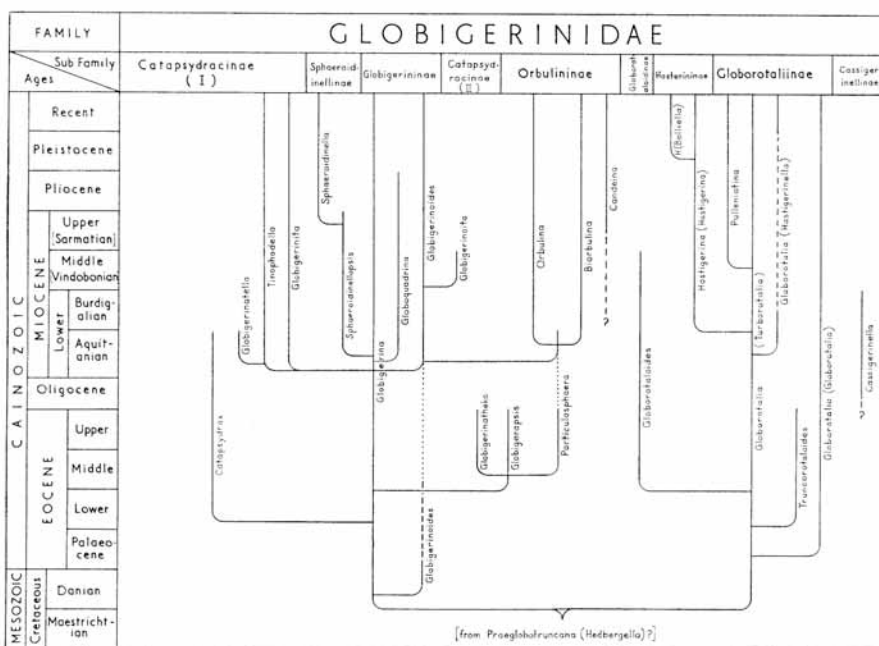
*Diagnosis.* Globigerinaceae with trochoid tests, dorsally evolute, ventrally more or less involute and umbilicate; primary aperture interiomarginal, intraumbilical or umbilical-extraumbilical, characteristically modified by an imperforate complex umbilical cover-plate (tegillum). Relict parts of primary apertures open into umbilicus beneath the tegillum, and thence to exterior through accessory apertures in the tegillum [Range: Turonian to Maestrichtian].

1. Primary aperture intraumbilical:

(a) With imperforate peripheral band, usually with carinae:  
 genus *Globotruncana* Cushman 1927 (Turonian to Maestrichtian), type species *Pulvinulina arca* Cushman 1926.

(Synonyms *Rosalinella* Marie 1941, type species *Rosalina linneiana* d'Orbigny 1839; *Margino-truncana* Hofker 1956, type species *Rosalina marginata* Reuss (1845) 1854; *Globotruncanita* Reiss 1957, type species *Rosalina stuarti* de Lapparent 1918.)

- (i) Chambers without costellae:  
Subgenus *Globotruncana* (Turonian to Maestrichtian).
- (ii) Chambers with meridionally arranged costellae more or less developed:  
Subgenus *Rugotruncana* Brönnimann and Brown 1955 (1956) (Santonian? to Campanian to Maestrichtian), type species *R. tilevi* Brönnimann and Brown 1955 (1956).  
(?Synonym *Bucherina* Brönnimann and Brown 1955 (1956), type species *B. sandidgei* Brönnimann and Brown 1955 (1956).)



TEXT-FIG. 3. Suggested phylogeny of the Globigerinidae (simplified). The Catapsydracinae has been subdivided arbitrarily into two parts, to emphasize its polyphyletic nature.

- (b) Without imperforate peripheral band or true carinae; costellae more or less well developed; with or without pseudocarinae:  
genus *Rugoglobigerina* Brönnimann 1952 (Turonian to Maestrichtian), type species *Globigerina rugosa* Plummer 1927.  
(Synonym *Kuglerina* Brönnimann and Brown 1955 (1956), type species *Rugoglobigerina rugosa rotundata* Brönnimann 1952.)
- (i) Chambers uniformly inflated throughout ontogeny and without pseudocarinae:  
Subgenus *Rugoglobigerina* (Turonian to Maestrichtian).
- (ii) Chambers in adult dorsally flattened, and/or with pseudocarinae:  
Subgenus *Trinitella* Brönnimann 1952 (Santonian? to Campanian to Maestrichtian), type species *T. scotti* Brönnimann 1952.

- (iii) Chambers in adult radially elongate:  
 Subgenus *Plummerita* Brönnimann 1952 (Maestrichtian) (new name for *Plummerella* Brönnimann 1952, non *Plummerella* de Long 1942, Insecta.), type species *Rugoglobigerina* (*Plummerella*) *hantkeninoides hantkeninoides* Brönnimann 1952.
2. Primary aperture umbilical–extraumbilical:  
 genus *Abathomphalus* Bolli, Loeblich, and Tappan 1957 (Maestrichtian), type species *Globotruncana mayaroensis* Bolli 1951.

#### SYSTEMATIC DESCRIPTIONS

##### Family GLOBIGERINIDAE Carpenter 1862

##### Subfamily HASTIGERININAE Bolli, Loeblich, and Tappan 1957, emended

*Emended diagnosis.* Globigerinidae with tests which are initially trochospiral but which become nearly, but imperfectly, symmetrically planispiral in the adult. In the young, the interiomarginal aperture is umbilical–extraumbilical–peripheral; in the adult, it becomes umbilical–extraumbilical–peripheral–equatorial, and may be bordered in advanced forms by a very narrow, partly or wholly perforate, thin lip, which is equally developed throughout the length of the aperture. The adult equatorial aperture is a broad arch, never subdivided or tripartite, and lacks asymmetrical imperforate apertural flanges. Relict apertures absent, except in loosely coiled adult specimens of some species, where the last chamber or chambers are not in direct contact with the preceding whorl; in such a case, the aperture of the penultimate chamber may remain open, facing the periphery of the preceding whorl. The juvenile chambers are subglobular; this form may be retained in the adult, or they may become depressed and subreniform, or radially elongate and subcylindrical or subconical. Tubulospines are not known.

*Remarks.* The Hastigerininae show evidence of descent from the Globorotaliinae in their imperfect planispiral coiling and *Globorotalia*-like initial stage which possesses an umbilical–extraumbilical aperture. This family is distinct from the Hantkeninidae in lacking imperforate apertural portici and in never attaining a truly planispiral symmetrical test.

##### Genus HASTIGERINA Thomson 1876 emended

*Type species* by original designation and monotypy: *Hastigerina murrayi* Thomson 1876 = *Nonionina pelagica* d'Orbigny 1839.

##### Subgenus HASTIGERINA Thomson 1876 sensu stricto

*Emended diagnosis.* Hastigerininae in which the adult chambers are subglobular or slightly depressed, not radially elongate.

##### Subgenus BOLLIELLA subgen. nov.

*Type species* here designated: *Hastigerina* (*Bolliella*) *adamsi* sp. nov.

*Diagnosis.* Hastigerininae in which the adult chambers are radially elongate.

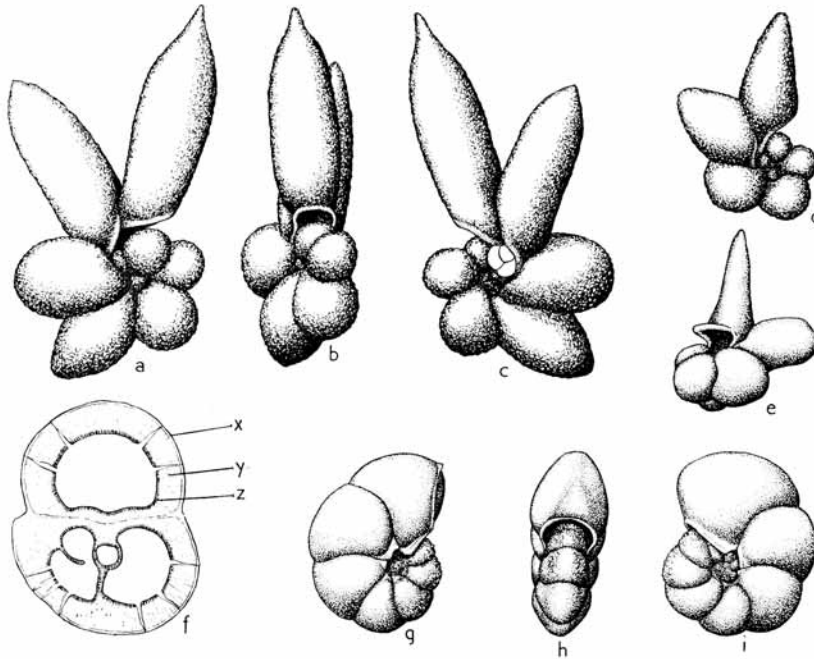
*Remarks.* This subgenus is named after Dr. H. M. Bolli, Caracas, Venezuela, in recognition of his work on planktonic foraminifera.

