

# Chapter 10

## The Buliminida

A study of foraminiferal assemblages of modern seas has disclosed striking correlations between form, structure and environment... Among species of *Bolivina*, *Bulimina* and *Uvigerina*, small, less ornamented types occur on the continental shelf and there is a progressive increase and differentiation of surface sculpture with increasing depth of water.

(Bandy, 1960)\*

The Buliminida include some of the most beautiful glassy Foraminifera—elongate spirals or columns of bubble-like chambers with comma-shaped or delicately siphonate apertures and compressed blades with barbed carinae. They are densely perforated and the pores, often of different sizes and shapes, may be arranged in different patterns. The external surface is often variously ornamented with costae, nodes or spines which appear to afford a peculiar adaptive advantage in the fine sediments of the deep ocean floor.

A characteristic feature is the toothplate connecting the aperture with the previous foramen. This varies from a simple trough-like or cornet-shaped structure to a rolled-up tube, and may protrude through the aperture like a cockscomb (figure 10.1). It has been investigated in detail under the optical microscope by Höglund (1947) and Hofker (1951, 1956) and illustrated by SEM (Glaçon and Sigal, 1974). Although Hofker stresses the value of the toothplate as a key to phylogenetic relationships in the group, it is still not clear what taxonomic weight can be put on these differences and further work by SEM is required.

The wall is calcitic and both hyaline radial and hyaline oblique structures occur. An attempt was made in the 'Treatise' to subdivide the group on the basis of these differences in wall structure with all the oblique genera removed to the Cassidulinacea. This move has broken down because variation occurs at the generic and the specific level. It was indicated by the results of Wood (1949a), who found that although *Ehrenbergina serra* sensu Brady is hyaline oblique, *E. hystrix* is

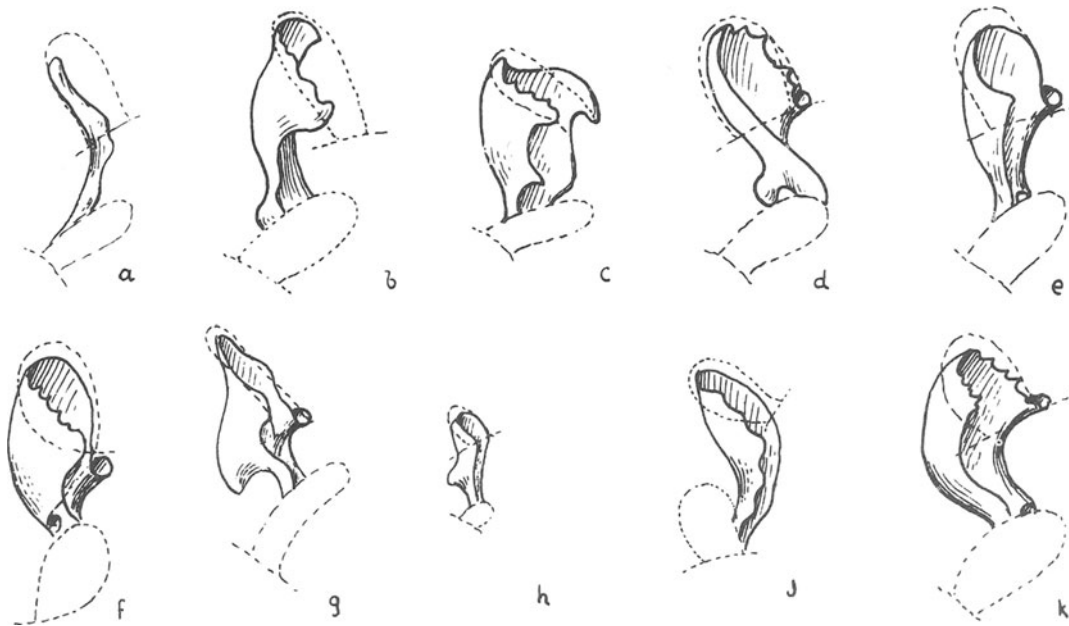
radial. *E. hystrix* var. *glabra*, however, is consistently hyaline oblique. He also discovered that *Pleurostomella subnodosa* sensu Brady is compound with an oblique inner layer and an outer pellicle of radially disposed crystals. These variations have been confirmed both in the Cassidulinidae (Feyling-Hanssen and Buzas, 1976) and in the Turriliniidae (Hansen, 1972).

As pointed out earlier (chapter 4), the wall in all the hyaline Foraminifera apart from the Nodosariida is regarded as fundamentally bilamellar. Sliter (1974), after a study of the ultrastructure of members of the Bolivinitidae and *Caucasina*, regarded them as 'essentially monolamellar' but with a surface veneer. He distinguished the following layers: a spongy organic lining, basal membrane, calcitic wall, calcitic veneer and outer membrane. Two calcitic lamellae are therefore present in the wall of each new chamber, as in strictly bilamellar forms. The pores are simple 'protopores' and lack sieve plates.

### CHAMBER FORM AND COILING MODES

As is well shown by the table of coiling modes (figure 4.3), almost 100 genera were placed in this order in the 'Treatise' (Loeblich and Tappan, 1964) and high trochoid arrangement is clearly dominant, reaching 70 per cent. Significantly, a similar high proportion is achieved only in the Lituolida. Biserial to uniserial arrangement reaches 17 per cent and enrolled biserial 10 per cent. Low trochoid and fully uniserial genera (in both generations) are rare, two only in each case. No unilocular forms were included in this group in the 'Treatise' but *Parafissurina*, and certain species placed in *Lagena*, probably belong here.

\*See Bandy (1960a).



**Figure 10.1** Toothplates in the Buliminidae. a *Praebulimina* sp., b *Bulimina trigonalis*, c *Bulimina rostrata*, d *Bulimina inflata*, e *Bulimina buchiana*, f *Bulimina marginata*, g *Reusella spinulosa*, h *Chrysalidinella*, j *Bulimina debelis*, k *Bulimina aculeata*. From Hofker (1951)

There are no attached forms and as in the case of the Nodosariida there are no examples of secondary subdivision of the chambers, although retral processes occur rarely.

The superfamilies and families are distinguished on the basis of chamber arrangement and aperture form. See the Summary Classification at the end of the chapter.

### Buliminacea

Trochospiral to triserial, biserial and uniserial genera, usually round or trigonal in section with globular chambers and umbilical, basal to comma-shaped aperture, are included in the Buliminacea. The aperture becomes terminal and round in advanced forms and finally produced with a turned out (everted or phialine) lip. The toothplate is trough-like or cornet shaped with free edge produced and wing-like or rolled up to form a tube.

Trochospiral genera with more than three chambers to the whorl, at least in the initial part, are included in the Turriliniidae. Triserial to uniserial genera with comma-shaped or terminal aperture are included in the Buliminidae. This family includes species with oval to slit-like pores, sometimes of two sizes in the same individual and in advanced forms the free edge of the toothplate

is rolled up and joins the anterior end of the aperture. Triserial to uniserial genera with produced aperture, characteristically with a long neck and phialine lip, are included in the Uvigeriniidae. Triserial to uniserial genera with triangular or arched chambers and basal to cribrate apertures are included in the Pavoniniidae.

