

THE STATUS OF *BOLLIELLA*, *BEELLA*, *PROTENTELLA* AND RELATED PLANKTONIC FORAMINIFERA BASED ON SURFACE ULTRASTRUCTURE

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ABSTRACT

Surface ultrastructure of the type species of *Bolliella*, *Beella*, *Protentella*, and *Clavatorella*, all of which exhibit radial elongation of adult chambers, have been examined using the scanning electron microscope to determine their taxonomic relationships. Based on surface ultrastructural and other characteristics, *Bolliella* is considered to be a subgenus of *Globigerinella*, *Beella* a subgenus of *Globigerina*, and *Clavatorella* a subgenus of *Protentella*. *Bolliella* and *Beella* differ from

Protentella and *Clavatorella* in possessing fine hispid test surfaces resulting from presence of spine bases even on adult tests. It is suggested that *Bolliella* evolved from *Globigerinella*, *Beella* from *Globigerina* while *Protentella* and *Clavatorella* appear to have descended from a *Globorotaloides* ancestor. The tendency towards streptospiral coiling in the adult tests of *Beella* suggests a phylogenetic relationship to *Hastigerinella*.

INTRODUCTION

Radial elongation of adult chambers or tendencies towards this occur in numerous Cenozoic planktonic foraminifera of both trochospiral and planispiral forms and has been used as a criterion to separate taxa at the generic or subgeneric level (Cushman, 1927; Bolli, Loeblich, and Tappan, 1957; Bolli, 1957; Banner and Blow, 1959, 1960; Lipps, 1964; and Blow, 1965).

Using the scanning electron microscope, we have examined the surface ultrastructure of the late Cenozoic Globigerinacea with radially elongate adult chambers to determine phylogenetic and taxonomic relationships.

HISTORY OF TAXONOMIC SUBDIVISION

Cushman (1927) proposed *Hastigerinella* (subfamily Globigerininae) as distinct from *Hastigerina* Thompson,

1876, by the trochospiral test and radial elongation of chambers. *Hastigerina digitata* Rhumbler was designated by Cushman as the type species of *Hastigerinella*. However, *H. digitata* of Rhumbler (1911) is not conspecific with *Globigerina digitata* Brady, 1879, which led Galloway (1933) to cite *Hastigerinella rhumbleri* n. sp., as the type species. Bolli, Loeblich, and Tappan (1957) and Bolli (1957) included *Globigerina digitata* Brady, *Hastigerinella bermudezi* Bolli, and *H. rhumbleri* Galloway, in *Hastigerinella*.

Banner and Blow (1959) proposed a new subgenus *Bolliella* with the type species *Hastigerina (Bolliella) adamsi* n. sp., for *Hastigerininae* in which the adult test is planispiral and chambers are radially elongate. Banner and Blow (1959) considered *Hastigerinella* Cushman to be a subgenus of *Globorotalia*, and regarded Brady's *Globigerina digitata* to belong to *Hastigerinella*. In 1960, Banner and Blow erected another subgenus *Beella* (type species, *G. digitata*) of the genus *Globorotalia* distinguished by the uniformly trochospiral test

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TABLE 1
Location of samples examined

	Core	Latitude	Longitude	Water depth	Age
1. Deep-sea cores					
<i>Bolliella adamsi</i> :	RIS 88 G. (S. Pacific)	16° 51' S.	145° 48' W.	2,760 m	Recent
<i>Beella digitata</i> :	Leg 21 (D.S.D.P.), Site 206, Core 3, Section 1, 90-92 cm, (Southwest Pacific)	32° 00' 75" S.	165° 27' 15" E.	3,196 m	Pleistocene
" "	Eltanin 48-13, 2-4 cm (S.E. Indian Ocean)	28° 30' 95" S.	93° 30' 30" E.	3,326 m	Pleistocene
<i>Beella praedigitata</i> :	CAP 38 BP (S. Pacific)	14° 16' S.	119° 11' W.	3,400 m	Pliocene
2. Out crop samples					
<i>Protentella proluxa</i> :	Luisian Stage, Newport Bay, California, middle Miocene (collected by J. H. Lipps)				
<i>Clavatorella bermudezi</i> :	Hut Bay Formation, Little Andaman, Bay of Bengal, middle Miocene (collected by M. S. Srinivasan)				
<i>Clavatorella nicobarensis</i> :	Sawai Bay Formation, Car Nicobar, Bay of Bengal, early Pliocene (collected by M. S. Srinivasan)				

throughout and radially elongate adult chambers. The subgenus *Bolliella* differs from *Beella* in possessing a planispiral test with radially elongate chambers in the adult. Lipps (1964) proposed a new genus *Protentella* (type species, *Protentella proluxa*) within the Hastigerininae as distinct from other Hastigerinids and Globigerinids by its planispiral test with radially elongate chambers in the adult and by smooth-walled texture. Loeblich and Tappan (1964) elevated *Bolliella* and *Beella* to generic status, and assigned the latter to family Globigerinidae. Consequent upon this agreement with the views of Loeblich and Tappan that *Beella* belongs to Globigerinidae, Blow (1965) introduced *Clavatorella* (type species, *Hastigerinella bermudezi* Bolli) for those trochospiral species which have radially elongate chambers and an aperture which is interiomarginal, umbilical-extra umbilical in position.

