

THE NATURE OF *GLOBANOMALINA* HAQUE

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ABSTRACT

The type descriptions and paratype specimens of the type-species of *Globanomalina* Haque, *G. ovalis* Haque, 1956, together with the type descriptions and ideotypes of *Globigerina pseudoiota* Hornibrook, 1958, are reassessed and the species are synonymous. The primary types of the taxa are of late Paleocene to earliest Eocene age (Zones P4–6). The genus *Globanomalina* Haque is trochospiral, microperforate and smooth-walled, and the generic name should be used for species of the lineage from *G. archeocompressa* (Blow) (beginning in earliest Paleocene, Zone P α) to *G. luxorensis* (Nakkady) (earliest Eocene, Zones P6–8). Contrary to recently published opinion, it is not a synonym of the planispiral, macroperforate genus *Pseudohastigerina* Banner and Blow (early Eocene, Zone P6, to early Oligocene, Zone P19), but is its immediate ancestor.

INTRODUCTION

In their most recent attempt to systematize comprehensively the genera of the Foraminiferida, Loeblich and Tappan (1988, p. 485) have repeated the opinion which they had held earlier (1964, p. C665), that the genus *Globanomalina* Haque, 1956, is a complete and senior synonym of the genus *Pseudohastigerina* Banner and Blow, 1959. This opinion was based upon a study of topotypes of each type species (*Globanomalina ovalis* Haque, 1956, and *Nonion micrus* Cole, 1927), as well as un-named "included species" (Loeblich and Tappan, 1988, p. 486), from which Loeblich and Tappan concluded that all of the species "commonly show evidence of their trochospiral ancestry in asymmetrical early whorls and aperture, although coiling is dominantly planispiral and the aperture equatorial."

My research shows that this conclusion is not only wrong taxonomically, in that it misrepresents the morphology of the primary species concerned and misuses this morphology in the diagnoses of the taxa, but that it is also misleading biostratigraphically. If the two genera are distinguished taxonomically on the basis of the observable morphology of their rigorously defined type species, then the biostratigrapher is provided with a generic distinction between Paleocene–early Eocene species (of *Globanomalina*) and early Eocene–early Oligocene species (of *Pseudohastigerina*), while the paleontologist can describe the evolution of stratigraphically late species of *Globanomalina* into early species of the new genus *Pseudohastigerina*. The two genera are different in coiling mode and apertural extent; if these morphological differences are not nomenclatorially distinguished here, then guidelines would be established which would play havoc with the taxonomy

(and the resulting biostratigraphy) of these and other groups of Globigerinina.

TAXONOMIC HISTORY AND STATUS

GLOBANOMALINA OVALIS HAQUE, 1956

The genus *Globanomalina* was proposed by Haque (1956, p. 147) with *G. ovalis* Haque, 1956, as its designated type species, originally retrieved from the Nammal Limestones and Shales of the Laki Series, exposed in the Nammal Gorge of the Salt Range in Pakistan. The specimen figured by Haque (1956, pl. 14, fig. 3a–c, enlarged and reproduced on Pl. 1, Fig. 1a–c) was the holotype of *G. ovalis*, and it was obtained from sample 62 of Haque's measured outcrop section. Although this sample came from a series referred by Haque (1956) to the lower Eocene, the sample also yielded planktonic foraminiferal taxa now known as *Morozovella aequa* (Cushman and Renz) and *M. acuta* (Toulmin), while *M. velascoensis* (Cushman) was believed to have its lowest occurrence only 20 feet higher in the section (Haque, 1956, pls. 1 and 35). It would now be referred to the late Paleocene, probably to Zones P4 (the *Planorotalites pseudomenardii* (Bolli) Zone) or P5 (the *M. velascoensis* (Cushman) Zone) as recognized by Toumarkine and Luterbacher (1985).

Globanomalina was said by Haque (1956) to have its chambers "arranged in a trochoid spiral . . . All the chambers are visible from the dorsal side, which may be flattened or convex. Ventral side completely involute, umbilicate." These features were not only drawn by Haque for the type species, *G. ovalis*, but for all other species included by him in the new genus; an example is *G. simplex* Haque (1956, p. 149, pl. 30, fig. 2a–c, reduced and reproduced here on Plate 1, Fig. 2a–c), which is recorded by Haque (1956, pl. 35) to have a range similar to that of *G. ovalis* in the Nammal Limestones and Shales.

Type specimens of all of the new species, including the holotype of *Globanomalina ovalis*, were to be deposited by Haque (1956, p. 2) with the Geological Survey of Pakistan at Quetta, Pakistan. Some paratypes were presented by Haque to the British Museum (Natural History) in September 1954 (as recorded by Berggren and others, 1967, p. 279), and, among them, the two paratypes of *G. ovalis* are now registered as specimens P.42400. These specimens are now re-illustrated (Pl. 1, Fig. 3a–c, and Pl. 2, Fig. 1a–c). The specimens essentially agree with both the description and the drawings of *G. ovalis* originally published by Haque (1956) and with the notes later published by Berggren and others (1967). On the umbilical side the species is involute, while on the spiral side it is evolute, with all the chambers of the earlier whorls still visible. The aperture (as described by Berggren and others, 1967)