The toothplate shows considerable variation in this superfamily, as revealed by the optical microscopic researches of Höglund (1947), Hofker (1951), Haynes (1954), Nørvang (1966, 1968a, 1968b), and SEM (Glaçon and Sigal, 1974; Scott, 1977). Hofker distinguished a number of genera largely upon the basis of this feature, as for instance *Euvigerina* which has a trough-like toothplate lacking the wing-like free edge of *Uvigerina*. However, there are similar differences between Palaeocene species still referred to *Bulimina*, such as *B. thanetensis* and the genoholotype *B. marginata* which has a rolled-up free edge. Before these differences are accepted as generic or even subgeneric further genera, especially *Neobulimina*, and a broad range of species must be examined. For the same reasons the Turriliniidae are distinguished from the Buliminidae here on the basis of their trochospiral arrangement rather than their supposed simpler toothplate, as in the 'Treatise'. This is because this structure has not been described in *Turrilina*, although the SEM photos of Hansen (1972) appear to show a cornet-

shaped toothplate with denticulate free edge, possibly not unlike that of *Stainforthia*. *Caucasina*, although hyaline oblique, is included here in the Turriliniidae, as is *Epistominella* which appears close to *Baggatella* despite its peripheral, rather than umbilical, aperture.

The Buliminidae like the Turriliniidae are regarded as including both hyaline radial and oblique genera and species. For this reason *Fursenkoina* and *Cassidella* are placed close to *Stainforthia*.

### Bolivinitacea

Compressed biserial to uniserial genera and enrolled biserial to uncoiled forms with aperture in the plane of compression, umbilical to terminal, are included in the superfamily Bolivinitacea.

The family Bolivinitidae includes the biserial to uniserial genera with aperture extending into the apertural face from the basal suture or becoming terminal or rounded. The Eouvigerinidae exhibit similar chamber arrangement but the aperture is terminal with a produced neck and lip. In contrast, the Islandiellidae are enrolled biserial to uncoiled with basal to subterminal aperture.

Most, if not all, of the genera in the Bolivinitidae appear to be hyaline radial, if we continue to exclude *Loxostomum*, following Loeblich and Tappan (1964). This can be justified on the grounds of complete absence of a toothplate in this genus, which is consistently present in other members of the superfamily. Indeed, Copestake (1978) suggests that the hyaline oblique *Loxostomum* gave rise to radial *Berthelinella* in the Lias. The Loxostomidae clearly require further study.

Although the Islandiellidae were originally distinguished as hyaline radial in wall structure, populations of *Islandiella islandica* from Rockall Trough and the North Sea are consistently hyaline oblique (specimens from G. Pearce and D. Masson collections, U.C.W.), although identical in other external and internal characters with the populations from Iceland originally studied by Nørvang (1958). If these populations can interbreed this represents variation in wall structure at the infraspecific level, as noted above in *Ehrenbergina*. Variation in wall structure at the specific level has also been confirmed in *Cassidulina* by Feyling-Hanssen and Buzas (1976). This has led these last authors to regroup *Islandiella* with *Cassidulina*. This course is not followed here because the Islandiellidae can be clearly differentiated upon the basis of the consistent presence of

a cornet-like toothplate, connecting the aperture with the previous foramen.

### Cassidulinacea

This superfamily includes triserial to biserial and uniserial genera and enrolled biserial to uncoiled forms with subterminal to terminal or peripheral aperture. The lower margin of the aperture is characteristically dentate and there is an internal tube or siphon, although this may be lost or reduced in advanced forms. The Pleurostomellidae include the triserial to biserial and uniserial genera, usually with globular and embracing chambers and crescentic aperture with dentate lower border and internal siphon. The siphon is much reduced in *Ellipsolingulina*. In the Cassidulinidae the toothplate is reduced to a short blade projecting internally from the inner border of the aperture and the chamber arrangement is enrolled biserial. In the streptospiral *Sphaeroidina* the toothplate is lost altogether but an external tooth is retained on the lower or outer border of the aperture, as in *Cassidulina*.

Most genera in the Pleurostomellidae are hyaline oblique but the unilocular *Parafissurina* is hyaline radial. For this reason it was transferred to the Glandulinidae in the 'Treatise'. However, the subterminal aperture beneath a hood and the long internal siphon indicate that an affinity with the Pleurostomellidae is more likely. *Sphaeroidina* was placed in a separate family in the 'Treatise', within the Buliminacea which were considered a radial group. It is here considered an advanced member of the Cassidulinidae, following Vašiček (1956). As noted above, a number of radial species of *Cassidulina* are now known, including *C. cushmani* and *C. delicata*, so a major objection to this course disappears.

### POSSIBLE EVOLUTIONARY RELATIONSHIPS

There are only doubtful records of the order in the Triassic, but both the Buliminacea and the Bolivinitacea are apparently present in the Jurassic. The Cassidulinacea arose in the Cretaceous and most families had appeared by the end of the period except the Pavoninidae, the Islandiellidae and the Cassidulinidae. All families show continued diversification with evolution of new genera through the Cenozoic.

Both Cushman (1948) and Glaessner (1945, see reprint 1963a) considered that the buliminaceans

were the most primitive group and probably arose from *Turrilina* and gave rise later to the bolivinitaceans and cassidulinaceans. Hofker (1951) in contrast, in the introductory part of his Siboga Report, considered the possibility that all three groups may have arisen separately from the agglutinating Valvulinidae. But later on he concluded that both the Buliminidae and Turrilinidae (Buliminellidae) arose separately from *Praebulimina*. He further proposed that the Bolivinitidae sprang from *Fursenkoina* (*Virgulina*), while *Cassidella* gave rise separately to the Cassidulinidae and the Pleurostomellidae. Loeblich and Tappan (1974) consider the possibility that *Deckerellina* (Palaeotextulariidae) was ancestral to the Buliminacea.

Pertinent to this discussion is the position of *Brizalina liassica* which is widespread in the Lower Jurassic. According to Nørvang (1957) and Witthuhn (1968) this species is aragonitic. *Neobulimina* has now been discovered in the Lias also (Copestake, 1978). The preservation of *Neobulimina bangae* and *B. liassica* in the Mochras Lias is identical. Copestake therefore suggests that both were aragonitic and that *N. bangae* gave rise to *Brizalina liassica* in the obtusum zone of the Sinemurian. This indicates to him that the Buliminida originated from the aragonitic Oberhauserellidae. On the other hand, the toothplate in these species is a broad, flat plate, different from the narrow trough-like toothplate in *Praebulimina*. Probably '*Neobulimina bangae*' and *Brizalina liassica*' represent a separate line of development in the aragonitic group and should be removed to the Robertinida (as here understood).