Thus, forms possessing radially elongate chambers with various coiling modes and apertural positions were grouped by Blow (1965) into three different genera belonging to three separate subfamilies: *Bolliella* (Hastigerininae), *Beella* (Globigerininae), and *Clavatorella* (Globorotaliinae). According to Blow (1965) *Hastigerinella* is a special case representing a combination of streptospiral coiling and radially elongate chambers. Banner and Blow (1959, 1960) and Blow (1965) believed that all these groups arose by parallel evolution in different stocks and are phylogenetically unrelated. Blow (1965) considered *Protentella* as a junior synonym of *Bolliella*. On the contrary, Lipps (1966) regarded *Clavatorella* as a junior synonym of *Protentella*. Thus, considerable confusion has prevailed concerning the validity and usage of *Bolliella*, *Protentella*, and *Clavatorella*.

The classification proposed for the Cenozoic Globigerinacea with radially elongate chambers by Banner and Blow (1959, 1960) and Blow (1965) is based on gross morphological characteristics such as coiling mode and apertural position. With the development of the scanning electron microscope, and its application to the study of surface ultrastructure of planktonic foraminifera (Bé and others, 1966; Collen and Vella, 1973; Srinivasan and Kennett, 1974a, b; Kennett and Srinivasan, in press; Walker and Vilks, 1973; Vilks and Walker, 1974), it is now possible to attain greater precision in taxonomy and phylogeny.

MATERIALS

Six planktonic foraminiferal species possessing radially elongate chambers or tendencies towards this have been examined in this study: *Bolliella adamsi* Banner and Blow (type species of *Bolliella* Banner and Blow, 1959), *Globigerina digitata* Brady (type species of *Beella* Banner and Blow, 1960), *Protentella proluxa* Lipps (type species of *Protentella* Lipps, 1964), *Hastigerinella bermudezi* Bolli (type species of *Clavatorella* Blow, 1965), *Globigerina praedigitata* Parker, and *Clavatorella nicobarensis* Srinivasan and Kennett. Specimens examined are from the following locations (see table 1).

MORPHOLOGICAL CHARACTERISTICS OF GENERA AND SUBGENERA

CHARACTERISTICS OF BOLLIELLA

Type species. *Bolliella adamsi* Banner and Blow.

The typical form of *Bolliella adamsi* has a planispiral adult test, trochospiral juvenile test (Parker, 1962),

TABLE 2
Comparison of surface ultrastructure between *Bolliella*, *Beella*, *Protentella* and *Clavatorella*

Planktonic foraminiferal species	Surface ultrastructure	Pores	Spines	Stratigraphic range
<i>Globigerinella</i> (<i>Bolliella</i>) <i>adamsi</i>	Finely hispid, with smooth, even, microcrystalline interpore area.	Circular to subcircular pores, varying in diameter from $4\ \mu$ to $6\ \mu$.	Knoblike spine bases in the adult.	Recent
<i>Globigerina</i> (<i>Beella</i>) <i>digitata</i>	Cancellate pattern of raised ridges surrounding the pores. Less densely hispid than <i>Globigerina</i> or <i>Bolliella</i> . The interpore area is uneven, microcrystalline, tending to be crystalline at spine bases.	Small circular to subcircular varying in diameter from $1\ \mu$ to $2\ \mu$.	Scattered knoblike spine bases present which are less densely packed than <i>Globigerina</i> .	Pleistocene to Recent
<i>G. (Beella)</i> <i>praedigitata</i>	"	"	"	Pliocene-late Miocene
<i>Protentella</i> (<i>Protentella</i>) <i>prolixa</i>	Surface smooth, characterized by a regular reticulate pattern of ridges and subhexagonal porepits. Interpore area even to uneven, microcrystalline in texture.	Circular to subcircular uniformly distributed throughout. Diameter varies from $2.5\ \mu$ to $4.5\ \mu$.	Absent in the adult. May be present in young stage.	middle Miocene
<i>Protentella</i> (<i>Clavatorella</i>) <i>bermudezi</i>	Surface smooth, characterized by a regular reticulate pattern of ridges and subhexagonal porepits. Interpore area smooth, with microcrystalline texture.	Circular to subcircular uniformly distributed throughout. Diameter varies from $2.5\ \mu$ to $5\ \mu$.	Absent in the adult. Present in young stage.	middle Miocene
<i>Protentella</i> (<i>Clavatorella</i>) <i>nicobarensis</i>	Surface covered with irregular plates of calcite giving a crisp sugary appearance. The porepits and the cancellate ridges almost obliterated.	Subcircular to circular uniformly distributed. Pore diameter varies from $1.5\ \mu$ to $2.5\ \mu$.	Absent in the adult.	early Pliocene