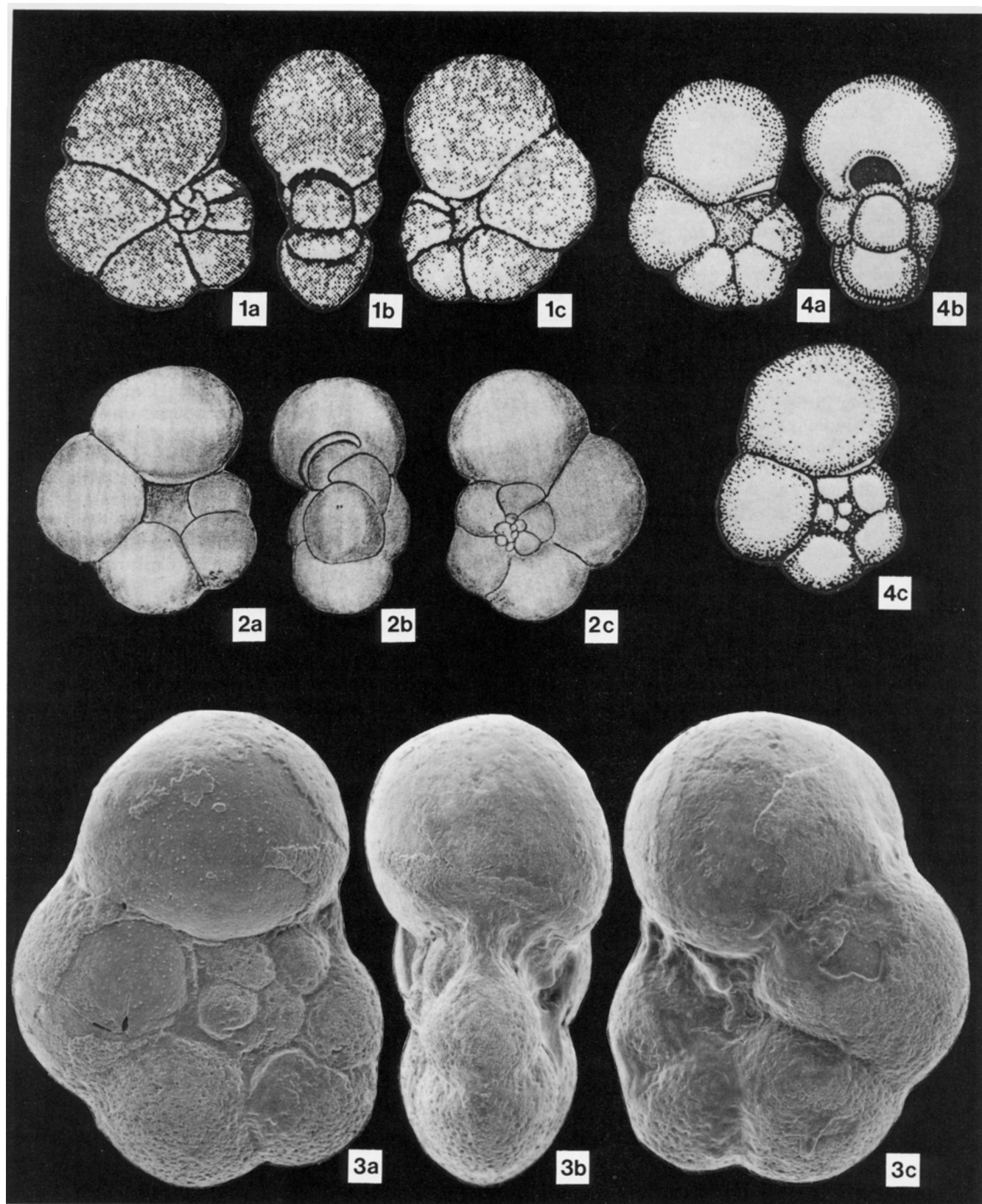


PLATE 1

1a-c *Globanomalina ovalis* Haque, 1956; original drawings of holotype, from Haque, 1956, pl. 14, fig. 3a-c, enlarged 300%, to give magnification of $\times 225$ if original estimate of magnification is used (" $\times$ ca. 75"), or, more probably, $\times 175$ if original measurements of specimen are used ("length . . . 0.26 mm"). **2a-c** *Globanomalina simplex* Haque, 1956; original drawings of holotype, from Haque, 1956, pl. 30, fig. 2a-c, reduced to 72.5% of original size, to give magnification of $\times 100$ if original estimates of magnification (" $\times$ ca. 142") or length of specimen

"is ventral and extends from the umbilicus to and around the periphery of the preceding whorl, but not along the dorsal suture on the dorsal side." As Haque wrote (1956, p. 148), "dorsal side flat or slightly convex, showing all the chambers. Ventral side completely involute, umbilicate . . . Aperture an elongate slit at the base of the last chamber of the outer whorl extending from the periphery to the umbilicus." Such trochospiral coiling, with such an asymmetrical, essentially umbilical-peripheral aperture, cannot (at least, should not) be confused with the planispiral coiling of the biumbilicate adult test, with its symmetrical, biumbilical-peripheral aperture, characteristic of all species of *Pseudohastigerina*, as that genus was originally defined (Banner and Blow, 1959, p. 19) and as it has subsequently been reliably used with full reference to its type species, *Nonion micrus* Cole (e.g., by Berggren and others, 1967; by Blow, 1979, p. 1178, who illustrated topotypes of *N. micrus*, Pl. 253; by Banner, 1982, p. 184, 206).

Loeblich and Tappan (1988, p. 485–486) were incorrect in stating that in both *Globanomalina* and *Pseudohastigerina* the "test [is] . . . biumbilicate . . . ; [the] aperture may extend to the umbilical area on one or both sides . . . ; . . . [the] coiling is dominantly planispiral and the aperture equatorial." For example, Loeblich and Tappan (1964, fig. 531.5a; 1988, pl. 531, fig. 7) illustrated a lateral view of a topotype with a concave spiral side which displays all the chambers of the early whorls of the trochospiral coil, and an aperture which covers the periphery of the penultimate whorl but which does not extend along the spiral (dorsal) side. The drawing is very like that given by Haque (1956) for the spiral side of the holotype (see Pl. 1, Fig. 1a), and conforms with the description given by Berggren and others (1967, p. 279, as noted above). The test shown by Loeblich and Tappan (1964, 1988) is not biumbilicate.