This leaves open the question of the origin of the Buliminida with *Praebulimina*, known from the Middle Jurassic, left as the most likely ancestral form. *Turrilina* is not known before the Eocene, so seems unlikely to represent a key, evolutionary link form. *Praebulimina* may have evolved from a triserial member of the Ataxophragmiidae with comma-shaped aperture and toothplate like *Eggerelloides* (see plate 7). *Eggerelloides* is not known before the late Cenozoic but the closely allied *Migros* is known from the Jurassic. The loosely spiral members of the Turrilinidae may have risen separately from a genus such as *Arenobulimina* and the low trochospiral genera appear to represent a distinct line of development within this group (subfamily Baggatellinae).

The Uvigerinidae probably also stem from *Praebulimina* but there may be two distinct lines: one leading from the Upper Cretaceous *Pseudouvigerina* to *Trifarina* in the Palaeocene and

*Siphouvigerina* and *Siphogenerina* in the Eocene, and the other to *Uvigerinella* in the Palaeocene and *Uvigerina* in the Eocene. The ancestral genus in the Pavoninidae is *Reussella* which may have arisen directly from *Bulimina* in the Eocene.

The Eouvigerinidae arose from among the Bolivinitidae (probably *Brizalina*) in the early Cretaceous and completely uniserial forms, *Siphonodosaria* and *Stilostomella*, had evolved by the end of the Period. As pointed out by Glaessner, *Islandiella* is apparently an enrolled bolivinitid and appears to have arisen near the Mesozoic/Cenozoic boundary from *Brizalina*. The secondarily uncoiled forms *Cassidulinoides* and *Ehrenbergina* appear in the Eocene and the completely uncoiled *Orthoplecta* in the Quaternary.

Although *Pleurostomella* is reported from the Lower Cretaceous, the apparently more primitive, triserial to biserial *Wheelerella* and *Bandyella* occur in the early Upper Cretaceous. These genera may be nearer to the ancestral form. Although Hofker produced convincing evidence to show that the siphon in early chambers of *Pleurostomella* is narrowly open, as in *Cassidella*, this genus is not recorded before the Upper Cretaceous. The origin of the Pleurostomellidae therefore remains in doubt. But it seems quite likely that *Cassidulina* arose from a compressed, biserial pleurostomellid like *Wheelerella* in which the subterminal aperture became a slit parallel to the periphery and the siphon was reduced as in *Ellipso-lingulina*.

All the families show a strong tendency to reduction in chamber number and appearance of uniserial growth. Unilocular genera apparently evolved in both the Uvigerinidae, '*Lagena*' with neck and phialine lip, and in the Pleurostomellidae, *Parafissurina*. This reduction in chamber number is generally accompanied by a change in the position of the aperture to terminal. However, it is noteworthy that in the Buliminidae, and especially in the Eouvigerinidae and Uvigerinidae, fully terminal apertures appear together with triserial and biserial chamber arrangement. Complication of the toothplate is seen particularly in the Buliminidae with rolled-up free edge in late Cenozoic *Bulimina* and double folding in *Globobulimina*, early in the Palaeogene.

Living individuals of the *Bulimina elongata* group occur with the apertural face adpressed to various firm substrates in Cardigan Bay, including mollusc shells (Haward and Haynes, 1976). The foraminifer clings by means of its pseudopods and ectoplasmic film, the test being held up at an angle of about 60°. The cylindrical form is relatively

stable hydrodynamically (see figure 4.7) and can be orientated down-current. The initial spine probably acts as a protective device. Other genera with basal and comma-shaped aperture probably adopt similar life positions, and also those genera with enlarged, flattened and often triangular face. Thus *Bolivinita* may occur upright on firm substrates like *Textularia truncata* in Cardigan Bay and orientate itself to the current in a similar fashion. But there seems little doubt that hydrodynamically unstable, elongate and carinate, blade forms, including most species of *Bolivina* and *Brizalina*, are gliding forms lying flat on the bottom (as seen in the photographs of culture dishes of *Bolivina doniezi*, published by Sliter, 1970). Interestingly, many develop longitudinal ornament like *Lingulina* and *Fronicularia*.

The movement of the aperture to the terminal position and development of a neck is considered to represent an adaptation connected with feeding at or below the sediment/water interface (as discussed in chapter 4 and in relation to similar trends in the Agglutinating Group and the Nodosariida). This is well seen in the Uvigerinidae and in the Pleurostomellidae where embracing, globular chambers (hydrodynamically stable) are characteristic, as in the Glandulinidae. This shape would help partially buried forms to overcome the difficulty of orientating to changing currents. In fully infaunal genera an elongate cylindrical shape is probably more adaptive.

Compared with the Nodosariida, the number of completely uniserial genera is low. This could be explained as indicating low numbers of fully infaunal genera. It is more simply explained as reflecting the high proportion of elongate trochospiral forms which could be regarded as pre-adapted to an infaunal life. In the Nodosariida, uncoiled genera tend to be assymetric in shape until the initial coil is lost. It is noteworthy that among the bolivinaceans the fully uniserial *Siphonodosaria* is the end product of a line of development from a blade form, the compressed biserial *Eouvigerina*. The complication of the evolutionary pathways followed by some families in this group is well illustrated by the reappearance of a close-coiled test form in the secondarily enrolled *Islandiella* and *Cassidulina*, presumably indicating a return to mobile surface feeding. But once again, by the Eocene, marked uncoiling trends supervene.

#### STRATIGRAPHICAL USE OF THE BULIMINIDA

The Buliminida became abundant by the Upper

Cretaceous and are characteristic of Cenozoic assemblages, especially in sediments representing Outer Shelf and Slope depths (see further below). Several families do not appear until the Tertiary and the time of first occurrence of many genera is stratigraphically useful. There is a strongly marked influx of new forms in the Eocene and this group has found particular application in the biostratigraphical zonation of the Middle Tertiary as well as in the Upper Cretaceous.

A number of authors have attempted to achieve the refinements possible through close definition of the species in particular lineages. In the Upper Cretaceous most attention has been paid to the *Bolivinoidea* group. Thus, Hiltermann and Koch (1950) found that the Senonian to Maastrichtian interval to N.W. Germany could be zoned on the series: *Bolivinoidea strigillata* — *B. decorata decorata*—*B. miliaris*—*B. decorata delicatula*—*B. draco draco*—*B. decorata gigantea*. With modifications this scheme has now been applied worldwide: in Australia (Edgell, 1954), England (Barr, 1966), France (Hinte, 1967), Libya (Barr, 1970) and the USA (Petters, 1977). Several lines are now recognisable and Petters distinguishes a central stock leading from *B. strigillata* through *B. culverensis*, *B. decoratus* and *B. miliaris* to *B. draco* and side lines to *B. giganteus* (raised to specific rank) and through *B. praelaevigatus* to *B. laevigatus*. The close similarity in the ranges of the main elements in this plexus in England and Libya are well shown in figure 10.2.

*Bolivinoidea* is useful only up to the Lower Maastrichtian and is replaced by other index benthonic species in the Upper Maastrichtian, but these include two species of *Pseudouvigerina* (Surlyk and Birkelund, 1977). The work on the Maastrichtian White Chalk by these authors is a good example of an integrated study of several faunal groups. As emphasised earlier, the student should note that although in this book we are dealing exclusively with Foraminifera their value is much increased when the results are combined with those of the study of other groups.