*Hastigerina (Bolliella) adamsi* sp. nov.

Text-figs. 4 a-d

*Globigerina digitata* Brady; Brady 1884 (part), *Challenger Exped. 1873-76 Rept., Zool.* 9 (pt. 22), pl. 82, figs. 6 [holotype], 7 [paratype] (not pl. 80).*Hastigerinella digitata* (Brady); Cushman, Todd, and Post 1954, p. 369, pl. 91, figs. 9, 10.

*Description.* The adult test is very slightly trochoid, being almost, but not perfectly, planispiral. The globular proloculum is followed by a whorl of about six rapidly enlarging subglobular chambers in the megalospheric generation; the microspheric



TEXT-FIG. 4. a-d, *Hastigerina (Bolliella) adamsi* sp. nov. a-c, holotype,  $\times 50$ , British Museum (Natural History) No. 1958.8.18.1. a, ventral view; b, edge view showing imperfect planispiral coiling; c, dorsal view showing extension of the aperture into a dorsal umbilicus (a juvenile foraminifer is attached to this side of the specimen, in the umbilicus). d, paratype,  $\times 50$ , B.M. (N.H.) No. 1958.8.18.2. e, *Globorotalia (Hastigerinella) digitata* (Brady), lectotype,  $\times 50$ , B.M. (N.H.) No. 1958.8.18.3. Ventral view refigured (this specimen was figured by Brady 1884, pl. 80, fig. 10, as *Globigerina digitata* Brady). f, *Sphaeroidinellopsis subdehiscens* (Blow); diagram after Blow 1959,  $\times 100$  approx., showing wall structure in this section: x, outer cortex, approx. 0.005 mm. thick; y, radial middle layer, approx. 0.05 mm. thick; z, inner radial layer. g-i, *Pseudohastigerina micra* (Cole),  $\times 100$ , from the Upper Eocene of Tanganyika. g, showing portici and position of relict apertures in the last two or three chambers; the last chamber of this specimen has been broken off. h, edge view showing apparently perfect planispiral coiling. i, side view showing portici of last two chambers (that of the last chamber is incomplete). B.M. (N.H.) No. P. 43657.

generation is not known. The juvenile aperture extends from the ventral umbilicus to the periphery and reaches an interiomarginal equatorial position, but is clearly asymmetrical and *Hastigerina*-like. In the succeeding whorl (also of about six chambers) the chambers are more nearly planispiral and become radially elongate without lateral compression; the chambers may become four times as high as broad. The later chambers are more loosely coiled, and by the end of the second whorl the test is almost equally biumbilicate, and the aperture has an equal extension into each umbilicus. A very thin and narrow, very finely perforate, apertural lip is present on the later chambers, extending back along the umbilical border of each chamber to meet the preceding chamber. The last formed adult chamber may be in contact only with the immediately preceding chamber, and not directly attached to the penultimate whorl; when this occurs, the primary apertures of the later chambers are not wholly closed, and remain open as relict apertures, which occur first on the ventral umbilical margin, and then (often by the third whorl) on both ventral and dorsal umbilical margins. The wall of the test is thin, uniformly and finely perforate, distinctly and uniformly hispid.

*Occurrence.* The type specimens were collected by the *Challenger* Expedition from 580 fathoms off the Kai (Ewab) Islands (*Challenger* Station 191A). The specimens collected by Cushman, Todd, and Post (1954) came from the outer slopes of Bikini Atoll and from Sylvania Guyot (1954, pp. 321–2). No records of fossil occurrences of this species are known to us.

*Types.* The holotype and paratype (Brady's figured specimens) are deposited in the British Museum (Natural History), *Challenger* Collection; Holotype—No. 1958.8.18.1. Paratype—No. 1958.8.18.2.

#### Subfamily SPHAERODINELLINAE new subfamily

#### Genus SPHAERODINELLA Cushman 1927, emended

*Type species* by original designation and monotypy: *Sphaeroidinella dehiscens* (Parker and Jones) = *Sphaeroidina bulloides* (d'Orbigny) var. *dehiscens* Parker and Jones 1865.

*Emended diagnosis.* Test trochoid throughout life; chambers rapidly enlarging, subglobular or subreniform, inflated, often becoming increasingly embracing in the adult. Primary wall calcareous, radial, coarsely perforate; pores usually broader in diameter at their inner ends than externally, where they narrow. Primary wall more or less covered by a secondary layer or layers of calcareous material, probably radial in structure, which is thickest near the apertures and in the sutures. The secondary layers of shell material (cortex) are shiny superficially in reflected light, and tend to restrict the pores of the primary wall, either greatly reducing the external openings or in some cases completely sealing them, especially in the apertural and adjacent sutural regions. The primary aperture is interiomarginal, intraumbilical throughout life, a low arch or slit; supplementary sutural apertures are present, at least in the adult. Both the primary and the supplementary apertures are furnished with lips, which may be smooth or crenulate, and which are often secondarily thickened with imperforate shell material (which is an extension of the cortex), and may become flange-like.

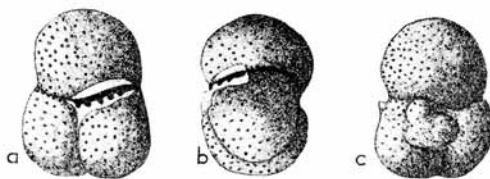
*Remarks.* Bolli, Loeblich, and Tappan (1957, pp. 32, 33, pl. 6, fig. 5) record and illustrate the presence of 'bullae' in some specimens of *Sphaeroidinella dehiscens*; we have seen similar structures on specimens of this species and believe them to be no more than thin-walled abortive chambers abnormally placed, more or less covering the sutures; we consider it probable that the structures seen by Bolli, Loeblich, and Tappan were the same. Similar structures have been observed by us in *Globigerinoides* where they are clearly aborted end chambers. Such abortive chambers are known in many genera of the Globigerinaceae, and are characterized by exceptionally thin walls, lack of hispidity, reduction of pore size, and erratic position. The erratic position and infrequent occurrence of abortive chambers serves to distinguish them clearly from true bullae. The cortex of *Sphaeroidinella* appears to be composed of less stable shell material than that of the primary wall, and is readily subject to loss, partial loss, or alteration during or after the process of fossilisation.

Genus SPHAEROIDINELLOPSIS gen. nov.

Text-figs. 4f, 5

*Type species* here designated: *Sphaeroidinellopsis subdehiscens* (Blow) = *Sphaeroidinella dehiscens subdehiscens* Blow 1959.

*Diagnosis.* Test trochoid throughout life; chambers regularly enlarging, subglobular, or subreniform, or showing a tendency to become radially elongate in the adult, or embracing. Wall structure similar to that of *Sphaeroidinella*, but in some species the cortex is less strongly developed. Primary aperture interior marginal, intraumbilical, a low arch or slit, furnished with a smooth or crenulate lip. No supplementary apertures are present.



TEXT-FIG. 5. *Sphaeroidinellopsis subdehiscens* (Blow), holotype,  $\times 47$ , after Blow 1959. a, ventral view; b, side view showing thickening of the outer cortex around the apertural margins; c, dorsal view.