usually five to six subglobular chambers in the final whorl with radially elongate chambers (pl. 1, figs. 1-4) and spinose surface when living (table 2). The distal end of some adult chambers in some individuals have short fingerlike extensions. SEM examination of the surface of final chamber shows uniformly distributed, circular to subcircular pores with scattered tubercles or knoblike spine bases on interpore areas. Otherwise, the interpore area is smooth with microcrystalline texture (pl. 1, fig. 5). The pores on the final chamber vary in diameter from $4\ \mu$ to $6\ \mu$. On earlier chambers, the spine bases tend to coalesce into irregular ridges and interpore areas have tendencies towards crystal growth forming coarser and more rugged topography. No crystals attain euhedral rhombohedral shape (pl. 1, fig. 6). The surface ultrastructure of *Bolliella* with circular pores and spine bases resembles *Globigerina* but spine

bases in *Bolliella* are few, knoblike, and scattered compared to *Globigerina* which has densely packed spine bases between numerous small pores. The surface ultrastructure of *Bolliella adamsi* is similar to *Globigerinella aequilateralis* suggesting a close affinity between the two as already pointed out by Banner and Blow (1960), Lipps (1966), and Parker (1967). Lipps (1966) placed *Bolliella* in synonymy with *Globigerinella* on the basis of wall structure. Following Parker (1962), he considered radial elongation of adult chambers in Globigerinacea to be no more than a supra-specific character. We consider that radial elongation of adult chambers in *Bolliella* justifies separation from *Globigerinella*, but on the other hand, close similarities in surface ultrastructure between the two taxa do not warrant separation at the generic level. Therefore, in order to demonstrate phylogenetic affinity between

Globigerinella and *Bolliella*, we prefer to retain the latter as a subgenus of *Globigerinella*. Further, because of the surface ultrastructure, and basic trochospiral coiling, we prefer to place *Globigerinella* and *Bolliella* in Globigerininae rather than Hastigerininae as suggested by Banner and Blow (1960).

CHARACTERISTICS OF BEELLA

Type species. *Beella digitata* (Brady).

Beella differs from *Bolliella* in possessing a trochospiral test and an umbilical aperture in the adult (pl. 1, figs. 9, 10; pl. 2, figs. 1, 2). Young individuals of *Beella digitata* have an extraumbilical aperture resembling *Globorotalia* (pl. 1, fig. 13) which becomes umbilical in the adult. The height of the spire varies considerably with growth of the individual becoming high spired in adults with a tendency towards streptospiral coiling. This suggests affinity with *Hastigerinella rhumbleri* Galloway (pl. 1, fig. 9). However, *Beella* is distinguished from *Hastigerinella* by lacking multiple hornlike chamber extensions and advanced streptospiral coiling.

The test surfaces of *Beella digitata* show a fine irregularly cancellate pattern of raised ridges surrounding the pores (pl. 1, figs. 12, 14). The final chamber of young individuals shows circular to subcircular pores and discrete tubercles representing spine bases (pl. 1, fig. 13). The surface topography of the final chamber on adult individuals is more rugged because of irregularly distributed tubercles on ridges. The pores are circular to subcircular, and small, varying in diameter from 1 μ to 2 μ (pl. 1, fig. 12). In adult individuals, pore pits are distinct and shallow. Occasionally, more

than one pore occurs in a single pore pit. The interpore area has a microcrystalline surface, and contains discrete tubercles that often coalesce to form ridges, forming a subhexagonal pattern to the pore pits (pl. 1, fig. 14). A smooth interpore area on some earlier chambers results from dissolution (pl. 2, fig. 4).

In general, the surface ultrastructure of *Beella digitata* is similar to, but much finer than, that of *Globigerina bulloides*. Although Parker (1962) noted its close affinity with *Globigerina*, she suggested that *Beella* may well be referred to *Hastigerinella*. Lipps (1966) considered *Beella* as a synonym of *Globigerina*. Banner and Blow (1960) regarded *Beella* as a subgenus of *Globorotalia* but later Blow (1969) considered it as a subgenus of *Globigerina*. We also prefer to retain *Beella* as a subgenus of *Globigerina* because of the radially elongate chambers, a finer surface ultrastructure than *Globigerina*, and a restricted stratigraphic occurrence (table 2).