*Uvigerina* is a very useful genus in stratigraphy from the Eocene onwards and Vella (1961) distinguished several lineages in the Tertiary of New Zealand. The generalised scheme given by Hornibrook (1968) is reproduced in figure 10.3. Further work world wide has been carried out by Papp and Schmid (1971), Schmid (1972), Boersma and Berggren (1972), Lamb and Hickernell (1972), Daniels and Spiegler (1977) and Boersma (1977), and seven zones can be distinguished in the Miocene of N.W. Germany on the basis of the *U. semiornata* and *U. pygmaea* groups.

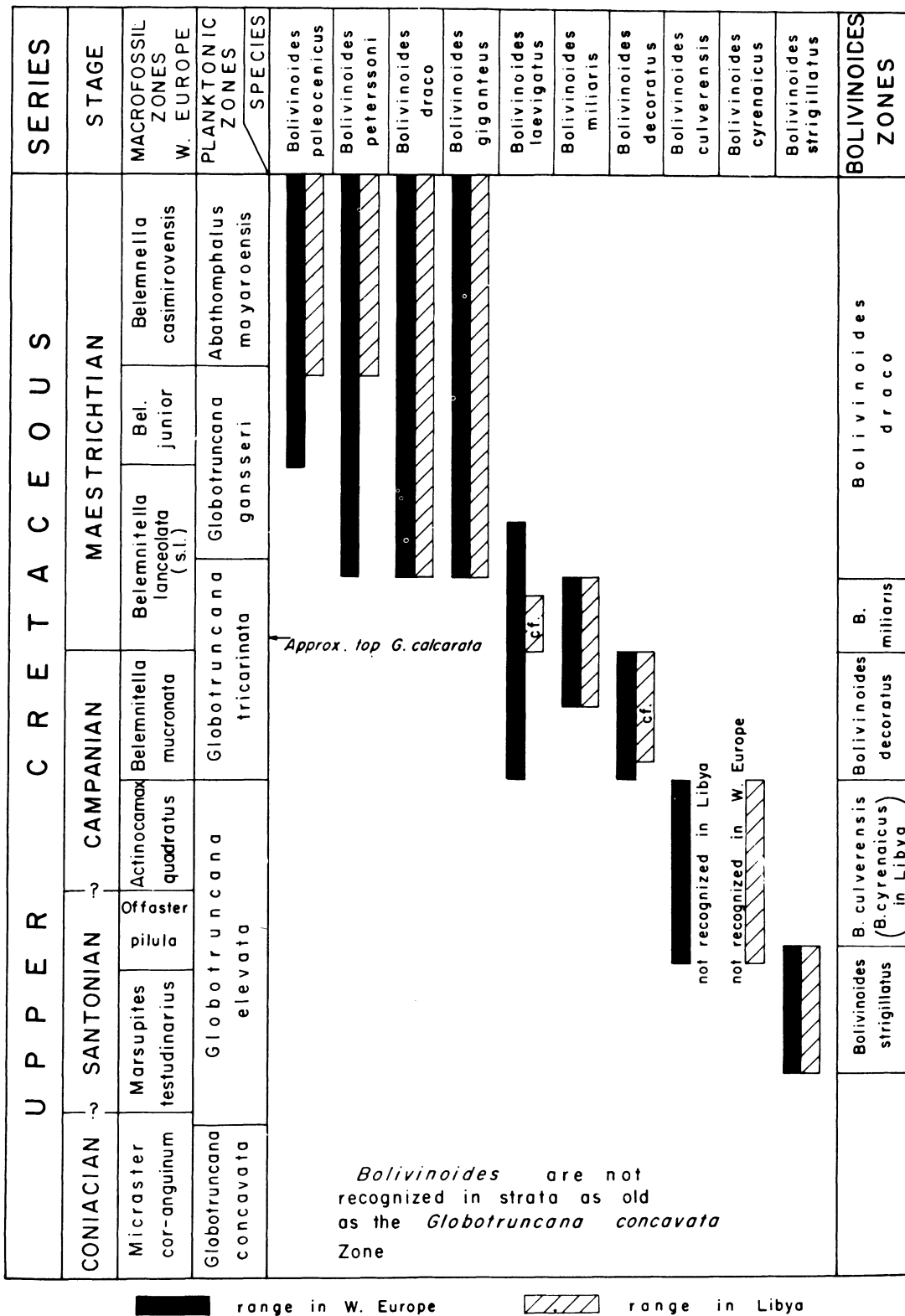


Figure 10.2 Comparison of the ranges of *Bolivinooides* species in N.W. Europe and the Tethyan Region. From Barr (1970)