GLOBIGERINA PSEUDOIOTA HORNIBROOK, 1958

Two years after Haque's publication, Hornibrook (1958a) (independently and without reference to Haque's work) described as a new species *Globigerina pseudoiota* from the Waipawan stage, Waipawa outcrop section, New Zealand. The Waipawan stage (the oldest stage of the Dannevirke Series) was regarded by Hornibrook (1958a, p. 26–27 and table 1) as Paleocene, equivalent to the Upper Lizard Springs Marl of Trinidad or the Upper Velasco Formation of Mexico; it contained the first *Acarinina* and *Morozovella*, but occurred above the Teurian stage (with post-Maestrichtian *Globigerinina*, including *Subbotina linaperta* (Finlay)) which would nowadays be considered to be early to middle Paleocene. *Morozovella crater* (Finlay) (which morphologically can be no more than a subspecies of

M. velascoensis (Cushman) *sensu stricto*) first appears in the Mangaorapan stage, which succeeds the Waipawan, and persists into the succeeding Heretaungan stage, where *Pseudohastigerina* (as "*Nonion*" *iota* Finlay) was believed to first appear. These records by Hornibrook alone might suggest an approximate correlation of the Waipawan stage with Zone P4, the Mangaorapan with Zone P5, and the Heretaungan with Zone P6 (as diagnosed by Toumarkine and Luterbacher, 1985). However, Jenkins (1971, p. 16, 40) believed that the Waipawa standard section included both late Paleocene and the earliest Eocene, with *P. micra*, *M. rex*, etc., occurring in its upper part. "*G.*" *pseudoiota* was considered by Jenkins (1971) to be a junior synonym of "*Nonion*" *wilcoxensis* Cushman and Ponton, 1932 (a species correctly referred to *Pseudohastigerina* by Berggren and others, 1967, and by Cordey and others, 1970), which Jenkins (1971) called *Globanomalina* and recorded from both the Waipawan and Mangaorapan parts of the Waipawa standard section. Nevertheless, the age of the primary types of *Globigerina pseudoiota* Hornibrook may be virtually the same as that of the primary types of *Globanomalina ovalis* Haque (i.e., in Zones P4 or P5, late Paleocene). *Globigerina pseudoiota* was originally described by Hornibrook (1958a, p. 34) as being "almost planispiral . . . The aperture . . . opening a little to one side of the plane of coiling." The holotype and one paratype were drawn (1958a, pl. 1, figs. 16–18), and these figures are enlarged and reproduced here (Pl. 1, Fig. 4a–c); they show the umbilical and axial views of the holotype (Pl. 1, Fig. 4a, b), with the spiral side of the paratype (Pl. 1, Fig. 4c) being evolute, revealing all the chambers of the earlier whorls. The tests are clearly trochospiral, but pseudoplanispirality is achieved in the last whorl, when the interiomarginal aperture becomes umbilical-extraumbilical-peripheral in extent. The tests are not described or depicted as being biumbilicate, and the aperture is not shown to be symmetrical, biumbilical-peripheral. The original description and figures (Hornibrook, 1958a, loc. cit.) show that this "extremely finely perforate" species is congeneric with *Globanomalina ovalis*.

In 1966, Hornibrook presented eight ideotypes, which had been collected 20 ft above the base of the Dannevirke Series at the "mouth of the Birch Stream" (Hornibrook, 1958b, p. 664) to the British Museum (Natural History) (registered as P.47456), and three are illustrated in this paper (Pls. 2, 3) to show the range of variation considered by Hornibrook to occur within his species. All specimens show that the test of this species is trochospiral, becoming pseudoplanispiral in the last whorl of some specimens. Trochospirality is clearly maintained uniformly throughout growth when the number of chambers in each whorl is reduced from a juvenile 6 to an adult 5 (Pl. 3, Figs. 1, 2; Pl. 1, Fig.

(0.46 mm) are used. 3a–c *Globanomalina ovalis* Haque, paratype, from the Nammal Limestones and Shales, Laki Series, Nammal Gorge, Salt Range, Pakistan, BM(NH) P.42400a, $\times 300$. 4a–c *Globigerina pseudoiota* Hornibrook, 1958 (= *Globanomalina ovalis*); original drawings of holotype (4a, b) and paratype (4c) from Hornibrook, 1958a, pl. 1, figs. 16–18, enlarged 225%, to give magnification $\times 158$.