SEM examination of the surface ultrastructure of *Beella praedigitata* (Parker) shows surface ultrastructure (pl. 2, figs. 3, 5–9) similar to its Pleistocene descendent *B. digitata*. The only difference between the two forms is a lack of fully developed radially elongate chambers in *B. praedigitata*, although the test shows a tendency towards radial elongation of the last chamber.

CHARACTERISTICS OF PROTENTELLA

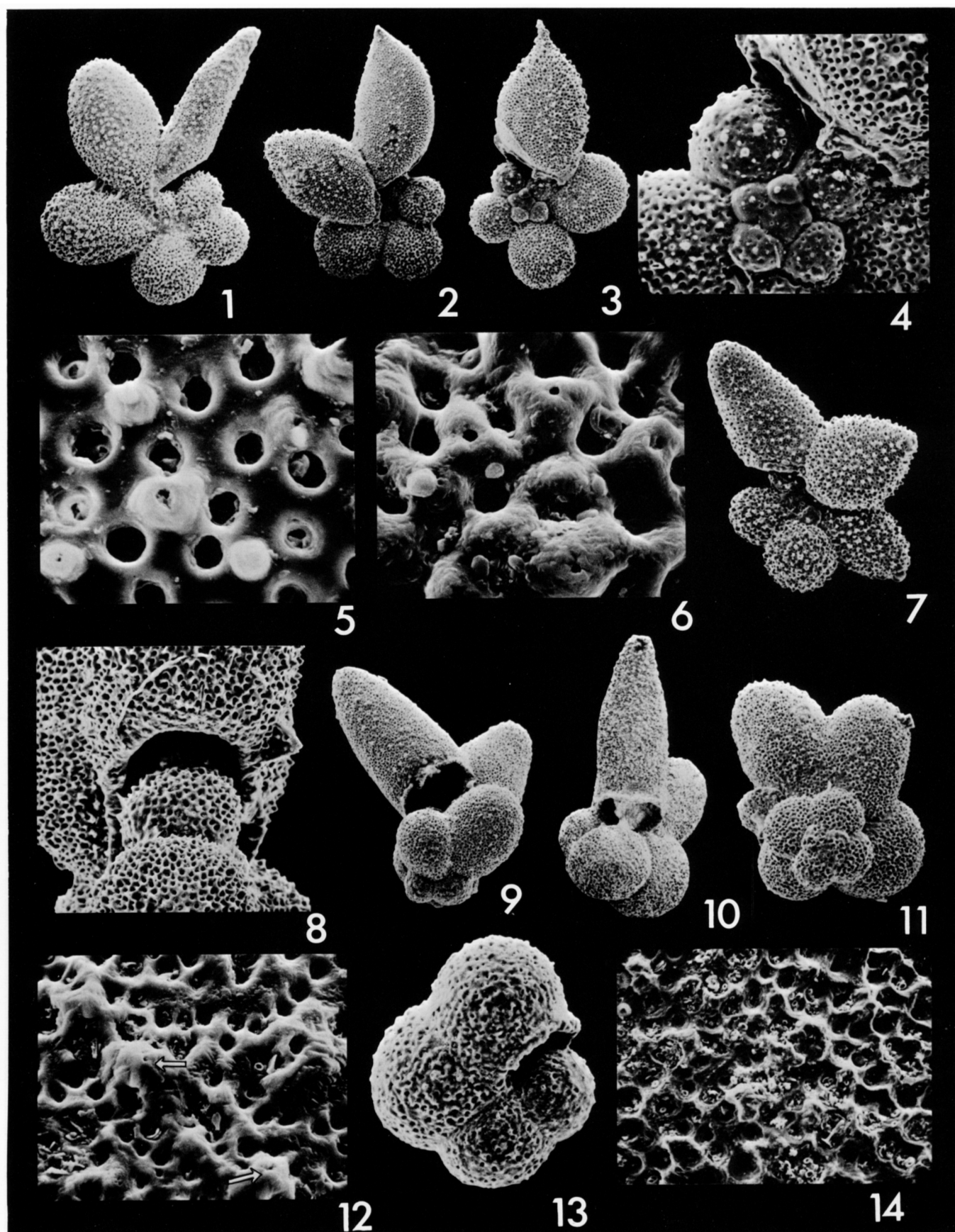
Type species. *Protentella proluxa* Lipps.