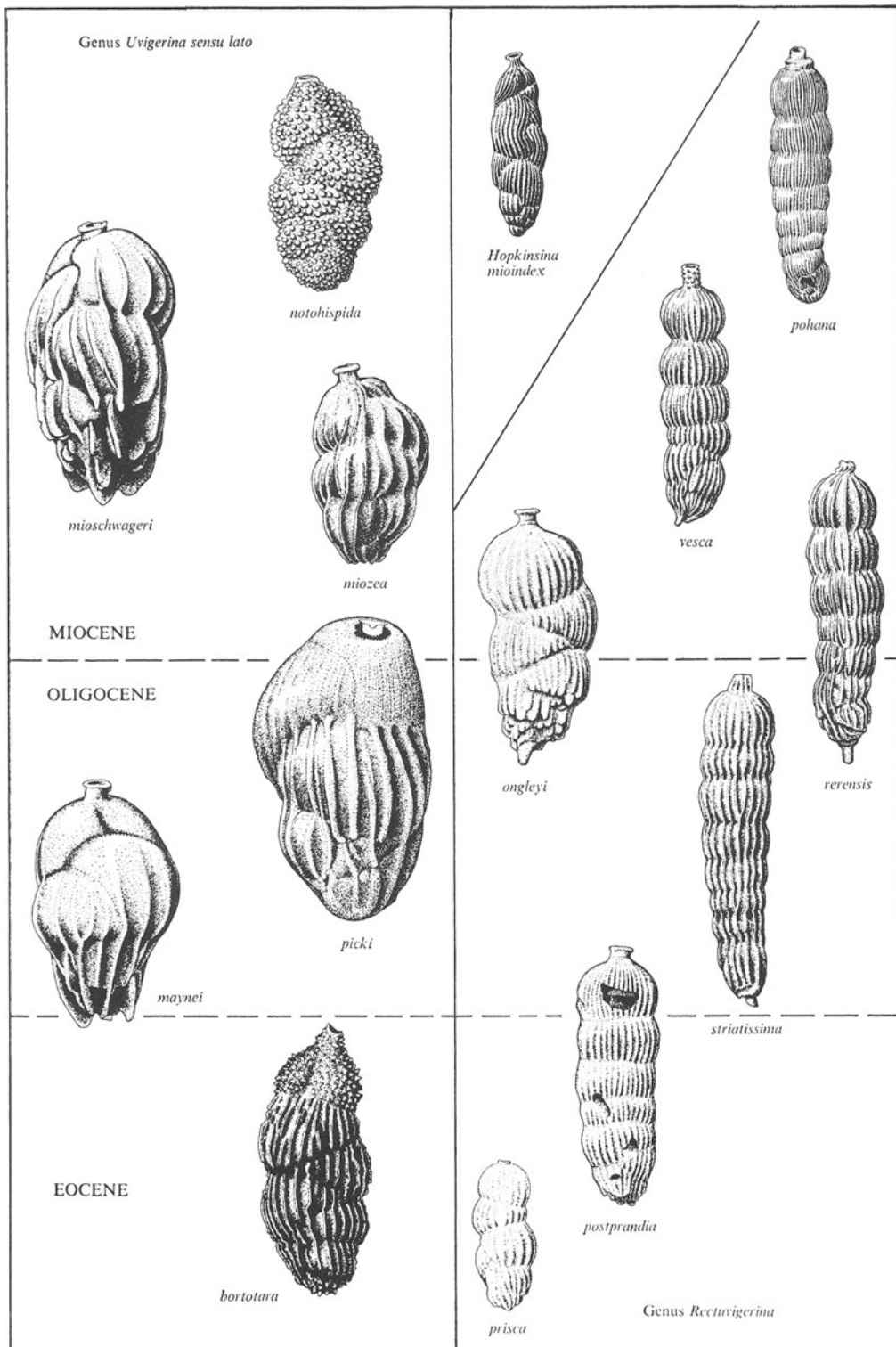


Figure 10.3 Sequence of uvigerinids in the New Zealand Tertiary. From Hornibrook (1968); illustrations by Brazier

According to Anne Boersma there are four time intervals with high numbers of new appearances of uvigerinids: Middle to late Eocene, early Oligocene, late Oligocene and early Miocene. She recognises three groups of species of *Uvigerina* on the basis of ornament—hispid, hispido-costate and costate—and regards them as an evolutionary series that first developed through the early Palaeogene but was repeated many times later in the Cenozoic. She also remarks on the cosmopolitan distribution of many species and their rapidity of dispersal around the world's oceans.

Evolutionary studies have also been made of *Ehrenbergina* and the results applied to Oligo-Miocene stratigraphy. Dorothee Spiegler (1973) has traced an evolutionary line from *E. variabilis variabilis* to *E. variabilis aculeata* in the Upper Oligocene and to *E. serrata serrata* and *E. serrata healyi* in the early Miocene in N.W. Germany. A parallel line is *E. variabilis variabilis* to *E. variabilis praepupa* and *E. pupa*. Both lines are considered to be examples of gradual change to more compact, solid forms. In New Zealand a parallel series has been used to define stage boundaries in the Lower Miocene. Formerly the base of the Otaian Stage was defined on the appearance of *E. healyi* which was considered to diverge to give *E. marwicki* and *E. willetti* in the Middle and Upper Otaian. Detailed measurements of the relation between length against gross inflation and length against width have been made by Scott (1973c). This work (figure 10.4) indicates that *E. healyi* and *E. marwicki* cannot be separated subspecifically and should both be referred to *E. marwicki*. *E. willetti* is considered a subspecies of *E. marwicki*. This has simplified treatment of this group and the species and subspecies can now be considered to jointly define the base of the Otaian.

## ECOLOGY

The Buliminida occur widely from shallow, coastal waters to the Abyssal Plain but are particularly abundant on the Outer Shelf and on the uppermost Continental Slope (Norton, 1930; Parker, 1948; Lowman, 1949; Phleger, 1960; Murray, 1973b; Boltovskoy and Wright, 1976). For example, of 30 species found living at depths from 796 to 6011 m in the Peru – Chile Trench, 18 (60 per cent) belong to this order (Bandy and Rodolfo, 1964). The most common genera are *Bolivina*, *Brizalina*, *Bulimina*, *Cassidulina*, *Epistominella*, *Trifarina* and *Uvigerina*. These are also the most common forms on the Slope off

Portugal (Seiler, 1975) and in the Bay of Biscay from 180 to 3000 m depth (Caralp *et al.*, 1970).

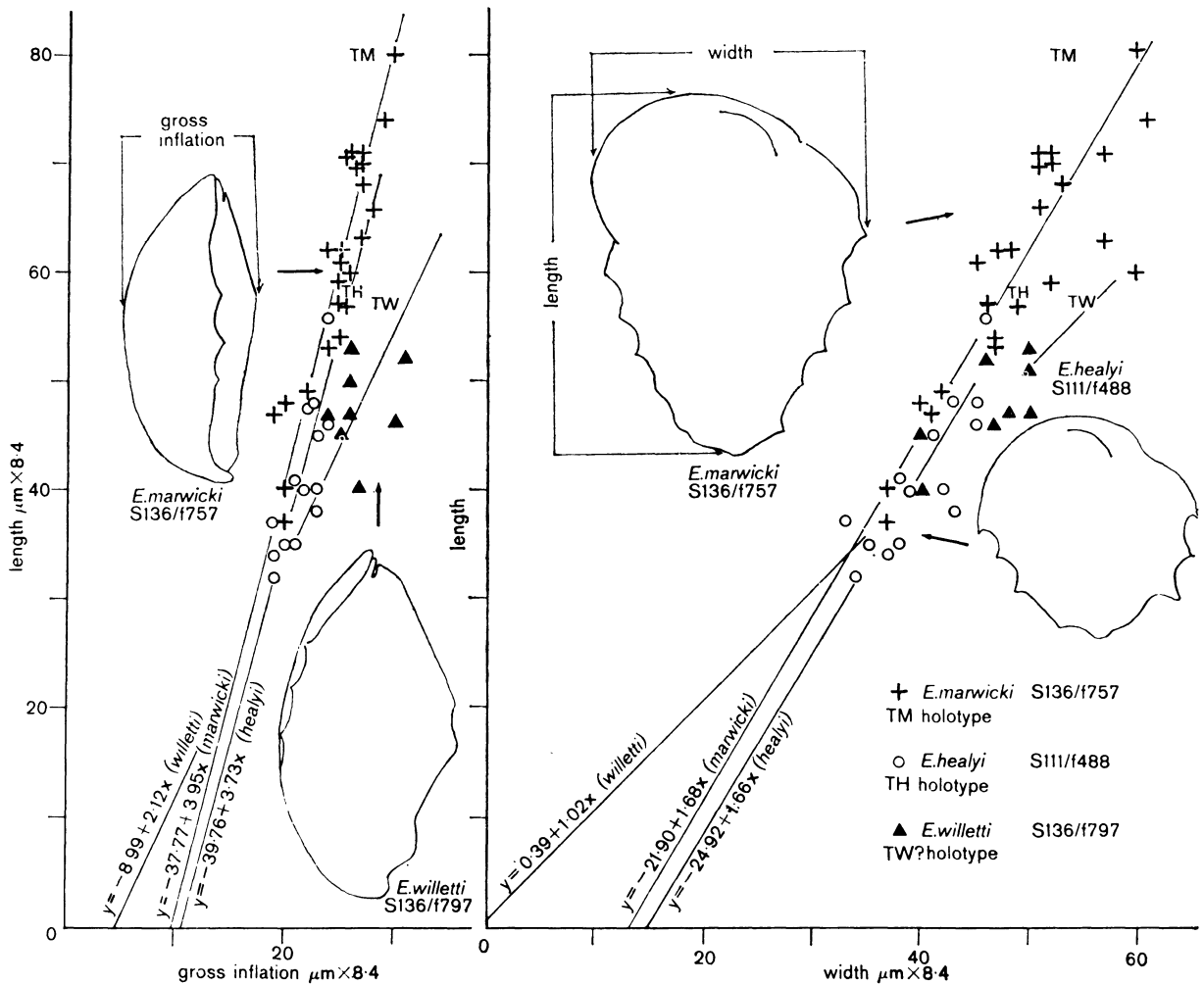
*Epistominella* is included in the list of genera that make up Brouwer's '*Cibicides wuellerstorfi* Fauna', characteristic of oceanic depths to 5000 m (1973). Strikingly, *Epistominella exigua* is the single most abundant species in Rockall Trough (Pearce, 1980).