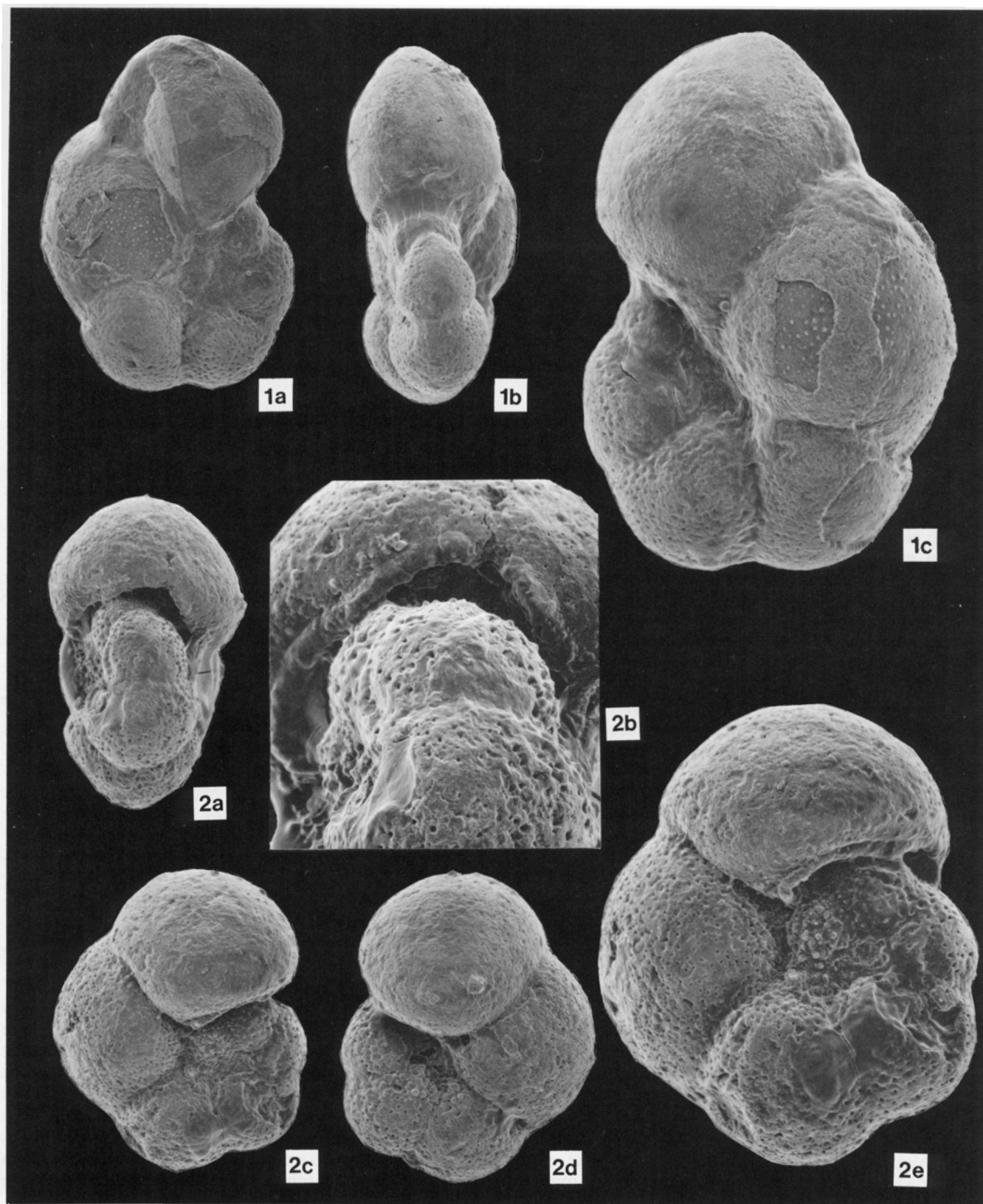


PLATE 2

1a-c *Globanomalina ovalis* Haque, 1956, paratype, from the Nammal Limestones and Shales, Laki Series, Nammal Gorge, Salt Range, Pakistan, BM(NH) P.42400b; last chambers have suffered some post-mortem (postburial) fracture and compression; loss of part of the walls of the last and penultimate chambers reveals internal molds of inner ends of the microperforations; apertural area shrouded in gum tragacanth, but apertural extent clearly similar to that in specimen figured below; **1a, b** $\times 200$; **1c** $\times 300$. **2a-e** *Globigerina pseudoiota* Hornibrook, 1958

4c); when the number of chambers per whorl is retained, throughout growth, as $5\frac{1}{2}$ –6, terminal pseudoplanispirality occurs (Pl. 2, Fig. 2a–e; Pl. 1, Fig. 4a, b). In this case, the last-formed chambers encroach onto the “dorsal” (spiral) sides of chambers of the penultimate whorl (Pl. 2, Fig. 2a, c, e); the “dorsal” sides of the trochospirally coiled earlier chambers are even then still clearly visible on the essentially evolute spiral side of the test. Even when terminal pseudoplanispirality is achieved, the aperture remains umbilical-peripheral (when seen from the umbilical side, Pl. 2, Fig. 2d), extending over the whole periphery of the penultimate whorl (as seen in axial view, Pl. 2; Fig. 2b), but it is present on the spiral side of only the last chamber (as seen clearly in tilted spiral-equatorial view, Pl. 2, Fig. 2e); it does not extend into a “dorsal” umbilicus, because there is no such structure, as the test is not planispiral. This is exactly the same in comparable paratypes of *Globanomalina ovalis* Haque (Pl. 2, Fig. 1a–c). Other ideotypes of *G. pseudoiota* lack the rapid enlargement of the final chambers, and do not attain terminal pseudoplanispirality, even though their tests may be as large as those which do. It may be noted that the newly figured, clearly trochospiral paratype of *G. ovalis* (Pl. 1, Fig. 3a–c), the originally figured paratype of *G. pseudoiota* (Pl. 1, Fig. 4c) and its similar newly figured ideotype (Pl. 3, Fig. 2a–d) are all about 0.3 mm in maximum diameter, and all are as big as the terminally pseudoplanispiral specimens of both taxa (Pl. 2, Figs. 1a–2e). The illustrated sequence of ideotypes of *G. pseudoiota* (Pl. 2, Fig. 2 to Pl. 3, Fig. 2) shows that a complete morphological grade exists between the clearly trochospiral and the terminally pseudoplanispiral tests; no taxonomic separation (at least, at full specific level) is practical or possible between them. The same is true of the comparable morphological variants of *G. ovalis*.

The ideotypes of *Globanomalina pseudoiota* from the mouth of the Birch Stream were considerably better preserved than the primary types, and clearly revealed to Hornibrook (1958b, p. 664), “the distinctly asymmetrical coiling and aperture” of the species. These specimens (including those illustrated here, Pls. 2, 3) were believed to be of Waipawan or Mangaorapan age, and had an illustrated asymmetry (Hornibrook, 1958b, p. 673, figs. 23, 26, 27) “typical of the whole sample [of conspecific specimens] from which they were selected.” Nevertheless, Hornibrook (1958b, p. 664) found that higher in the same section, in beds ascribed to the Heretaungan, “both symmetrical and asymmetrical forms occur. In the more compressed, narrower . . . test they resemble *iota* [“*Nonion*” *iota* Finlay, vel *Pseudohastigerina*] more than *pseudoiota* yet . . . they are intermediate between the two.” It is highly

probable that this was the fossil record of the continuous, apparently unpunctuated evolution of *Globanomalina* (*G. ovalis* and its immediate descendant, discussed below, *G. luxorensis*) into *Pseudohastigerina wilcoxensis* (Cushman and Ponton), which happened in Zone P6 according to Toumarkine and Luterbacher (1985, p. 101) or highest P6/basal P7 according to Blow (1979, p. 1193–1198).

SUMMARY

The tests of the types of *Globanomalina ovalis* (and of the types and ideotypes of its synonym *G. pseudoiota*) have a coiling mode and a wall surface which are not only different from those of *Pseudohastigerina* and the other members of the superfamily Hantkeniacea Cushman but which are trochospiral and microperforate, as were those of the presumed Paleocene ancestors (see below). Therefore, *Globanomalina* must have both its generic diagnosis and its suprageneric taxonomy emended from those published by previous authors (including Loeblich and Tappan, 1988).