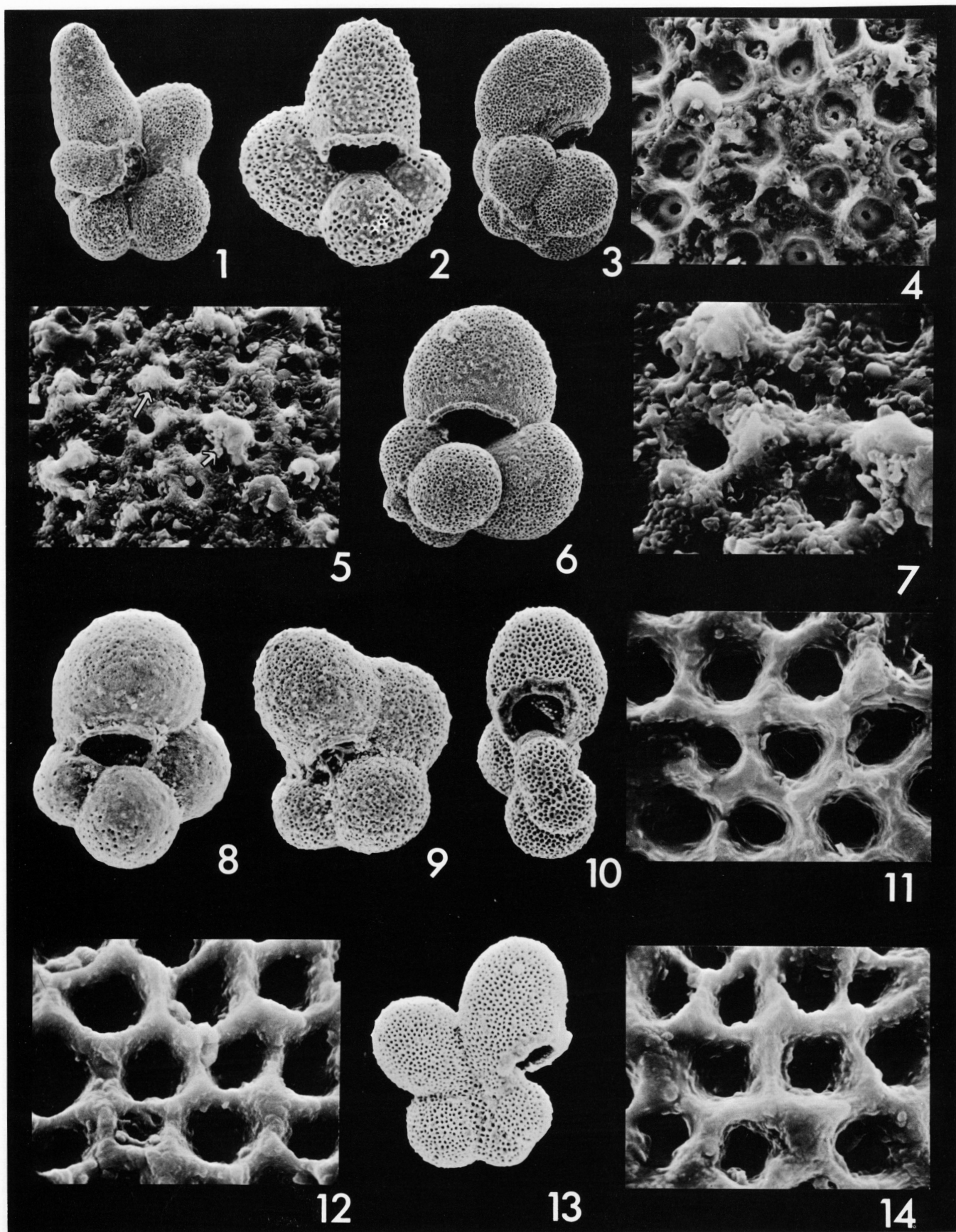
Protentella proluxa Lipps is characterized by a planispiral, involute, bi-umbilical test, with radially elongate

PLATE 1

- 1–8 *Globigerinella (Bolliella) adamsi* (Banner and Blow). R1S 88 G; 16° 51' S., 145° 48' W., 2,760 m. Recent. 1. Hypotype, side view (note the hispidity of the surface), $\times 102$. 2. Hypotype, side view, $\times 90$. 3. Juvenile specimen, dorsal view showing trochospiral coiling and a short fingerlike extension on the last chamber, $\times 108$. 4. Enlarged view of early chambers showing the proloculum followed by a whorl of about five rapidly enlarging chambers, $\times 318$. 5. Enlarged view of the final chamber showing circular pores, knoblike spine bases and smooth microcrystalline interpore area, $\times 2,000$. 6. Enlarged view of the earliest chamber on the last whorl. Note the circular pores and the coalescing spine bases forming irregular ridges. There is a tendency on the interpore region for crystalline thickening, $\times 2,000$. 7. Hypotype, side view showing hispidity