*Cassidulina*, *Trifarina* and *Uvigerina* in particular can withstand subzero temperatures and are strong elements in temperate and high latitude faunas. *Uvigerina* is found down to the CCD and it is interesting that *Stilostomella antillea* is found live at 6011 m in the Peru – Chile Trench. This parallels the ability of certain shallow marine calcareous forams to penetrate low alkalinity environments where, after death, the abandoned tests are rapidly dissolved. *Cassidulina* is the most abundant genus in the Malin Sea (N.E. Atlantic). *C. laevigata* makes up more than 20 per cent of the total fauna and at the top of the Slope exceeds 30 000 individuals per 10 ml volume sample. *Cassidulina obtusa* also exceeds 5000 individuals per 10 ml (Pendlebury, 1974).

*Cassidulina* is very abundant nearshore in cold waters and occurs close to melting glaciers in Spitzbergen (Nagy, 1965). As might be expected, it has found particular application in palaeo-ecological interpretation in the Quaternary (Feyling-Hanssen *et al.*, 1971; Norris, 1972). *Uvigerina* has also been used as a cold-water indicator and Lutze (1978) in a study of JOIDES cores from between the Canaries and Africa finds that the *Uvigerina* maximum coincides with a Neogene cooling trend well shown by the planktonic Foraminifera. This genus appears to build its test in isotopic equilibrium with sea water (Shackleton, 1974) and variations in oxygen isotope ratios in Quaternary species can be related to climatic fluctuations (see chapter 14 for an extended treatment of oxygen isotope work on Foraminifera). In addition, variations in carbon-13 in *Uvigerina* through the late Pleistocene and Holocene can be related to a two-thirds reduction in tropical rainforests (which contain more than half the total carbon) at the height of the last glaciation, followed by their expansion to half as much again over their present area in the subsequent pluvial (Shackleton, 1977c). So remarkably, the test of a small, deep-water foram is found to faithfully monitor dramatic changes in the terrestrial, plant biosphere.

In part, the success of this group at great depths is related to their ability to tolerate lowered oxygen levels. This is indicated by a study of samples from the oxygen minimum zone of the Chilean Shelf (0.14 ml/l to 0.31 ml/l). They con-





**Figure 10.4** Analysis of variability in *Ehrenbergina marwicki*, *E. willetti* and *E. healyi*. Length is plotted against gross inflation and against width. From Scott (1973c). The formula for the straight line or reduced major axis is  $Y = ax + b$ , where  $x = \text{length}$ ,  $Y = \text{length/width}$ ,  $a = \text{growth ratio}$ , and  $b = \text{initial growth index}$

tain an impoverished and stunted fauna. *Bolivina* and *Brizalina* are least affected, followed by *Cassidulina* and *Epistominella*. *Bolivina* and *Brizalina* appear to be able to tolerate levels as low as 0.10 ml/l (Boltovskoy, 1972).

Traced from the Shelf on to the Slope the Bulminida, especially *Bolivina*, *Bulimina* and *Uvigerina*, show marked morphological trends (Bandy, 1960a). The Shelf species are less ornamented and there is progressive increase and differentiation of surface sculpture down the Slope (figure 10.5). Bathyal species are also larger, as has been noted earlier in the case of other groups. These trends have been confirmed by the work of Patsy Smith (1963), Lutze (1964) and Boersma (1977). They also occur at the infra-

specific level and *Bolivina argentina*, studied by Lutze, shows an increase in overall length, strength of costae and length of initial spine down the Slope.

The complexity of the environment, and the care with which the microfaunas of the Slope must be interpreted, is emphasised by recent work. Assemblage zones tend to be more marked than in the Abyss or on the Shelf. This is explained as the result of 'intense resource competition' accentuated in certain areas by restricting, low oxygen levels (Rowe and Haedrich, 1978). The Upper Slope fauna is transitional between seasonally variable Shelf conditions with high rates of recycling of organic matter and the non-seasonal Abyss with low rates of recycling. The biomass

BULIMINID MORPHOGROUPS	SHELF (NERITIC)			SLOPE (BATHYAL)		
	INNER	MIDDLE	OUTER	UPPER	MIDDLE	LOWER
<b>BULIMINACEA</b>						
Bulimina		denudata				
sparse spines	--			-----		
spinose fringe	--	marginata				
spinose (large)					striata mexicana	
costate (small)					rostrata	
smooth (large)				affinis		
Buliminella						
smooth (small)		-----				
Epistominella						
rounded (small)	-----					
globose			--			
angular						
Stainforthia						
appressed		schreibersiana		-----		
Uvigerina			tenuistriata		nodosa	
striate		--				
costate				--	peregrina	
costate/spinose						dirupta
spinose						proboscidea
papillate						senticosa
<b>BOLIVINITINACEA</b>						
Bolivina	striatula					
striate (irreg. small)		acutula		-----		
striate (reg. medium)	-----					
smooth (small)		quadrata				
sinuate sutures (small)	--		vaughani			
limbate or sinuate (med. to large)					argentea, plicata and spissa	
Bolivinita						
<b>CASSIDULINACEA</b>						
Cassidulina		limbata		subglobosa		
large angular						
large globose		--				
large biumbonate			minuta		translucens	
small rounded						
small angular						
uncoiled					delicata and laevigata	

Figure 10.5 Distribution of morphogroups of buliminids in the modern oceans. After Bandy (1960a)

decreases exponentially with depth, and selection favours species that can find and utilise packaged detritus such as faecal pellets and carcasses. The Buliminida are, perhaps, specially adapted to exploit organic detritus of this sort.

An important discovery of Rowe and Haedrich is that whereas benthic fish dominate between 1000 and 1400 m, the fauna becomes dominated by echinoderms at mid-Slope. In the Slope and Basin area off California, Douglas and Heitman (1978) find that the mud-eating macrobenthos, including echinoderms, is limited by low oxygen

levels. This leads to the paradoxical result that the standing crop of living forams in the oxygen minimum area is 100/cm<sup>3</sup>, whereas it is only ±1/cm<sup>3</sup> in the high oxygen areas due to control by the macrobenthos. This underlines the importance of the adaptation of buliminids to low oxygen levels.