*Remarks.* This genus is distinguished from *Sphaeroidinella* by its lack of supplementary sutural apertures in the adult, notwithstanding that in some species (e.g. *S. seminulina kochi* (Caudri)) the dorsal sutures are very deeply incised. '*Sphaeroidinella*' *senni* Beckmann is of doubtful generic position, but lacks a cortex and thickened apertural lips and does not belong to the Sphaeroidinellinae. We consider that *Globigerina seminulina* Schwager 1866 (= *S. disjuncta* Finlay 1940), *Globigerina kochi* Caudri 1934 (= *S. rutschi* Cushman and Renz 1941 [part, holotyp $\epsilon$ ] = *G. grimsdalei* Keijzer 1945), and *S. multiloba* LeRoy 1944 belong to *Sphaeroidinellopsis*.

## Subfamily GLOBOROTALIINAE Cushman 1927 emended

*Emended diagnosis.* Globigerinidae with tests which are trochoid throughout life, dorsally evolute, ventrally more or less involute and umbilicate; the test possesses a ventral, interiomarginal, umbilical-extraumbilical primary aperture, which may possess a thin, more or less perforate, symmetrical, narrow lip, which usually extends the full length of the aperture and is of uniform breadth. In some specialized forms dorsal (sutural) supplementary apertures may be present.

*Remarks.* The Globorotaliinae (emend.) differ from the Globigerininae by possessing a primary aperture which extends out of the umbilicus, but which does not become peripheral and equatorial as in the Hastigerininae. No bullae are present. The Globorotaliinae are clearly separated from the Hantkeninidae by their lack of imperforate apertural portici, and from the Globotruncanidae by their lack of umbilical tegilla.

## Genus GLOBOROTALIA Cushman 1927, sensu lato, emended

*Type species* by original designation: *Pulvinulina menardii* (d'Orbigny) var. *tumida* Brady 1877.

*Emended diagnosis.* Globorotaliinae which lack dorsal, sutural, supplementary apertures.

## Subgenus HASTIGERINELLA Cushman 1927, emended

*Type species* by original designation: *Hastigerina digitata* Rhumbler 1911 (not *Globigerina digitata* Brady 1879) = *Hastigerinella rhumbleri* Galloway 1933 (nom. nov.).

*Emended diagnosis.* *Globorotalia* in which the adult chambers become radially elongate, and which possess no carinae.

*Remarks.* This subgenus differs from *Globorotalia* (*Turborotalia*) in the same way as *Praeglobotruncana* (*Clavihedbergella*) differs from *Praeglobotruncana* (*Hedbergella*). It differs from *P.* (*Clavihedbergella*) in lacking the asymmetric imperforate portici of that genus, and from *Hastigerina* (*Bolliella*) in possessing neither a peripheral, equatorial aperture nor a biumbilicate test.

*Globorotalia* (*Hastigerinella*) *digitata* (Brady) emended

Text-fig. 4e

*Globigerina digitata* Brady (part) 1879, *Quart. J. Micr. Soc. London*, n.s., **19**, p. 286 (no figures).  
*Globigerina digitata* Brady; Brady (part) 1884, *Challenger Exped. 1873-76 Rept.*, **Zool.** **9** (pt. 22), pl. 80, fig. 10 (lectotype, here designated); pl. 80, figs. 6-9 (not pl. 82).  
*Globigerina digitata* Brady; Phleger, Parker, and Peirson 1953, p. 12, pl. 1, figs. 9, 10.  
*Globigerina* (*Globigerinella*) *digitata* Brady; Hofker 1956, p. 225, pl. 34, figs. 6-7 only.  
*Hastigerinella digitata* (Brady); Bolli, Loeblich, and Tappan 1957, p. 32, pl. 5, fig. 3.

*Description.* The test is distinctly and nearly uniformly trochoid throughout life, evolute dorsally and involute ventrally, with a small umbilicus. In the megalospheric form the globular proloculum is followed by a whorl of about four rapidly enlarging, subglobular chambers, each possessing a semicircular unlippered aperture, umbilical—slightly extraumbilical in position. This whorl is followed by a second trochoid whorl of about five



rapidly enlarging chambers, in which the aperture broadens until it becomes a high arch, increasingly extraumbilical in extent, later reaching, but not extending over and beyond, the periphery. In the adult, a very narrow, thin, perforate apertural lip is developed. In the last whorl the chambers become radially elongate without lateral compression, and become two to three times higher than broad. The wall is finely and uniformly perforate and very slightly roughened superficially; it is distinctly less hispid and more finely perforate than *Hastigerina (Bolliella) adamsi* sp. nov.

*Remarks.* When Brady first described *Globigerina digitata* (1879), no specimens were illustrated; in his subsequent figures (Brady 1884, pls. 80, 82) two species and genera were included under this name, and no type specimen was designated. Subsequent records by other authors are confused in consequence, the two forms not being distinguished. By designating a lectotype here, we are able to divide Brady's figured specimens, and to show that they exemplify the phenomenon of radial elongation of the adult chambers in the Globorotaliinae and in the Hastigeriniinae (*Hastigerina (Bolliella) adamsi* nov.), paralleling similar morphological developments known in the Rotaliporinae (*Praeglobotruncana (Clavhedbergella)*) and the Planomaliniinae (*Planomalina (Hastigerinoides)*). All these subgenera appear to be phylogenetic end-forms, leaving no descendants, and have shorter stratigraphic ranges than the genera to which they belong.

*Occurrence.* The lectotype (here designated) and topotypes figured by Brady (1884, pl. 80) were collected by the *Challenger* Expedition at station 338, from 1,990 fathoms in the North Atlantic. This species has been recorded from Recent seas by Phleger, Parker, and Peirson (1953), Hofker (1956), and Bolli, Loeblich, and Tappan (1957), but apparently it has never been found fossil.

*Lectotype.* The lectotype of *Globigerina digitata* Brady 1879, is in the British Museum (Natural History), No. 1958.8.18.3.

Family HANTKENINIDAE Cushman 1927, emended

Subfamily ROTALIPORINAE Sigal 1958, emended

Genus PRAEGLOBOTRUNCANA Bermúdez 1952, emended

*Type species* by original designation: *Globorotalia delrioensis* Plummer 1931.

*Emended diagnosis.* Test trochoid, evolute dorsally, more or less involute and umbilicate ventrally. Chambers subglobular, or reniform, or compressed, or radially elongate. Periphery rounded or truncate, or subacute, with or without imperforate peripheral bands and carinae. Primary aperture is interiomarginal, umbilical-extraumbilical, bordered by an asymmetric imperforate porticus. The portici of the last whorl do not fuse, and the relict parts of primary apertures of the last whorl open directly to the exterior through the umbilicus. Neither supplementary nor accessory apertures are present.

Subgenus PRAEGLOBOTRUNCANA Bermúdez 1952, emended

*Emended diagnosis.* *Praeglobotruncana* which possess an imperforate peripheral band and a carina or carinae. The carina may not be fully developed on the last formed chamber. Adult chambers not radially elongate.

*Remarks.* This subgenus differs from *Rotalipora* in lacking supplementary apertures, and from *Abathomphalus* in lacking a tegillum.

Subgenus HEDBERGELLA Brönnimann and Brown 1958, emended

*Type species* by original designation: *Anomalina lorneiana* (d'Orbigny) var. *trocoidea* Gandolfi 1942.

*Emended diagnosis.* *Praeglobotruncana* in which there are no imperforate peripheral bands or carinae, and in which the adult chambers are not radially elongate, but which are uniformly subglobular or subreniform.

*Remarks.* *Praeglobotruncana* (*Hedbergella*) differs from *Ticinella* in lacking the distally fused portici characteristic of that genus; it is not surely known to possess dorsal pseudo-carinae, which often occur in *Ticinella*. Costellae do not occur.

It was the apparent intention of Brönnimann and Brown (1955 (1956)) to erect a genus to cover a group of simple Cretaceous 'globigerines' which were unkeeled and possessed no tegilla, and yet which were distinct from true *Globigerina* d'Orbigny. This genus was named *Hedbergina* and was based, unfortunately, upon *G. seminolensis* Harlton 1927, as type species. However, as pointed out by Bolli, Loeblich, and Tappan (1957, pp. 39, 40), the holotype of *G. seminolensis* is the only known specimen. It is badly preserved, and the umbilical apertural characters are indeterminate. No topotype material of this species can be obtained as its true provenance is unknown. Subsequently, Brönnimann and Brown (1958) proposed the genus *Hedbergella* as a 'new name' (*sic*) for the same morphological group, designating *Anomalina lorneiana* (d'Orb.) var. *trocoidea* Gandolfi 1942, as the type species. We believe that the species *Globigerina seminolensis* Harlton, and consequently the genus *Hedbergina* Brönnimann and Brown, should be regarded as *nomina dubia* and it is our intention to make application for it to be considered as such to the Secretary to the International Commission on Zoological Nomenclature.