- of the surface, $\times 140$. 8. Enlarged apertural view; showing virtually planispiral coiling in the adult, $\times 280$. 9–14 *Globigerina (Beella) digitata* Brady. DSDP Leg 21, Site 206, Core 1, Section 1, 65–67 cm. 9. Hypotype, ventral view showing slightly displaced last chamber. Note the coiling of the test which is tending towards streptospiral approaching *Hastigerinella*, $\times 150$. 10. Hypotype, ventral view, $\times 113$. 11. Hypotype, dorsal view, $\times 157$. 12. Enlarged view of the penultimate chamber showing circular to subcircular pores and raised ridges. Spine bases marked by arrows, $\times 2,100$. 13. Juvenile specimen, showing extraumbilical aperture. Also note the pores and discrete tubercles representing the spine bases, $\times 363$. 14. Enlarged view of the final chamber, showing cancellate pattern of raised ridges surrounding the pores, $\times 1,130$.





adult chambers. The wall is smooth, finely and uniformly perforate without any sign of spine bases on adult chambers (pl. 2, figs. 10, 13). We have not been able to obtain any juvenile specimens to see that these contain spines or spine bases. Lipps (1964), however, reported slight surficial knobs which may represent spine bases, but we have not confirmed this.

The surface ultrastructure of *Protentella* differs from both *Bolliella* and *Beella* in having no spine bases, thus lacking the characteristic hispid test surface of the latter two taxa (table 2). The surface ultrastructure on the final chamber of *P. proluxa* is a regular reticulate pattern of ridges forming circular to subcircular or subhexagonal pore pits, this same pattern persisting on most earlier chambers (pl. 2, figs. 11, 12, 14). The pores are uniform, regularly distributed throughout the test, with pore diameter varying from $2.5\ \mu$ to $4.5\ \mu$. The pores are bordered by steeply rising cancellate ridges of varying heights. The interpore area is almost smooth, microcrystalline without any discernible rhombohedral crystals even at magnification $\times 5,000$ (pl. 2, figs. 11, 12, 14). Blow (1965) considered *Protentella* to be a junior synonym of *Bolliella*, and further suggested that *P. proluxa* may be a junior synonym of *Bolliella adamsi*. However, we find that *Bolliella adamsi* (pl. 1, figs. 5, 6) has fine hispid surface and spine bases, thus resembling *Globigerinella*. *Protentella proluxa* (pl. 2, figs. 11, 12, 14) differs distinctly in having a cancellate pattern of steeply rising ridges, lacks spine bases or hispid test surface and thus resembles *Globorotaloides* in surface ultrastructure. Because of these differences we retain *Protentella* as a valid genus.

CHARACTERISTICS OF CLAVATORELLA

Type species. Clavatorella bermudezi (Bolli).

Clavatorella bermudezi has a low trochospiral test which is evolute on the dorsal side throughout. The chambers are subspherical or ovate in early stages but later become radially elongate (pl. 3, figs. 3, 4, 8). This form is also distinguished from *Bolliella*, *Beella*, and *Protentella* by the diagnostic adult chambers, which are much more separated at their attenuated proximal ends. Young individuals of *C. bermudezi* (pl. 3, fig. 4) have distinct spines but, as in *Protentella*, they are totally lost in adult forms. The surface ultrastructure on the final chamber of *C. bermudezi* is identical to that of *P. proluxa*. The surfaces of almost all chambers have regular, uniformly distributed circular to subcircular or subhexagonal pore pits (pl. 3, figs. 2, 5, 6). The pores on the final chamber vary in diameter from $2.5\ \mu$ to $5\ \mu$. Like *Protentella*, the pores are bordered by steep microcrystalline ridges of varying heights.

Blow (1965) considered *Clavatorella* to have evolved from a globorotaliid ancestor and later Blow (1969) regarded this taxon to be a subgenus of *Globorotalia*. Lipps (1966) observed that the wall structure of *Clavatorella bermudezi* is similar to *Protentella* and *Globigerina*, and unlike the globorotaliids which Blow (1965, 1969) thought were most closely related. Therefore, Lipps (1966) placed *Clavatorella* in synonymy with *Protentella*. Fleisher (1974), however, considered that *Protentella* is distinct from *Clavatorella* by having weakly developed pore pits and lacking a cancellate texture or regular pattern of pore distribution. His illustration (1974, pl. 5, fig. 6) showing surface detail

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PLATE 2

- 1-2, 4 *Globigerina* (*Beella*) *digitata* Brady. Eltanin, 48-13, $28^{\circ} 30' 95''$ S., $93^{\circ} 30' 30''$ E., 3,326 m. 1. Hypotype, ventral view, showing misplaced kummerform chamber, $\times 180$. 2. Hypotype, ventral view showing umbilical aperture, $\times 233$. 4. Enlarged view of the earliest chamber on last whorl. Note the flattened interpore area caused by dissolution, $\times 2,050$.
- 3, 5-9 *Globigerina* (*Beella*) *praedigitata* Parker. CAP 38 BP, $14^{\circ} 16'$ S., $119^{\circ} 11'$ W., 3,400 m. 3. Hypotype, side view, $\times 131$. 5. Enlarged view of the final chamber showing circular pores and raised spine bases (shown by arrows). Also note the granular interpore area resulting from secondary thickening, $\times 1,920$. 6. Hypotype, ventral view, $\times 150$. 7. Further enlargement of fig. 5, $\times 4,800$. 8. Hypotype, ventral view, $\times 320$. 9.