A further important factor is that bottom currents are most active at the Shelf break (off New England, Ross and MacIlvaine, 1978). This may cause winnowing and concentration of dead tests and also movement down the Slope.

## FURTHER READING

- Barr, F. T. (1966). The foraminiferal genus *Bolivinooides* from the Upper Cretaceous of the British Isles. *Palaeontology*, **9**(2):220–243
- Barr, F. T. (1970). The foraminiferal genus *Bolivinooides* from the Upper Cretaceous of Libya. *J. Paleont.*, **44**(4):642–654
- Bertels, Alwine (1972). Buliminacea y Cassidulinacea (Foraminiferida) guiás del Cretácico superior (Maastrichtiano medio) y Terciario inferior (Daniano inferior) de la República Argentina. *Revta esp. Micropaleont.*, **4**(3):327–353
- Boltovskoy, E. (1972). Nota sobre los valores mínimos de oxigenación que pueden soportar los foraminíferos bentónicos. *Boln Soc. Biol. Concepcion*, **44**:135–143
- Caralp, M., Lamy, A. and Pujos, M. (1970). Contribution à la connaissance de la distribution bathymétrique des Foraminifères dans le Golfe de Gascogne. *Revta esp. Micropaleont*, **2**(1):55–84
- Cushman, J. (1937). A monograph of the subfamily Virguliniinae of the foraminiferal family Buliminidae. *Spec. Publs Cushman Lab.*, **9**:1–228
- Cushman, J. A. and Parker, Frances L. (1937). Notes on some European Eocene species of *Bulimina*. *Contr. Cushman Lab. Foramin. Res.*, **13**(2):46–54
- Cushman, J. A. and Parker, Frances L. (1940). The species of the genus *Bulimina* having Recent types. *Contr. Cushman Lab. foramin. Res.*, **16**(1):7–23
- Cushman, J. A. and Parker, Frances L. (1947). *Bulimina* and related foraminiferal genera. *Prof. Pap. U.S. geol. Surv.*, **210D**:55–176
- Glacon, Georgette and Sigal, J. (1974). Morphologie de l'appendice buccal chez *Caucasina* (Foraminifère), suivie d'une comparaison avec celui de divers genres de Buliminidae. *Revta esp. Micropaleont.*, **6**(2):209–227
- Hansen, H. J. (1972). Two species of Foraminifera of the genus *Turrilina* with different wall structure. *Lethaia*, **5**(1):39–45
- Hinte, J. E. van. (1967). *Bolivinooides* from the Campanian type section. *Proc K. ned. Akad. Wet.*, ser. B, **70**(3), 254–263
- Hofker, J. (1956). Foraminifera Dentata. Foraminifera of Santa Cruz and Thatch Islands, Virginia Archipelago, West Indies. *Spolia zool. Mus. haun.*, **15**:1–237
- Lutze, G. F. (1964). Statistical investigations on the variation of *Bolivina argentea* Cushman. *Contr. Cushman Fdn foramin. Res.*, **15**(3):105–116
- Nørvang, A. (1958). *Islandiella* n.g. and *Cassidulina* d'Orbigny. *Vidensk. Medd. fra Dansk naturh. Foren.*, **120**:25–41
- Scott, G. H. (1973). *Ehrenbergina* (Foraminiferida); variability and application to lower Miocene biostratigraphy in New Zealand. *N.Z.Jl Geol. Geophys.*, **16**(1):52–67
- Scott, G. H. (1978). Shell design in *Bolivinita quadralata*, *B. pohana*, and *B. compressa* (Foraminiferida). *N.Z.Jl Geol. Geophys.*, **21**(1):85–95
- Shackleton, N. J. (1977). Carbon-13 in *Uvigerina*; tropical rainforest history and the equatorial Pacific carbonate dissolution cycles: pp. 401–427 in *The Fate of Fossil Fuel CO<sub>2</sub> in the Oceans* (Anderson, N. R. et al., Eds). Plenum Press, New York.
- Sliter, W. V. (1970). *Bolivina doniezi* Cushman & Wickenden in clone culture. *Contr. Cushman Fdn foramin. Res.*, **21**(3):87–99
- Surlyk, F. and Birkelund, T. (1977). An integrated stratigraphical study of fossil assemblages from the Maastrichtian White Chalk of Northwestern Europe: pp. 257–281 in *Concepts and Methods of Biostratigraphy* (Kauffman, E. G. and Hazel, J. E., Eds). Dowden, Hutchinson and Ross, Penn.
- Vella, P. (1961). Upper Oligocene and Miocene uvigerinid foraminifera from Raukumara Peninsula, New Zealand. *Micropaleontology*, **7**(4):467–483

## SUMMARY CLASSIFICATION

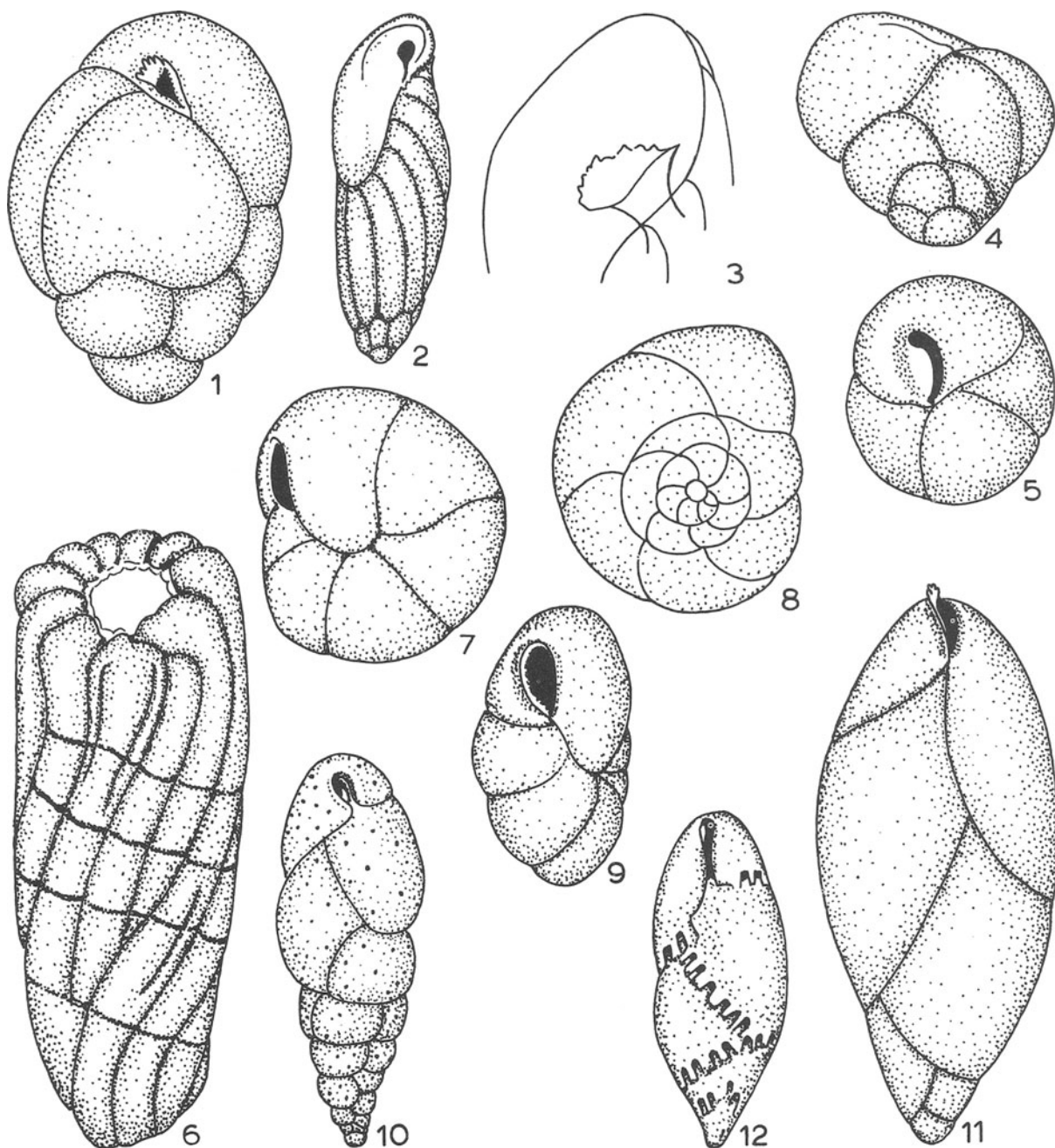
## MAIN FAMILIES AND IMPORTANT GENERA OF BULIMINIDA