Subgenus CLAVIHEDBERGELLA subgen. nov.

*Type species* here designated: *Praeglobotruncana* (*Clavihedbergella*) *subcretacea* (Tappan) = *Hastigerinella subcretacea* Tappan 1943, p. 513, pl. 83, fig. 4.

*Diagnosis.* Test trochoid, evolute dorsally, more or less involute ventrally and umbilicate. Early chambers subglobular, later becoming increasingly elongate in a radial direction. Wall generally hispid, uniformly perforate, lacking imperforate peripheral bands, carinae or costellae. Aperture ventral, interior marginal, umbilical-extraumbilical, sometimes reaching periphery of the preceding whorl but not extending on to the dorsal surface or becoming equatorial. Test not biumbilicate. Apertures furnished with portici, but lacking tegilla or bullae. No supplementary or accessory apertures, but relict apertures may be present.

*Remarks.* This subgenus differs from *Praeglobotruncana* (*Praeglobotruncana*) in lacking an imperforate peripheral band and in possessing radially elongate chambers in the adult. It differs from *P.* (*Hedbergella*) in possessing radially elongate adult chambers, and is related to that subgenus in the same way as *Globorotalia* (*Hastigerinella*) is related to *G.* (*Turborotalia*). It differs from *G.* (*Hastigerinella*) in possessing characteristically

Hantkeninid portici, and it may be distinguished from *Planomalina* (*Hastigerinoides*) by its lack of an equatorial primary aperture and its uniumbilicate test.

*Hastigerinella simplex* Morrow 1934, and *Hastigerinoides simplicissima* Magné and Sigal 1954, are also considered to belong to *Praeglobotruncana* (*Clavihedbergella*).

Subfamily PLANOMALININAE Bolli, Loeblich, and Tappan 1957, emended

Genus PSEUDOHASTIGERINA gen. nov.

Text-figs. 4 g, h, i

Type species here designated: *Pseudohastigerina micra* (Cole) = *Nonion micrus* Cole 1927 (*Bull. Amer. Paleont.* 14 (51), p. 22, pl. 5, fig. 12).

*Diagnosis.* Test planispirally coiled throughout in the megalospheric form, biumbilicate. Aperture is a low, interiomarginal, equatorial, symmetrical arch, extending into the umbilici, not subdivided or elongate in the plane of coiling, furnished with an imperforate porticus. The porticus is narrowest at its mid-point (that is, in the part immediately above the periphery of the preceding whorl), and broadens slightly towards the dorsal and ventral umbilici. Very small relict apertures present at umbilical margins of last two or three chambers only, and the portici are only clearly visible on these chambers. The chambers are subglobular, or slightly depressed, and enlarge regularly; they are not radially elongate or furnished with tubulospines. The wall is uniformly perforate, with no imperforate peripheral bands or carinae, and more or less hispid; the hispidity usually becomes obsolete in the adult.

*Remarks.* This genus is morphologically intermediate between the Planomaliniinae and the Hantkeniniinae. It is distinguished from *Planomalina* (*Globigerinelloides*) by its strongly reduced relict apertures, and the consequent lack of visible portici except on the last few chambers. It differs from *Schackoia* (sensu lato) by its lack of radial extensions of the chambers, and by its true planispiral coiling in the megalospheric form. *Pseudohastigerina* differs from the Hantkeniniinae (emended) by its lack of an apertural elongation in the plane of coiling, by its less strongly developed portici (which do not form distinct lateral flanges), and by its lack of chamber elongation or tubulospines. We believe that an (as yet) unrecorded species of this genus is probably ancestral to the Hantkeniniinae; greater development laterally of the portici, elongation of the aperture in the plane of coiling and the appearance of tubulospines would produce the subgenus *Hantkenina* (*Aragonella*); subsequent modification of the aperture would lead to *Hantkenina* sensu stricto and to *Cribrhantkenina*. Parallel modifications of the aperture, but associated with chamber elongation rather than with the development of tubulospines, probably gave rise to *Clavigerinella*.

*Pseudohastigerina micra* is hispid on the earliest parts of the last whorl; this is a feature common to the Globigerinaceae, and is distinct from *Nonion*, which is also clearly distinguished by its microgranular wall structure. An ancestral form to *Pseudohastigerina* may prove to be *Protelphidium* Haynes (1956, pp. 86–87), but the aperture is not adequately enough known in this genus to enable its relationships to be ascertained; Haynes (1956, pl. 16, fig. 9) illustrates the type species, *P. hofkeri*, as having a *Nonion*-like aperture without portici. *Nonion sublaeve* ten Dam, placed by Haynes in *Protelphidium* (op. cit., p. 87), seems unrelated to *Pseudohastigerina*.

*Pseudohastigerina* differs from *Hastigerina* by its true planispiral coiling throughout ontogeny, and by its possession of apertural portici.

*Occurrence.* *Nonion micrus* was first recorded from the Guayabal Formation of Mexico by Cole (1927, p. 22); he considered that this was probably equivalent to the Upper Claiborne, and is probably Middle Eocene in age. This species has been recorded subsequently from the higher parts of the Lower Eocene to the top of the Upper Eocene (e.g. Hornibrook 1958, pp. 29, 34 [as '*Globigerinella*' *iota* (Finlay)]; Bolli 1957, p. 161; Subbotina 1953, p. 88; &c.). Bykova (1953, p. 86) has recorded *G. micra* (Cole) from beds in the Tadjikistan depression, which are probably of Upper Palaeocene age; her specimen was not illustrated, however, and her determination cannot be checked. *G. naguwichiensis* Myatliuk probably belongs to this genus, but its age is not well known; Myatliuk (1950, p. 281) thought it to be possibly Oligocene. No species referable to this genus have been recorded from beds of other than Palaeogene age. Specimens of '*G. aspera* (Ehrenberg)', recorded by Haynes (1956, p. 98) from the Palaeocene Thanet Beds of East Kent, may prove to belong to *Pseudohastigerina*; his specimens require further study, but they may confirm the suspected Palaeocene occurrence of this genus.

#### DISCUSSION

We have already pointed out in the introduction to this work those morphological characters which we consider to be of fundamental taxonomic importance. We have endeavoured to base our classification on characters which occur only singly and are not repeated. However, many of the more obvious characters of the Globigerinaceae are apparently repeated, and occur in a repetitive manner in widely divergent stocks. Unfortunately, many previous workers have only recognized these more obvious characters, so that in the results of their work, the ranges of the genera, as interpreted by them, are much extended in geological time. This work illustrates the importance of those less obvious apertural structures which in the past have been largely neglected, and which may be broadly analogous to such structures as the toothplates of the Buliminidae, &c.

Moreover, having recognized the importance of these structures associated with the apertures, we have been led to reinvestigate other characters, such as 'keels', which in the past have been considered homologous in many different genera. Our results indicate that structures such as the 'keel' are also fundamentally different in different stocks, and confirm our views, not only of the taxonomic importance of the individual apertural structures, but also as to the validity of the phylogeny our classification suggests. We believe that all the subfamilies employed here (with the single major exception of the polyphyletic but taxonomically convenient Catapsydracinae) are biologically natural groupings (text-figs. 2, 3).

The more obvious differences of test shape, used by past authors to define their genera and to illustrate their phylogenetic concepts, and which we believe to occur iteratively in distantly related or unrelated stocks, include radial elongation of adult chambers, acquisition of supplementary apertures, planispirality, umbilical cover-plates, 'keels', &c. Some aspects of these characters are discussed below.