SYSTEMATIC TAXONOMIC EMENDATION

Superfamily GLOBOROTALIACEA Cushman, 1927

Family EOGLOBIGERINIDAE Blow, 1979

Genus *Globanomalina* Haque, 1956, emended

Type species (O.D.): *Globanomalina ovalis*
Haque, 1956

Diagnostic description. Test trochospiral, with five to seven chambers in each whorl; spiral side slightly convex or flat or slightly concave; umbilical side with a narrow umbilicus; chambers throughout growth are inflated, subovoid, and spiral and intercameral sutures are depressed; periphery is typically rounded but may become very bluntly subangular in terminal growth, but never carinate; aperture is interiomarginal, a low slit-like opening, extending from the umbilicus to the periphery of the penultimate whorl, which it may reach or even surround, but not extending into or along the spiral suture; aperture is furnished with a porticus-like lip, which is typically imperforate and which tends to broaden posteriorly; the wall is microperforate, with narrow perforations opening exteriorly into low, bluntly margined perforation pits; no spines, pustules or spine bases, no acutely margined, polygonal perforation pits (not hispid or cancellate).

Remarks. The genus differs from *Eoglobigerina* Morozova, 1959, in having an intraextraumbilical aperture and not one which is merely anteroextraumbilical (as defined by Li Qianyu, 1987) and in being microperforate. *Globanomalina* differs not so much by its larger size (topotype *E. eobulloides* Morozova, 1959,

(= *Globanomalina ovalis*), ideotype, from 20 feet above the base of the Dannevirke Series, mouth of the Birch Stream, loc. S68/781, New Zealand, BM(NH) P.47456a; 6 chambers in the last whorl and final aperture extends on to the spiral side of the test; 2a, 2c, 2d, all $\times 200$; 2b, enlarged detail of 2a, slightly tilted, showing asymmetrically broader opening of the circum-peripheral aperture towards the umbilical side, $\times 460$; 2e, specimen seen on spiral side (as in 2c, but tilted), showing typical restriction of the aperture, on that side, to the last chamber, $\times 300$.

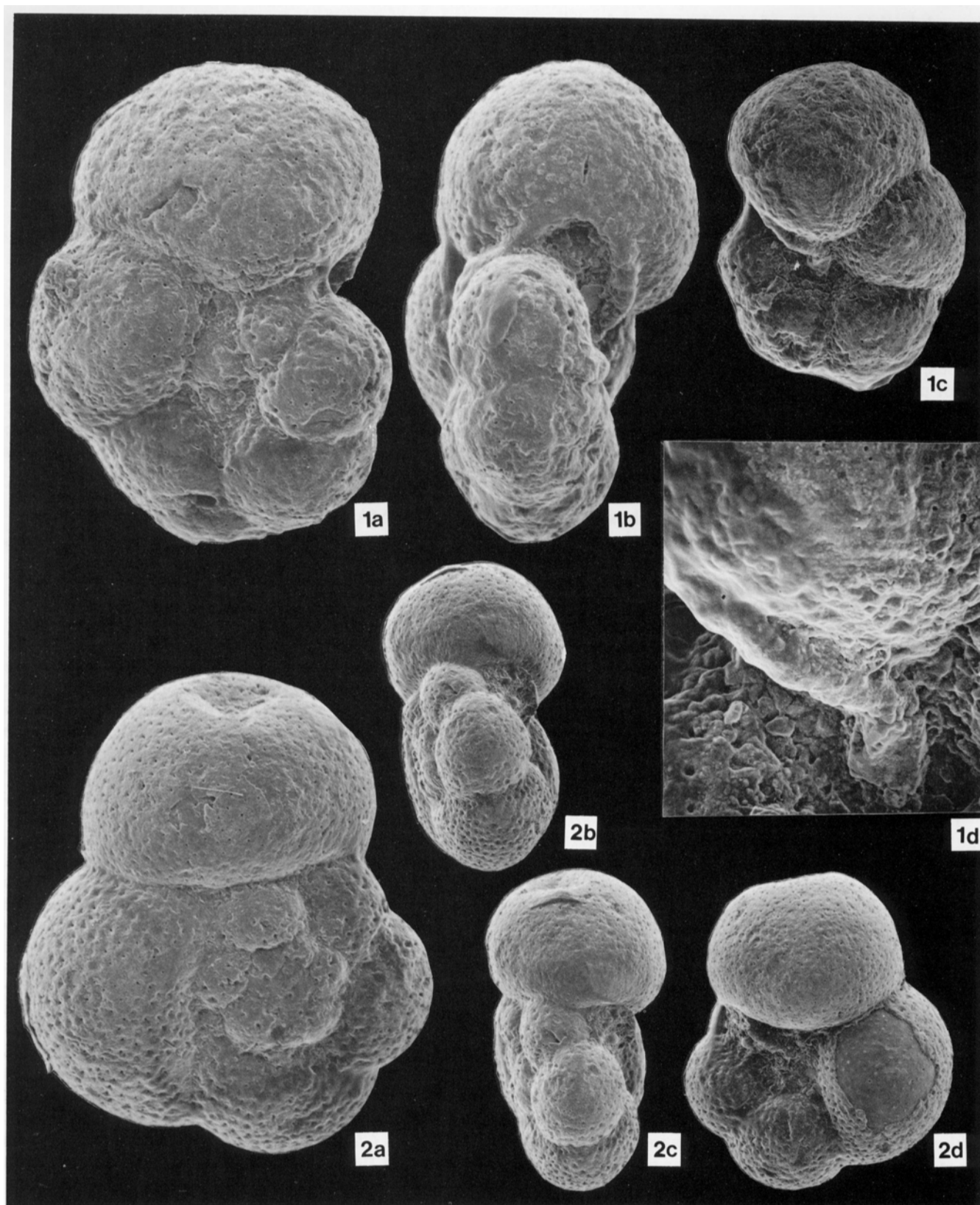


PLATE 3

1a-d, 2a-d *Globigerina pseudoiota* Hornibrook, 1958 (= *Globanomalina ovalis* Haque), ideotypes, from 20 feet above base of Dannevirke Series, at the mouth of the Birch Stream, New Zealand, BM(NH) P.47456b and P.47456c, showing progressively increased restriction of the aperture to the umbilical side with reduction in the number of chambers in the last whorl; also showing the microperforate walls, with superficial