- Hypotype, ventral view, showing tendency towards the radial elongation of the last chamber, $\times 240$.
- 10-14 *Protentella* (*Protentella*) *proluxe* Lipps. Luisian Stage, Newport Bay, California. 10. Topotype, apertural view, $\times 320$. 11. Enlarged view of the final chamber showing subcircular to circular, uniformly distributed pores and microcrystalline interpore ridges, $\times 5,000$. 12. Enlarged view of the final chamber showing subcircular to subhexagonal pore pits and steeply rising cancellate ridges of varying heights, $\times 4,900$. 13. Topotype, side view. Note the absence of hispidity of the surface, $\times 320$. 14. Enlarged view of the earliest chamber on the last whorl. In comparison with figures 11 and 12 note uniform pore distribution and even diameter of pores from the earliest to final chamber, $\times 5,000$.

of the final chamber of *P. proluxa* is of a highly corroded specimen (as in the specimen of *P. bermudezi* shown in pl. 3, fig. 6) and does not show distinct steep cancellate ridges producing subcircular to subhexagonal pore pits.

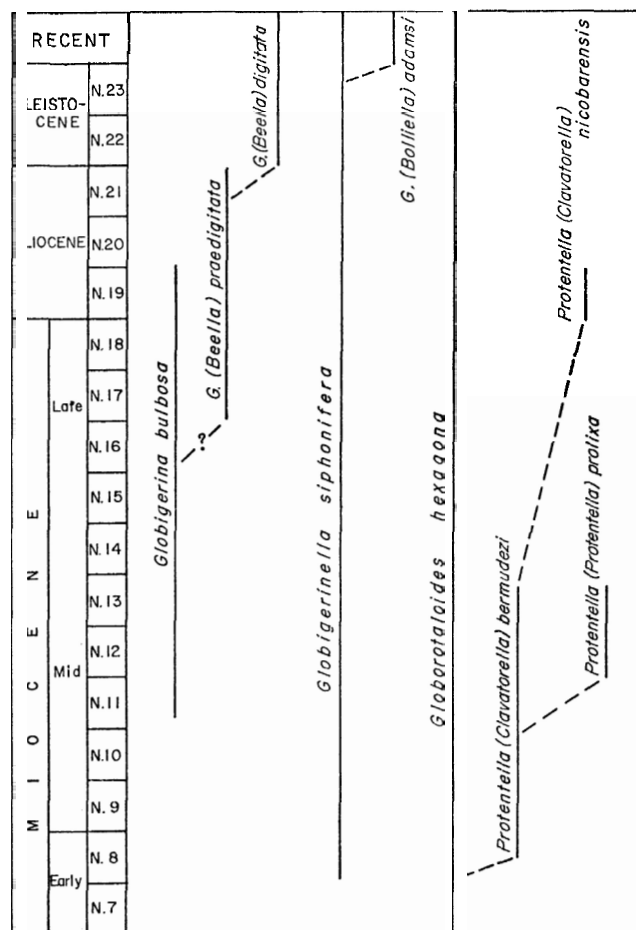
Our studies show that *Clavatorella* and *Protentella* have similar surface ultrastructure, and even the size, shape, and distribution of pores on the test are identical, suggesting a close affinity between the two (pl. 2, fig. 12; pl. 3, fig. 2). Although the wall structures are the same, as observed by Lipps (1966), we believe that the difference in the degree of trochospiral coiling in later stages between *Clavatorella* and *Protentella* justifies separation of *Clavatorella* at least as a subgenus of *Protentella*.

Status of *Clavatorella nicobarensis* Srinivasan and Kennett

Srinivasan and Kennett (1974a) described *Clavatorella nicobarensis* from the Pliocene of Nicobar Islands, Bay of Bengal, and considered this species to have descended from *Clavatorella bermudezi* (Bolli). On the evidence of surface ultrastructure these authors regarded *C. nicobarensis* to be related to *Beella digitata* but further work suggests that this is not the case. Surface ultrastructural studies of the holotype and paratypes of *C. nicobarensis* show that the entire test is covered with irregular plates of calcite (pl. 3, figs. 7, 9–13), which almost obliterates the pores and gives a crisp sugary appearance to the test surface. No definite pattern of crystals can be observed, even at higher magnifications. Careful examination of the test surface, however, reveals generally circular to subcircular pore pits, bordered by cancellate ridges (pl. 3, fig. 10), diagnostic of *Protentella* and *Clavatorella*. As is the case of *C. bermudezi*, we place *C. nicobarensis* in the genus *Protentella*, subgenus *Clavatorella*.