The gross aspects of the 'keels' seen in the solid specimens of *Globotruncana*, *Globo-*

*rotalia*, *Ticinella*, *Rotalipora*, and *Praeglobotruncana* are, in many species, apparently similar; but in thin section and under high magnification subtle but significant differences are apparent (Pls. 2, 3). In *Ticinella roberti* (Gandolfi) and *T. helvetica* (Bolli) the 'keel' is seen to be no more than an external perforate thickening of the dorsal periphery, fully contiguous with the primary wall, and of fundamentally similar structure (Pl. 3). It appears to be secondary and superficial, and has been shown by Schijfsma (1955) to develop proterogenetically in *T. helvetica* from a 'grosse globigerine', which is referable to *Praeglobotruncana* (*Hedbergella*). Evidence from specimens seen by us from East Africa confirm Reiss's (1957) conclusions as to the eventual fusion of the portici in the later ontogeny of *T. helvetica*, but our sectioned specimens do not confirm his belief in the imperforate nature of the 'keel'. Consequently, we consider this 'keel' to be a pseudocarina, and not a true carina (Pl. 3, fig. 2b).

In the well-known evolutionary sequence '*Globorotalia fohsi barisanensis*'-'*G. fohsi fohsi*'-'*G. fohsi lobata*'-'*G. fohsi robusta*' (Bolli 1950; Blow 1959), we find that *barisanensis* is without any sort of 'keel' or marginal thickening, and the chamber wall is uniformly perforate throughout (Pl. 1, fig. 1); in advanced forms of '*fohsi fohsi*' there is a beginning in the last few chambers of a thickening of the peripheral margin, which is, however, still fully perforate (Pl. 1, fig. 2). In '*fohsi lobata*' the perforate peripheral thickening (which is termed here pseudocarina) is increasingly emphasized, and an imperforate, apparently exogenous layer is laid down on the thickened margins of the last one or two chambers (Pl. 1, fig. 3). It is at this stage that we consider that a true carina is developed. The imperforate layer gradually increases in strength and thickness, and proceeds palingenetically throughout the whole test to give the most advanced and final subspecies '*fohsi robusta*' (Pl. 1, fig. 4). We regard the 'keel' to be a true carina when imperforate shell material makes its appearance, and believe that this character can be used to subdivide the many species ascribed to *Globorotalia* (s.l.). We have found that in thin sections of *Globorotalia menardii tumida* the 'keel' consists of distinctly imperforate shell material, whereas in *G. centralis* the wall is uniformly perforate throughout. Accordingly the supraspecific taxa *Globorotalia* and *Turborotalia* are employed here, based on the presence or absence of a true carina. We regard these taxa as only of subgeneric status, since gradations from forms without any 'keels' to forms with pseudocarinae, and from these to other forms with true carinae, are known not only in the evolutionary series outlined above but also in other lineages, such as those discussed by Blow (1959), including that leading from *G. (T.) praescitula* to *G. (G.) menardii menardii*.

In *Globotruncana*, the imperforate peripheral band is broad, and always bears two imperforate ridges (here termed carinae); some species may appear to possess one carina only (e.g. *G. stuarti*), but this always dichotomises to produce two carinae, one running dorsally and the other ventrally, a character never seen in the Globorotaliinae. No transitions from pseudocarinae to true carinae are known in the Globotruncanidae as here emended, although pseudocarinae occur in *Rugoglobigerina* (*Trinitella*). In species of *Globotruncana* where the carinae are widely spaced, as in *G. tricarinata*, the perforations of the test wall end abruptly against the margins of the imperforate peripheral band, which extends the full breadth of the wall between the carinae, and which appears to possess a texture different from both that of the perforate parts of the *Globotruncana* wall and from the imperforate parts of the wall of *Globorotalia*. It is not unlikely that the actual nature of the imperforate carinae of *Globotruncana* is different from that of the

carinae of *Globorotalia*; further work, using other techniques, is necessary and this is in progress.

The acquisition of planispiral or nearly planispiral modes of coiling is accompanied by a migration of the primary ventral interiomarginal aperture to an equatorial position. This has occurred in the Planomaliniinae, Hantkeniniinae and Hastigeriniinae, without radical change in the fundamental nature of the apertural accessory structures; thus, portici have not been lost in the Planomaliniinae or Hantkeniniinae, but in some cases have even been accentuated. In the Hastigeriniinae the lipped Globorotaliid aperture is preserved. However, some further specialized modifications of the shape of the primary aperture may occur in some genera; in *Planomalina* (*Globigerinelloides*) and in *Schacko-ina* (*Leupoldina*) the primary interiomarginal equatorial aperture tends to become bipartite, with enlargement laterally, giving incipient biseriality in the later chambers. The last one or two chambers may become fully biserial, and the primary aperture becomes fully divided and opens only on the lateral shoulders of the penultimate whorl (Subbotina 1953, pl. 13, figs. 8*b*, 9*b*, 11*b*; Bolli 1957, pl. 2, figs. 7*a*, 8*a*). This character is not known in other subfamilies. With the achievement of planispirality and equatorial apertures in the Hantkeniniinae, elongation of the aperture normal to the axis of coiling also occurs, but the lateral accentuation of the aperture is by no means diminished, at least in *Hantkenina* itself. On the other hand, there is no fundamental modification of the *Globorotalia*-like aperture in *Hastigerina*; no elongation or other modification is present, save that of an extension of the aperture over and beyond the periphery on to the dorsal surface. This seems to be associated with the fact that complete and true planispirality has not yet been attained.

A tendency towards planispirality may be recognized in morphologically advanced

#### EXPLANATION OF PLATE I

Thin sections photographed to show carina development in some Globorotaliinae.

Fig. 1. *Globorotalia* (*Turborotalia*) *fohsi barisanensis* (LeRoy), from the Lower Burdigalian, Pozón Formation, near Pozón, Eastern Falcón, Venezuela; 1*a*, axial section,  $\times 125$  approx.; 1*b*, same specimen, peripheral part of a chamber in the last whorl, showing uniformly perforate structure (the pores are partly infilled with ferruginous material),  $\times 500$  approx.

Fig. 2. *Globorotalia* (*Turborotalia*) *fohsi fohsi* Cushman and Ellis, from the Middle Burdigalian, Pozón Formation, near Pozón, E. Falcón, Venezuela; 2*a*, axial section,  $\times 125$  approx.; 2*b*, same specimen, periphery of a late chamber, showing development of a fully perforate pseudocarina,  $\times 1,000$  approx.; 2*c*, same specimen, periphery of an earlier chamber, showing perforate structure without formation of a pseudocarina,  $\times 1,000$  approx.

Fig. 3. *Globorotalia* (*Globorotalia*) *lobata lobata* Bermúdez, from the lower part of the Upper Burdigalian, Pozón Formation, near Pozón, E. Falcón, Venezuela; 3*a*, axial section,  $\times 125$  approx.; 3*b*, same specimen, periphery of a late chamber, showing formation of a wedge of imperforate radial shell material at the extreme periphery,  $\times 1,000$  approx.; 3*c*, same specimen, periphery of an earlier chamber, showing retention of a uniformly perforate wall-structure in the early part of the test,  $\times 500$  approx. The appearance of imperforate peripheral shell material (a morphologically primitive carina) is taken as the arbitrary distinction between *Globorotalia* sensu stricto and *Globorotalia* (*Turborotalia*) in this and other evolutionary series.

Fig. 4. *Globorotalia* (*Globorotalia*) *lobata robusta* (Bolli), from the Upper Burdigalian, Pozón Formation, near Pozón, Venezuela; 4*a*, axial section, showing development of a carina throughout the last whorl,  $\times 125$  approx.; 4*b*, the peripheral carina, showing its radial structure and the inner residuum of perforate material overlain by thick imperforate layers,  $\times 500$  approx.

forms of other genera, such as *Praeglobotruncana* (*Hedbergella*) and *Rugoglobigerina*. *P. (H.) gautierensis* (Brönnimann) and *R. macrocephala* (Brönnimann) both possess flattened or concave dorsal surfaces and very low trochospiral tests.