the type species of *Eoglobigerina*, is illustrated by Loeblich and Tappan, 1988, pl. 513, to reach almost 0.25 mm maximum diameter, while *G. ovalis*, as on Pl. 1, reaches 0.3 mm) but by the flatness (Pl. 1, Fig. 3a-c) or concavity (Pl. 2, Fig. 1a-c) often assumed by its spiral side. Even when the spiral side of *Globanomalina* is at its maximum concavity (e.g., Pl. 2, Fig. 2a, b), it is still evolute and the aperture enters no umbilicus there; this is a clear distinction from *Pseudohastigerina* Banner and Blow, 1959 (and from all the Hantkeninacea Cushman, 1927, as defined by Loeblich and Tappan, 1988), which is biumbilicate and planispiral. *Globanomalina* differs from all of the Globigerinitidae Bermudez, including the Tenuitellinae Banner (as both are redefined by Li Qianyu, 1987), by lacking superficial scattered pustules on its walls, and from them, as well as from all of the Praehedbergellidae (as defined by Banner and Desai, 1988), by possessing perforation pits (the microperforations of the Praehedbergellidae open from completely smooth walls). *Globanomalina* lacks the macroperforate walls with polygonal (and pustular or spinose), acutely margined perforation pits and cancellate appearance of post-Eocene genera (such as *Paragloborotalia* Cifelli, 1982).

The loss of canaliculi and their perforations at the periphery of trochospiral tests has been preliminary to the repeated evolution of a keel in many families of the Globigerinina since the Aptian. As discussed by Banner and Desai (1988), the acquisition of a keel must have been advantageous to the lineage in which it evolved, and could have been related to the development of more efficient pseudopodial functions. Certainly, the phylogenetic descendants of typical *Globanomalina* (e.g., *G. chapmani* (Parr), Zones P3-6) included species which became carinate (e.g., "*Planorotalites*" *pseudomenardii* Bolli, Zones P4-7) while remaining microperforate (and smooth). Such species should be distinguished from the macroperforate (and more distinctly muricate) genus *Planorotalites* Morozova (e.g., its type species, *P. pseudoscitula* (Glaessner), Zones P10-13), but that is a matter beyond the scope of this paper. Nevertheless, they represented a different evolutionary development, along a separate path, from that of the other descendant, *Pseudohastigerina*. Like all other planispiral globigerines of the Cenozoic, *Pseudohastigerina* never became carinate. In the Cenozoic, descendants of a peripherally perforate globigerine lineage became either carinate or planispiral; these two morphocharacters were incompatible and never occurred together in the Cenozoic.

By the above emended diagnosis and differentiation for *Globanomalina*, other species which belong to this genus include "*Globigerina*" *compressa* Plummer, 1926, "*G.*" *danica* Bang, 1969, and similar early Paleocene species, for which no other appropriate generic

name currently applies, but which (as discussed below) are phyletically close to the microperforate *Globanomalina*-*Pseudohastigerina* lineage. Consequently, the stratigraphic range of *Globanomalina* is believed to be from early Danian, early Paleocene (Zone P α), to earliest Eocene (Zone P7-?8) (see below).

Globanomalina ovalis Haque, 1956, emended Plates 1-3

Globanomalina ovalis HAQUE, 1956, p. 148, pl. 14, fig. 3a-c.
Globigerina pseudoiota HORNIBROOK, 1958a, p. 34, pl. 1, figs. 16-18.

Description. *Globanomalina* as here defined, with six chambers per whorl initially, sometimes retaining this number in the last-formed whorl but sometimes reducing it to five; the rate of chamber volume increase with chamber addition is approximately the same in each form, so that (a) when the chamber number is reduced (e.g., to five in the last whorl) the spiral side of the test remains completely evolute and flat or slightly convex in shape, or (b) when the final chamber number is not reduced (e.g., is retained at about six in the last whorl) the final chambers overlap slightly onto the spiral side, so that that side becomes incompletely evolute and slightly concave in shape; wall is microperforate, with perforation canaliculi about 1 μ m in diameter, opening into broadly and bluntly rounded perforation pits about 10 μ m in diameter (the perforation pits are deeper on the earlier chambers which have had their walls thickened by test growth); maximum diameter achieved is about 0.34 mm.

Remarks. Both the paratypes and holotype of *Globanomalina ovalis* and the ideotypes, paratype, and holotype of "*Globigerina pseudoiota*" contain specimens which are terminally five- or six-chambered and no taxonomic distinction on this criterion is practical, possible or sensible. The primary types of *G. ovalis* were originally drawn as being more compressed laterally (as seen in axial view, Pl. 1, Fig. 1b) than those of "*G. pseudoiota*" Pl. 1, Fig. 4b), but comparison of the other specimens figured here (e.g., Pl. 2) shows that no separation between the taxa can be successful on this basis: the specimen which is peripherally most angular (Pl. 2, Fig. 1b) has a crushed and deformed last chamber (Pl. 2, Fig. 1a), and there can be no distinction within the range of variation shown by the other specimens. All other characters (e.g., perforation size as seen externally, as in Pl. 2, Fig. 2e, or as internal casts as on Pl. 1, Fig. 3a, or as both) appear to be the same. Consequently, the two taxa are believed to be synonyms. As noted above, the biostratigraphic age of the species is believed to be Zones P4-6, late Paleocene to earliest Eocene.

It has been suggested (Banner, 1982, p. 158) that

perforation pits which become deeper as the wall thickens in earlier chambers. 1a-d, 5½ chambers in the last whorl, P.47456b; 1a, b $\times$ 400, 1c $\times$ 267, 1d, the imperforate, porticus-like lip, $\times$ 870. 2a-d, 5½ chambers in the penultimate whorl but only 5 chambers in the last whorl, P.47456c; 2a $\times$ 300; 2b-d $\times$ 200.