DISCUSSION

Blow (1965) classified forms having radially elongate chambers into three main groups, each having a distinct coiling mode and apertural position: 1. Planispiral coiling and equatorial aperture, *Bolliella* (Hastigerininae); 2. Trochospiral test and umbilical aperture, *Beella* (Globigerininae); and 3. Trochospiral coiling and extraumbilical aperture, *Clavatorella* (Globorotalinae). He considered *Hastigerinella* to be a special case representing a combination of streptospiral coiling and radially elongate chambers. According to Banner and



TEXT FIGURE 1

Phylogeny of *Bolliella*, *Beella*, *Protentella* and related planktonic foraminifera as suggested by surface ultrastructure and other morphological features.

Blow (1960) and Blow (1965) these groups arose by parallel evolution in different stocks and represent unrelated phylogenetic end forms. Parker (1962) and Lipps (1966) considered radial elongation of adult chambers to be a specific characteristic in some genera and therefore considered *Bolliella* and *Beella* as synonyms of *Globigerinella* and *Globigerina* respectively. Despite this, Lipps (1966) retained *Protentella* at the generic level and considered *Clavatorella* to be a synonym of *Protentella* on the basis of wall structure.

Examination of the surface ultrastructure of *Bolliella* Banner and Blow, *Beella* Banner and Blow, *Protentella* Lipps, and *Clavatorella* Blow show that *Bolliella* is more closely related to *Globigerinella* as already observed by Banner and Blow (1959) and Parker (1962), and that

Beella is similar to *Globigerina*, although it has a much finer surface ultrastructure (text fig. 1, table 2). The surface ultrastructure of *Protentella* is identical to that of *Clavatorella*, but the two forms differ in the degree of trochospiral coiling in the adult. Thus, in contrast to the statement of Banner and Blow (1960) and Blow (1965), ultrastructural characteristics suggest a close affinity between *Bolliella* and *Beella* on the one hand and *Protentella* and *Clavatorella* on the other. Furthermore, the tendencies towards streptospiral coiling in adult individuals of *Beella digitata* (pl. 1, fig. 9) suggests that *Hastigerinella* may have developed from *Beella*, by acquiring advanced streptospiral coiling and by developing bifurcation of adult chambers.

Blow (1965) considered *Clavatorella* to have evolved from a globorotaliid ancestor. According to Fleisher (1974), *Clavatorella bermudezi* evolved from *Globorotaloides variabilis* in the latest early Miocene. Our studies support the observations of Fleisher (1974) that there is a close similarity in the surface ultrastructure between *P. (C.) bermudezi* and *Globorotaloides hexagona*. We believe that *Protentella (Protentella) proluxa* and *Protentella (Clavatorella) bermudezi* both evolved from a *Globorotaloides* ancestor.

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PLATE 3

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- 1 *Protentella* (*Protentella*) *prolixa* Lipps. Apertural view showing virtually planispiral coiling. Also note the uniformly distributed pores throughout the test; same location as plate 2, figure 10, $\times 637$.
- 2-6, 8 *Protentella* (*Clavatorella*) *bermudezi* (Bolli). Hut Bay Formation, Little Andaman Island, Bay of Bengal. 2. Enlarged view of the final chamber. Note the sub-circular to subhexagonal pore pits, bordered by steep microcrystalline ridges of varying heights, $\times 2,180$. 3. Hypotype, ventral view, $\times 190$. 4. Juvenile specimen, ventral view. Note the projecting spines and knoblike spine bases on the test, $\times 304$. 5. Enlarged view of the final chamber showing the effect of dissolution, $\times 2,100$. 6. Enlarged view of the final chamber. Note the absence of ridges and the even interpore region caused by dissolution, $\times 1,900$. 8. Hypotype, dorsal view, $\times 241$.
- 7, 9-13 *Protentella* (*Clavatorella*) *nicobarensis* (Srinivasan and Kennett). Sawai Bay Formation, Car Nicobar Island, Bay of Bengal. 7. Paratype, oblique axial view to show that the aperture does not extend onto the dorsal side, $\times 980$. 9. Enlarged view of the final chamber. Note the surface, covered by irregular development of calcite crystals giving a crisp sugary appearance to the test. The crystal growth almost obliterates the pores, $\times 1,900$. 10. Further enlargement of figure 9. Note the circular to subcircular pore pits bordered by cancellate ridges, $\times 5,000$. 11. Holotype, ventral view, $\times 214$. 12. Paratype, oblique axial view, $\times 238$. 13. Topotype, ventral view, $\times 320$.