Radial elongation, or a tendency towards this, occurs commonly in nearly all the families and subfamilies, in both planispiral and trochoid tests, but it is most noticeable in those in which the coiling is either planispiral or very low trochospiral and which do not possess carinae. In general, three broad morphological types seem to occur independently in unrelated stocks. Broadly elongate clavate chambers occur in the Cretaceous *Praeglobotruncana* (*Clavihedbergella*), *Schackoia* (*Leupoldina*) and *Planomalina* (*Hastigerinoides*), the Eocene *Clavigerinella*, and the Neogene *Globorotalia* (*Hastigerinella*) and *Hastigerina* (*Bolliella*). Narrowly elongate, digitate chambers occur in the Cretaceous *Schackoia* (*Schackoia*), *Rugoglobigerina* (*Plummerita*), some species of *Planomalina* (*Hastigerinoides*) (e.g. *P. (H.) alexanderi* (Cushman)), in some specimens of the Palaeogene *Clavigerinella jarvisi* (Cushman) and in some individuals of Recent *Globorotalia* (*Hastigerinella*) *digitata* (Brady). True tubulospines, which differ from the chamber elongations of *Schackoia* (*Schackoia*) by their thickened walls and much reduced lumina, occur only in the Palaeogene *Hantkenina* and *Cribrorhantkenina*. Tendencies towards radial elongation of the adult chambers have been observed in other genera; both *Globigerina inaequispira* Subbotina and *G. bulbosa* LeRoy show deep separation and slight elongation of the later chambers. It is probable that this character has arisen independently within individual genera as well as within individual lineages. Thus, the early stages of the Lower Miocene *Globorotalia* (*Hastigerinella*) *bermudezi* (Bolli) are those of a *Globorotalia* (*Turborotalia*) (Blow 1959); Blow (loc. cit.) has pointed out that there appears to be no direct relationship between this species and any known Recent species of *G. (Hastigerinella)*.

Supplementary sutural apertures have been acquired in the Rotaliporinae (*Hantkeninidae*) and in most subfamilies of the Globigerinidae. The Cretaceous Rotaliporinae are clearly distinguished by possessing supplementary sutural apertures on the ventral side only, in contrast to the almost invariably dorsal sutural supplementary apertures of the Cainozoic Globigerinidae. No other Cretaceous group besides the Rotaliporinae is known to possess true supplementary apertures, although accessory apertures and relict apertures are common. In the Globigerinidae supplementary sutural apertures are associated with either normal trochospiral coiling and a retention of a primary aperture (e.g. *Truncorotaloides*, *Globigerinoides*) or with the development of highly involute tests (tending to become spherical) associated with reduction or loss of an external primary aperture (e.g. *Globigerapsis*, *Porticulasphaera*). In extreme spherical forms (e.g. *Globigerinatella*, *Orbulina*) areal supplementary apertures occur. Whereas *Globigerinoides triloba* (s.l.) has been shown by Bolli (1957, *Bull. U.S. Nat. Mus.* **215**, p. 110) and by Blow (1959) to develop from a form similar to that illustrated by Fornasini (1897) as *Globigerina trilocularis* d'Orbigny in the Middle Aquitanian, Blow (loc. cit.) has demonstrated that *Globigerinoides bollii* originates in the Upper Burdigalian from a different species of *Globigerina*. This indicates that the genus *Globigerinoides* itself is polyphyletic. Similarly, it is probable that *Truncorotaloides topilensis* and *T. rohri* have originated from two distinctly different species of *Globorotalia* (s.l.), at two distinctly different times within the Palaeogene.

Umbilical plate-like structures are known throughout the Mesozoic and Cainozoic,

## EXPLANATION OF PLATE 2

Thin sections photographed to compare carina development in different families of the Globigerinaceae.

Fig. 1. *Globorotalia (Globorotalia) menardii menardii* (d'Orbigny), from the Burdigalian, approx. 2 miles SSW. of Kilindone, Mafia Island, Tanganyika; British Petroleum Co. Ltd., Sample No. S.P. 56/30'; 1a, axial section,  $\times 125$  approx.; 1b and 1c, same specimen, the periphery of early and late parts of the last whorl, showing radial perforations in the lateral parts of the test wall contrasting with the imperforate carina; 1b,  $\times 500$  approx.; 1c,  $\times 1,000$  approx.; the carina is morphologically advanced even in geologically early specimens of this species, and the crystalline radial structure of the carina is frequently obscure.

Fig. 2. *Globotruncana (Globotruncana) elevata stuartiformis* Dalbiez, from the Campanian, approx. 4 miles west of Lindi, Tanganyika; British Petroleum Co. Ltd., Sample No. FCRM. 1524; 2a, axial section,  $\times 83$  approx.; 2b and 2c, same specimen, the periphery of early and late parts of the last whorl, showing radial perforations in the lateral parts of the test wall ending abruptly against the imperforate carina, both  $\times 500$  approx.; in this plane of section, the carina shows no indication of its anterior dichotomy, and appears superficially similar to that of *Globorotalia (G.) menardii menardii*.

Fig. 3. *Globotruncana (Globotruncana) tricarinata coronata* (Bolli), from the Campanian, approx. 3½ miles from Lindi Bridge, Tanganyika; British Petroleum Co. Ltd., Sample No. PEK. 5570; 3a, axial section,  $\times 125$  approx.; 3b, same specimen, the periphery of a late part of the last whorl, showing the broad, imperforate peripheral band with two carinae, and the abrupt termination against it of the radial perforations of the adjacent chamber walls,  $\times 500$  approx.

Fig. 4. *Rotalipora globotruncanoides* Sigal, from the Cenomanian, approx. 5 miles south-west of Lindi, Tanganyika; British Petroleum Co. Ltd., Sample No. FCRM. 2050; 4a, axial section,  $\times 83$  approx.; 4b, same specimen, the periphery of the last whorl, showing the imperforate carina and the abrupt ending of the perforations against it,  $\times 500$  approx.

## EXPLANATION OF PLATE 3

Fig. 1. *Praeglobotruncana (Hedbergella) sp.* (= the 'grosse globigerine' of Schijfsma (1955)), from the Turonian of the BP-Shell Petroleum Development Co. (Tanganyika) Ltd. test-well Lindi No. 2, near Lindi, Tanganyika; British Petroleum Co. Ltd., Sample No. Lindi No. 2, 334 ft.; 1a, axial section,  $\times 125$  approx.; 1b, same specimen, periphery of the last whorl. Showing uniformly perforate structure, but slightly flattened dorsal surface,  $\times 500$  approx.

Fig. 2. *Ticinella helvetica* (Bolli), from the Turonian, approximately 8½ miles north west of Lindi, Tanganyika; British Petroleum Co. Ltd. Sample No. FCRM. 1907; 2a, axial section,  $\times 110$  approx.; 2b, same specimen, periphery of last whorl, showing perforate thickening (pseudocarina), and more strongly flattened dorsal surface,  $\times 1,000$  approx.

Fig. 3. *Ticinella roberti* (Gandolfi), from the Upper Albian or Lower Cenomanian of the BP-Shell Petroleum Development Co. (Tanganyika) Ltd. Test Well Wingayongo G.1 (90 ft.), Luhohi River, approximately 3½ miles west of Wingayongo Hill, Tanganyika; axial section,  $\times 110$  approx.

Fig. 4. *Praeglobotruncana (Praeglobotruncana) cf. stephani* (Gandolfi), from the Upper Cenomanian of the BP-Shell Petroleum Development Co. (Tanganyika) Ltd. Test Well Lindi No. 2 (829 ft.), near Lindi, Tanganyika; 4a, axial section,  $\times 110$  approx.; 4b, same specimen, periphery of the early part of the last whorl, showing imperforate peripheral band and development of a broad carina,  $\times 500$  approx.; 4c, same specimen, periphery of the last chamber, showing imperforate area, without development of a carina,  $\times 1,000$  approx.

Fig. 5. *Globotruncana (Globotruncana) arca* (Cushman), from the Campanian near Kilwa cross-roads, Tanganyika; British Petroleum Co. Ltd., Sample No. RS. 48; deformed specimen, the two carinae typical of this species being present on one side of the test, but being represented by a 'single' carina on the other side; 5a, axial section,  $\times 125$  approx.; 5b, same specimen, showing the normal development of the imperforate peripheral band on an otherwise abnormal chamber,  $\times 500$  approx.