Globanomalina luxorensis (Nakkady) should be regarded as the senior synonym of *G. ovalis* Haque. The type specimens of *Anomalina luxorensis* Nakkady (1950, p. 691, pl. 90, figs. 39–41) are deposited in the British Museum (Natural History) (registered as P.41697, holotype, and P.41892, four paratypes). They were obtained by Nakkady from the topmost Esna Shale at Abu Durba, southwest Sinai. This horizon was referred by Nakkady to the youngest Paleocene, immediately below beds referred to the Lower Eocene; however, *Morozovella velascoensis* (Cushman) occurs 150–300 m below this (Nakkady, 1950, p. 680–682, with unpublished notes deposited in the BM(NH), and the *M. velascoensis* specimens registered as P.41771) with *M. marginodentata* (Subbotina) (P.41768, recorded by Nakkady, 1950, as “*Globorotalia crassata* (Cushman) var. *aequa* Cushman & Renz”) also occurring 250 m below. It is not possible from the published and unpublished notes, and from the registered specimens, to be sure of the biostratigraphic age of *G. luxorensis*, but it is probable that its type horizon is within the Zone P6–7 interval. The type specimens should be referred to the earliest Eocene (*sensu* Toumarkine and Luterbacher, 1985, p. 100); it is likely that they are the same age or about a zone younger than the type *G. ovalis*. Re-examination of the types shows that *G. luxorensis* is very similar to *G. ovalis* but that it is distinguishable from it; *G. luxorensis* is more compressed laterally, its chambers are less inflated, and its intercameral sutures are less indented and more curved. All observed primary types of *G. luxorensis* have 6–6½ chambers in the last whorl. Its junior synonym, the equally compressed “*Globorotalia*” *pseudochapmani* Gohrbandt, 1967 (which occurs with a Zone P7–8 assemblage in Austria) has types with 6–7 chambers in the terminal whorl. It is probable that *G. luxorensis* is the intermediate form in the unpunctuated evolution from *G. ovalis* to *Pseudohastigerina wilcoxensis* (Cushman and Ponton). Drawings of a specimen referable to *G. luxorensis* were included within their concept of *P. wilcoxensis* by Toumarkine and Luterbacher (1985, p. 107, fig. 12.12a–c; not fig. 12.9–11).

THE PHYLOGENY OF *GLOBANOMALINA*

The oldest Danian, earliest Paleocene (Zone Pα), contains the oldest known microperforate, trochospiral, Cenozoic Globigerinina with an intraextraumbilical aperture. These include the species described by Blow (1979) as “*Globorotalia (Turborotalia)*” *archeocompressa* Blow (1979, pl. 56, figs. 1, 2, and pl. 58, figs. 2, 6–9) and “*G. (T.)*” *longiapertura* Blow (1979, pl. 58, figs. 3–5, and pl. 63, figs. 1–9). The latter is a junior synonym of “*Globigerina*” *eugubina* Luterbacher & Premoli Silva, 1964, which is the type species of *Parvularugoglobigerina* Hofker, 1978 (Li Qianyu, 1987, p. 313; Loeblich and Tappan, 1988, p. 474, pl. 513). Such species are not cancellate or hispid; their wall surfaces are not well known, but they may well possess the shallow, rounded-edge perforation pits of

typical *Globanomalina*. They are distinct from similar Zone Pα macroperforate taxa (such as “*G. (T.)*” *polycamera* (Khalilov) of Blow, 1979, pl. 59, figs. 1–4, 6).

The macroperforate, trochospiral, acarinate, intraextraumbilically apertured taxa were well established by the end of the early Paleocene and the beginning of the middle Paleocene (as with “*G. (T.)*” *pseudobulloides* (Plummer), of which a strict topotype from Zone P2 was illustrated by Blow, 1979, pl. 248, figs. 6–8). In the middle Paleocene they became strongly muricate (as *Acarinina* spp.) and then muricocarinata (*Morozovella* spp., from *M. conicotruncata* (Subbotina), Zone P3, onwards). These macroperforate taxa may well have had their origin with Danian *Eoglobigerina* Morozova, which is equally macroperforate (see the topotype of its type species, *E. eobulloides* (Morozova), illustrated by Loeblich and Tappan, 1988, pl. 513, figs. 1–3, and *E. eobulloides simplicissima* Blow, from Zone Pα, pictured by Blow, 1979, pl. 57, figs. 3, 4).

In contrast, the phylogeny of the microperforate forms never produced heavily muricate (or muricocarinata) taxa. Their origin is obscure; it may have been with microperforate, anteroumbilically apertured species which have been placed with *Eoglobigerina* (such as *E. fodina* Blow, 1979, pl. 57, figs. 5, 6, from Zone Pα) or with the intraextraumbilically apertured *Bléfuscuiana* spp. (Banner and Desai, 1988, Cretaceous). Nevertheless, they proceeded to evolve smoothly along two, principal phylogenetic lines. One retained trochospirality but developed a smooth, peripheral carina (“*Planorotalites*” spp., with “*P.*” *pseudomenardii* (Bolli) in Zone P4), while the other became planispiral and evolved into *Pseudohastigerina* in the early Eocene. Both of these have been (separately) noted above, but only the second will be discussed here.

The *Parvularugoglobigerina eugubina* line, with its narrowly elevated, peripherally highly arched, extraumbilical aperture (analogous to that of the late Eocene *Praetenuitella impariapertura* Li Qianyu), seems short lived (Zone Pα) and phyletically and taxonomically distinct (because of its aperture, slowly enlarging chambers and slowly opening spiral suture).

The main lineage, with the unelevated, narrow, intraextraumbilical aperture, from *Globanomalina archeocompressa* (Blow) (also Zone Pα) evolved through *G. compressa* (Plummer) (*Globigerina compressa* Plummer, 1926; Zones P1–3, see Blow, 1979, pl. 75, figs. 9–11, P1, and pl. 78, figs. 5–11, P2, etc.), to *Globanomalina chapmani* (Parr) (*Globorotalia chapmani* Parr, 1938; Zones P3–6; synonyms *G. ehrenbergi* Bolli, 1957, and *G. troelseni* Loeblich & Tappan, 1957; see Toumarkine and Luterbacher, 1985, p. 107–108). In these taxa, there is the distinctive increase in the rate of chamber enlargement, and an increasingly rapid opening of the curve of the spiral suture, which led to the concavity of the spiral side in its immediate descendants, the terminally 5- to 6-chambered forms of *Globanomalina ovalis* Haque (Zones P5–6) and the 6½- to 7-chambered forms of *G. luxorensis* Nakkady

(P6–?8). These taxa evolved directly into the truly planispiral, 6½- to 7-chambered, typical *Pseudohastigerina wilcoxensis* (Cushman & Ponton), as depicted by Cordey and others (1970, figs. 1–6), even though toptype assemblages of *P. wilcoxensis* (from the Bashi Marl, Ozark, Alabama, of the *M. subbotinae* Zone, according to Berggren and others, 1967, which equates to late Zone P6, according to Toumarkine and Luterbacher, 1985) contain both true *P. wilcoxensis* (as figured by Berggren and others, 1967, text-fig. 2s–v) and the immediately ancestral species of *Globanomalina* (op. cit., loc. cit., text-fig. 2p–o).