Fig. 6. *Pseudohastigerina micra* (Cole), from the Upper Eocene, approximately 2½ miles south-west of Mhanya, Lindi District, Tanganyika; British Petroleum Co. Ltd., Sample No. FCRM. 1923; 6a, equatorial section,  $\times 125$  approx.; 6b, same specimen, showing monolamellar and imperforate nature of the septa,  $\times 500$  approx.



but are of completely different type and origin in the two eras. In the Cretaceous such plate-like structures within the umbilici appear to have been formed in at least two ways. The origins of the tegilla in the Globotruncanidae are not known, but from their detailed morphology and their arrangement relative to the chambers ('protruded umbilical cover-plate' of Brönnimann and Brown 1955 (1956), p. 509 et seq.) they are clearly different from the plates formed in *Ticinella* from fused elongate portici ('depressed umbilical cover-plate' of Brönnimann and Brown, loc. cit.). In the case of the fundamentally distinct bullae, characteristic of the Globorotaloidinae and Catapsydracinae, it is probable that this structure has arisen independently in different genera, possibly in different ways. Blow (1959) believes that the bulla of *Tinophodella ambitacrena* (i.e. *Globigerinita naparimaensis* of Blow 1959, not of Brönnimann 1951, emended by Loeblich and Tappan 1957) has arisen from the well-marked lip of *Globigerina juvenilis* Bolli, indicating no close genetic relationship with other bulla-bearing forms. It has already been noted in this paper that *Globigerinatheka* possesses a *Globigerapsis* juvenile stage, and it is probable that *Globigerinatheka* is descended from *Globigerapsis*. Similarly, *Globigerinoita* has a juvenile *Globigerinoidea* stage, and is probably descended directly from that genus. Even within the genus *Catapsydrax*, it is highly probable that polyphyleticism will become apparent when the interrelationships of its species become better known. The subfamily Catapsydracinae is therefore a polyphyletic group of specialized end-forms, which possesses unity only in the uniformity of its specialized characters, but which possesses definite stratigraphic value. No bullae are indisputably known in the Mesozoic.

From the above discussion, it is clear that great care must be exercised in determining the relative taxonomic importance of the morphological characters present in the Globigerinaceae. It is felt that the use of non-iterative characters in the higher taxa, and the discriminating use of iterative characters in the lower taxa, has produced a classification which (with the exception of the Catapsydracinae) closely approaches a natural order, and which is both stratigraphically and biologically significant.

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#### GLOSSARY

As some new terms have been introduced in this paper, and others modified or restricted in their usage, a short list of definitions is given below.

*Apertures, accessory:* apertures which do not open directly from the lumina of the primary chambers, but which open from beneath structures accessory to the primary aperture or the primary chambers  
*Apertures, equatorial:* apertures which are symmetrical to the plane of coiling, extending from the

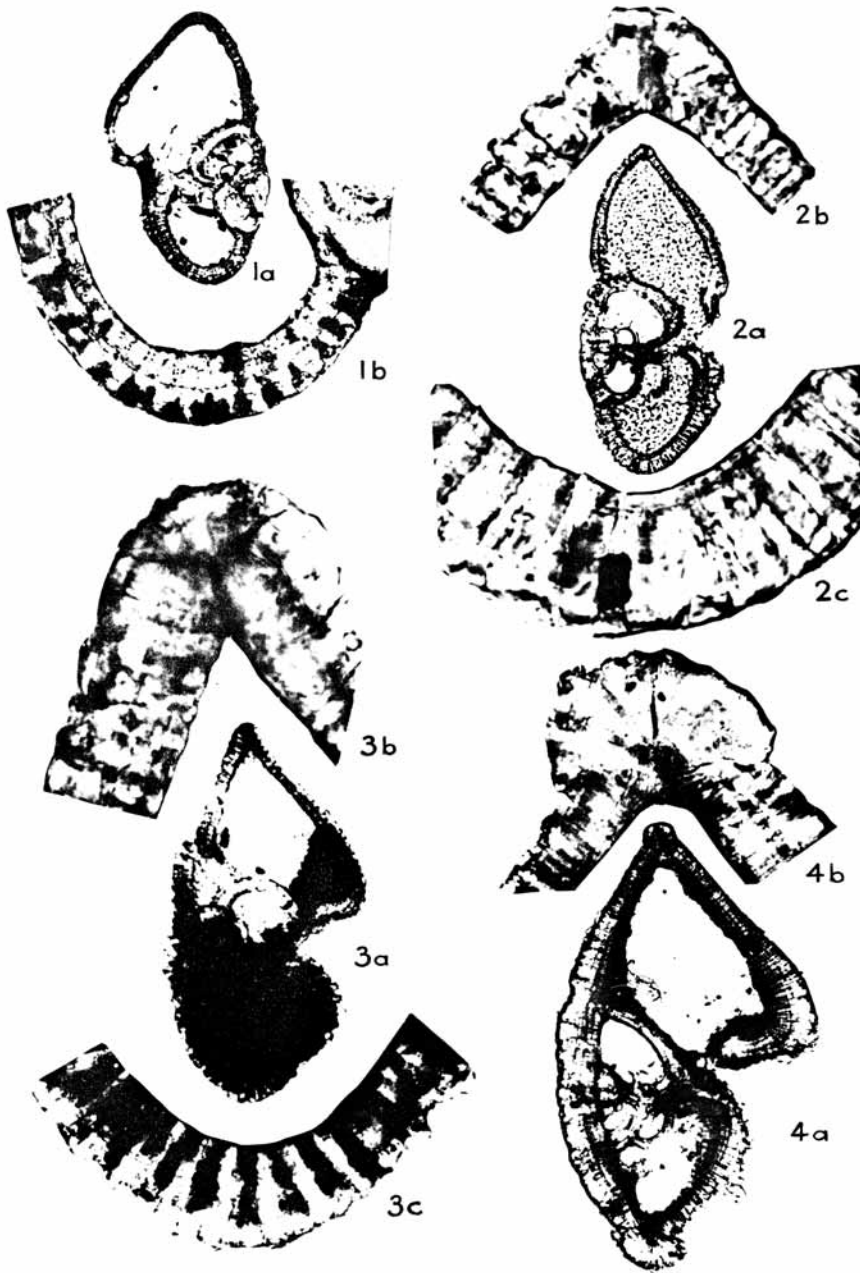
- ventral to the dorsal side of the test (most perfectly and symmetrically developed in planispiral, biumbilicate tests).
- Apertures, extraumbilical*: apertures which, although ventral in position, extend, in part at least, outside the umbilicus.
- Apertures, intraumbilical*: apertures which open into the umbilicus of the test and which do not extend outside it.
- Aperture, primary*: the single, principal aperture opening to the exterior from the lumen of the last-formed primary chamber, constant in position within the subfamily; typically the largest external aperture.
- Apertures, relict*: those parts of the primary apertures of chambers, other than the last-formed, which remain open to the exterior when successive chambers are added (the parts which no longer open to the exterior often becoming the septal apertures, communicating between successive chambers).
- Apertures, supplementary*: apertures opening to the exterior directly from the lumen of a primary chamber, which are additional to the primary aperture (often sutural in position, but may be areal in the apertural face).
- Apertures, umbilical*: apertures which open, in part at least, into the umbilicus of the test.
- Bulla*: a perforate, inflated, plate-like structure which covers the umbilicus (and sometimes the supplementary apertures) in the Catapsydracinae and Globorotaloidinae; accessory apertures are present at the margins of the bulla, or areally within it.
- Carina*: an imperforate, ridge-like thickening of the chamber wall, present on the periphery of the test, lying in the plane of coiling.
- Costellae*: ridge-like thickenings present on the dorsal and/or ventral chamber walls, typically running in a meridional direction, to converge at a 'pole' situated at the mid-point of the chamber periphery (maximum development in *Rugoglobigerina* s.s.), but sometimes running in directions normal or oblique to the periphery (e.g. *Globotruncana* (*Rugotruncana*) spp.).
- Dorsal*: the more evolute side of a trochospirally coiled test, usually, but not always, lacking an umbilicus.
- Lip*: a fairly narrow structure which appears to be a reflexed continuation of the actual chamber wall, projecting above and along an interiomarginal aperture or surrounding an areal aperture; typically symmetrically developed about the aperture (i.e. of uniform breadth throughout its length, or of maximum breadth at its mid-point).
- Porticus*: an imperforate, narrow or broad structure projecting from, and apparently additional to, the chamber wall, above and along an interiomarginal aperture; typically asymmetrically developed about the aperture (i.e. broadening towards one end of the aperture (typically the posterior end), where it often becomes flap-like or flange-like); portici may remain separate, or may fuse.
- Pseudocarina*: a perforate, ridge-like thickening of the peripheral part of the chamber wall, lying approximately in the plane of coiling.
- Tegillum*: a complex, often irregular structure of imperforate plates which covers the umbilicus; it may cover apertural portici (which are revealed when the tegillum is broken off), and is often pierced by accessory apertures; the later-formed plates may extend the full breadth of the umbilicus, and fuse on to the walls of chambers oppositely placed.
- Umbilical teeth*: lips which are exceptionally broad in their mid parts, so that they project as sub-triangular, perforate flaps into the umbilicus.
- Ventral*: the more involute side of a trochospirally coiled test, typically possessing an umbilicus.

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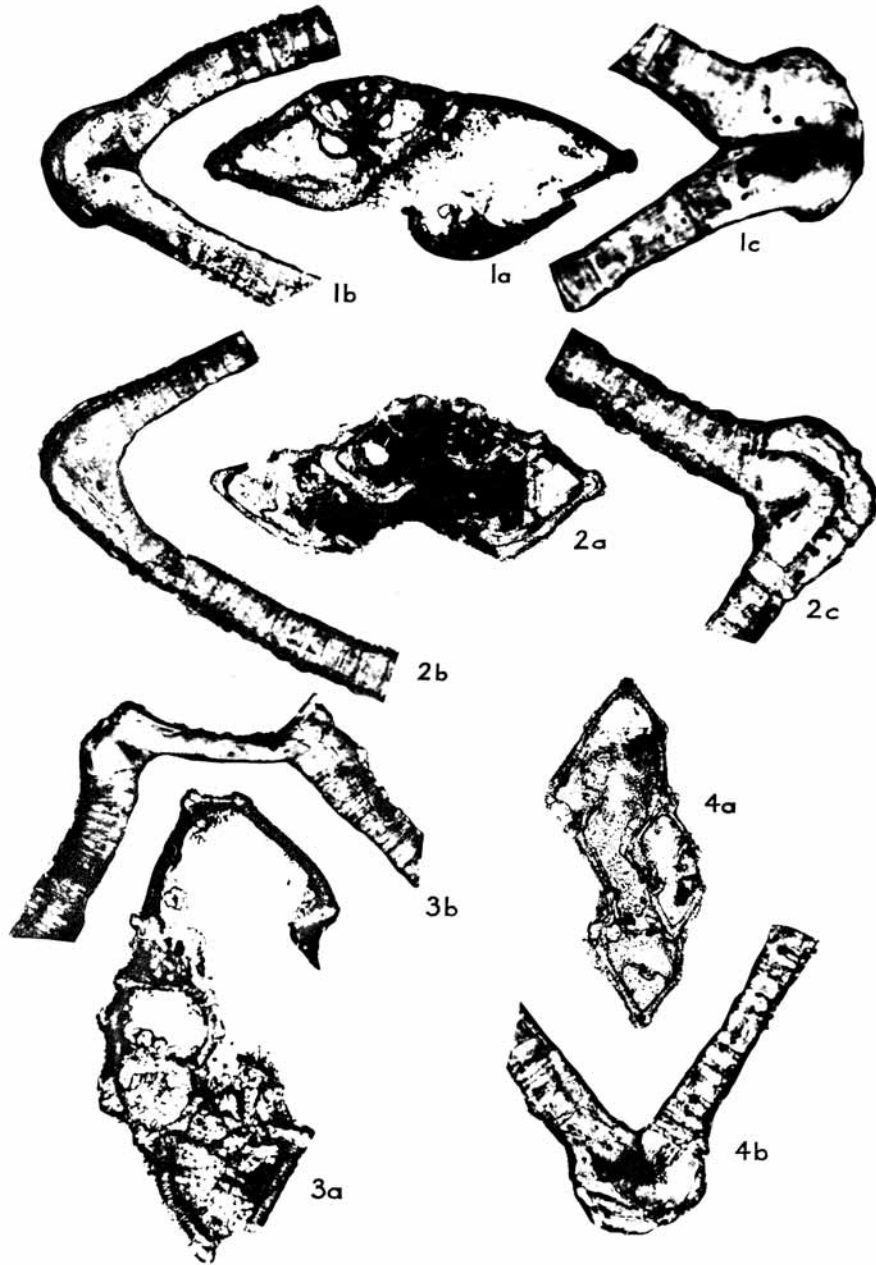
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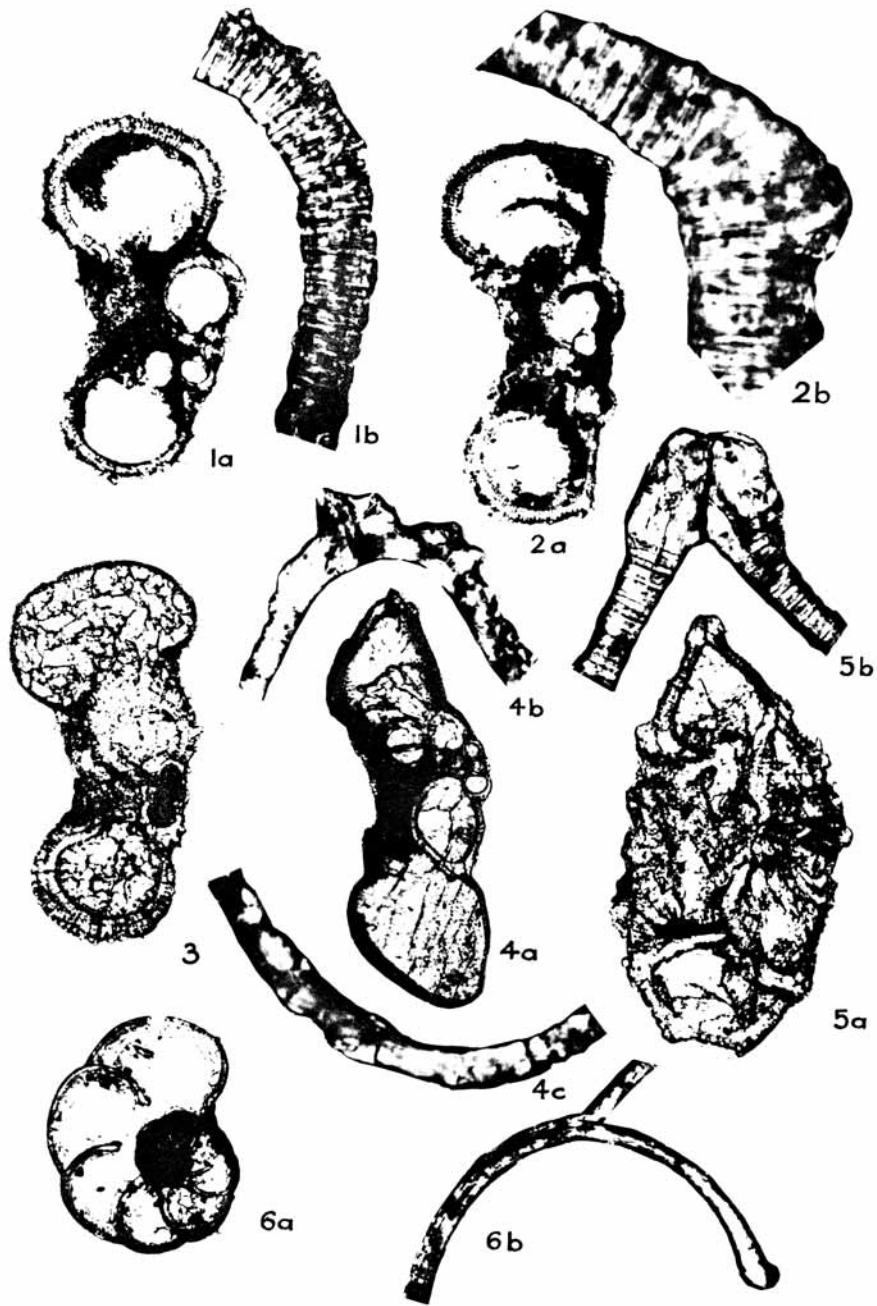
F. T. BANNER and W. H. BLOW  
British Petroleum Co. Ltd.,  
Research Station,  
Sunbury-on-Thames,  
Middlesex



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