It is such assemblages, containing specimens referable to both genera, *Globanomalina* and *Pseudohastigerina*, which have led to the confusion between them. Such confusion does not arise in the intervals of the Dano-Paleocene or the middle Eocene to early Oligocene, because it was only in the earliest Eocene (Zones P6–?8) that the two genera co-existed.

The attainment of true planispirality, and a biumbilicate test, is emphasized in (rare) specimens of *P. wilcoxensis* by the bipartite division of the aperture, symmetrically forming two separate openings, one on each side of the planispiral test (as drawn in Berggren and others 1967, text-figs. 6, 4a–6c, and in *P. sharkriverensis* Berggren & Olsson, SEM imaged by Blow, 1979, pl. 252, figs. 5–9). Such a bilaterally symmetrical morphology could not be achieved by the asymmetrical, only pseudoplanispiral, late and phyletically advanced species of *Globanomalina*.

With *Pseudohastigerina* evolved smooth macroperforate tests. The distance between perforations became similar to their diameters, the perforation pits disappeared and the perforations themselves enlarged to about 1.7 µm diameter (as depicted for *P. wilcoxensis*, Zone P7, and *P. sharkriverensis*, Zone P9, by Blow, 1979, pl. 252), and to about 2.5 µm in the type species (*P. micra* Cole), as shown from Zones P9–12, loc. cit., pl. 253). As observed by Li Qianyu (1987), this was preliminary to a late Eocene (Zone P15) reversion to both microperforate walls and pseudoplanispirality (true trochospirality) in the evolution of the first tenuitellids (*Praetenuitella impariapertura* Li, *P. patefacta* Li, etc.), with pustules scattered on otherwise smooth wall surfaces (there were no perforation pits). True *Pseudohastigerina* spp. persisted, however, biostratigraphically as high as Zone P19, early Oligocene (Bolli and Saunders, 1985).

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REFERENCES

- BANNER, F. T., 1982, A classification and introduction to the Globigerinacea, in Banner, F. T., and Lord, A. R. (eds.), *Aspects of Micropalaeontology. Papers presented to Professor Tom Barnard: Allen and Unwin, London*, p. 142–239.
- , and BLOW, W. H., 1959, The classification and stratigraphical distribution of the Globigerinaceae: *Palaeontology*, v. 2, p. 1–27.
- , and DESAI, D., 1988, Early Cretaceous Globigerinina, with especial reference to the Aptian assemblages of Speeton (North Yorkshire, England): *Journal of Micropaleontology*, v. 7 (2), p. 143–185.
- BERGGREN, W. A., OLSSON, R. K., and REYMENT, R. A., 1967, Origin and development of the foraminiferal genus *Pseudohastigerina* Banner and Blow, 1959: *Micropaleontology*, v. 13, p. 265–288.
- BLOW, W. H., 1979, The Cainozoic Globigerinida. A study of the morphology, taxonomy, evolutionary relationships and the stratigraphical distribution of some Globigerinida (mainly Globigerinacea): E. J. Brill, Leiden, 3 v., 1413 p.
- BOLLI, H. M., and SAUNDERS, J. B., 1985, Oligocene to Holocene low latitude planktic foraminifera, in Bolli, H. M., Saunders, J. B., and Perch-Nielsen, K. (eds.), *Plankton Stratigraphy*: Cambridge University Press, Cambridge, UK, p. 155–262.
- CORDEY, W. G., BERGGREN, W. A., and OLSSON, R. K., 1970, Phylogenetic trends in the planktonic foraminiferal genus *Pseudohastigerina* Banner and Blow, 1959: *Micropaleontology*, v. 16, p. 235–242.
- GOHRBANDT, K. H. A., 1967, Some new planktonic foraminiferal species from the Austrian Eocene: *Micropaleontology*, v. 13, p. 319–326.
- HAQUE, A. F. M. M., 1956, The foraminifera of the Ranikot and the Laki of the Nammal Gorge, Salt Range: *Palaeontologia Pakistanica. Memoirs of the Geological Survey of Pakistan*, v. 1, p. 1–293.
- HORNIBROOK, N. DE B., 1958a, New Zealand Upper Cretaceous and Tertiary foraminiferal zones and some overseas correlations: *Micropaleontology*, v. 4, p. 25–38.
- , 1958b, New Zealand Foraminifera: Key species in stratigraphy—No. 6: *New Zealand Journal of Geology and Geophysics*, v. 1, p. 653–676.
- JENKINS, D. G., 1971, New Zealand Planaktonic Foraminifera: *New Zealand Geological Survey, Paleontological Bulletin* 42, 278 p.
- LI QIANYU, 1987, Origin, phylogenetic development and systematic taxonomy of the *Tenuitella* plexus (Globigerinitidae, Globigerinina): *Journal of Foraminiferal Research*, v. 17, p. 298–320.
- LOEBLICH, A. R., JR., and TAPPAN, H., 1964, Sarcodina, chiefly "Thecamoebians" and Foraminiferida, in Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology: Geological Society of America and University of Kansas Press, New York and Lawrence, KS, Part C Protista* (2), 2 v., 900 p.
- , and ———, 1988, Foraminiferal genera and their classification: Van Nostrand Reinhold Company, New York, NY, v. 1, 970 p., v. 2, 212 p.
- NAKKADY, S. E., 1950, A new foraminiferal fauna from the Esna Shales and Upper Cretaceous Chalk of Egypt: *Journal of Paleontology*, v. 24, p. 675–692.
- TOUMARKINE, M., and LUTERBACHER, H., 1985, Paleocene and Eocene planktic foraminifera, in Bolli, H. M., Saunders, J. B., and Perch-Nielsen, K. (eds.), *Plankton Stratigraphy*: Cambridge University Press, Cambridge, UK, p. 87–154.

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