<b>BULIMINIDA</b>	wall hyaline, oblique or radial, bilamellar; aperture characteristically comma-shaped or a slit, terminal and produced in advanced forms, with internal toothplate connected to previous foramen; Jur. – Rec. Key figures 10.6 and 10.7.
<b>BULIMINACEA</b>	trochospiral to triserial, biserial and uniserial; aperture umbilical, basal or comma-shaped, terminal in advanced forms, may be replaced by multiple openings or trematophore; broad toothplate with free border that may join anterior end of aperture; most genera hyaline radial; Jur. – Rec. Key figure 10.6.
<b>BULIMINIDAE</b>	triserial to biserial and uniserial; aperture comma-shaped or terminal and round; Jur. – Rec.
<i>Bulimina</i> (no. 10)	triserial; aperture extending into apertural face from basal suture; toothplate with produced or rolled-up free border; Pal. – Rec. (simple trough-like tooth = <i>Praebulimina</i> , Mid. Jur. – U. Cret.; trigonal also = <i>Pyramidina</i> , U. Cret.; biserial in adult also = <i>Neobulimina</i> , Cret.; biserial to uniserial also = <i>Rectobulimina</i> , Cret.).
<i>Praeglobobulimina</i> (no. 11)	triserial with globular, strongly overlapping chambers; aperture extending up from basal suture; free edge of toothplate folded and joined to anterior end of aperture, tip protrudes like cockscomb; Pal. – Rec. (terminal aperture and toothplate double folded = <i>Globobulimina</i> ).
<i>Stainforthia</i> (no. 13)	narrowly elongate, triserial (at least in B form) to twisted biserial; aperture narrowly comma-shaped in marked depression; flaring toothplate with serrated free edge; Eoc. – Rec. (hyaline oblique without apertural depression = <i>Fursenkoina</i> , U. Cret. – Rec.; simple trough-like tooth also = <i>Cassidella</i> , U. Cret. – Rec.).
<i>Virgulinella</i> (no. 12)	triserial to biserial with retral processes and sutural pores; aperture extending up from basal suture with reduced toothplate; Neo. (porous trematophore but toothplate absent = <i>Delosina</i> , Rec.).
<b>TURRILINIDAE</b>	trochospiral with more than 3 chambers to the whorl; aperture high arch or comma-shaped; toothplate simple, trough-like or cornet-shaped; U. Cret. – Rec.
<i>Turrilina</i> (no. 1)	high trochoid with 4 chambers in each whorl, globular; aperture a high arch; Eoc. – Olig.
<i>Buliminella</i> (nos. 2/3)	numerous high chambers in drawn-out spiral; aperture comma-shaped in depression; toothplate with saw edge; U. Cret. – Rec. (aperture terminal, round = <i>Buliminellita</i> , Eoc. – Mio.; aperture cribrate and toothplate lost = <i>Sporobuliminella</i> , U. Cret.).
<i>Buliminoides</i> (no. 6)	low chambers in drawn-out spiral coiled round open umbilicus—formed by resorption in adult; Olig. – Rec.

- Baggatella*  
(nos. 4/5) low trochoid with narrowly comma-shaped aperture extending from umbilicus into apertural face; Eoc. – Rec. (aperture parallel to periphery = *Epistominella* (nos. 7–9), Pal. – Rec.; trochoid to triserial = *Caucasina*, U. Cret. – Mio.).
- UVIGERINIDAE triserial to biserial or uniserial; aperture terminal with neck; simple toothplate; U. Cret. – Rec.
- Uvigerinella*  
(no. 16) triserial, aperture subterminal with high collar, connected by suture to basal suture; Pal. – Rec.
- Uvigerina*  
(no. 14) triserial, aperture produced with phialine lip; toothplate with flaring free edge; Eoc. – Rec. (biserial adult = *Hopkinsina*; triangular in section = *Pseudo-uvigerina*, U. Cret.).
- Trifarina*  
(no. 15) triserial to uniserial, triangular with keeled margins; U. Pal. – Rec. (round in section = *Rectuvigerina*, M. Eoc. – Rec.; triserial to biserial and uniserial also = *Elhasaella* Haman (1978), Maas.; uniserial chambers loosely attached = *Siphouvigerina* (no. 17), Olig. – Rec.; triserial initial part only in B form = *Siphogenerina*, Eoc. – Rec.).
- PAVONINIDAE triserial to biserial and uniserial, uniserial chambers triangular or strongly arched; simple toothplate, lost in adult; aperture multiple in advanced forms; Eoc. – Rec.
- Reussella*  
(no. 18) triserial, sharply angular; aperture a basal slit with cornet-shaped toothplate; Eoc. – Rec. (cribrate = *Fijiella*, Rec.).
- Chrysalidinella*  
(no. 20) triserial to uniserial, triangular or quadrangular; aperture terminal, multiple; toothplate lost in uniserial part; Eoc. – Rec. (uniserial part round in section = *Tubulogenerina*, Eoc. – Mio.).
- Pavonina*  
(no. 19) triserial to biserial and uniserial with high arched chambers; aperture replaced by multiple pores, no toothplate; Mio – Rec.
- BOLIVINITACEA compressed biserial to uniserial (rarely with planispiral initial part) or enrolled biserial to uncoiled; aperture comma-shaped or a slit in the plane of compression, becoming terminal and produced in advanced forms; toothplate simple, trough-like or cornet-shaped, wall usually hyaline radial; Jur. – Rec. Key figure 10.7.
- n. superfam.
- BOLIVINITIDAE compressed biserial to uniserial (rarely with planispiral initial part); aperture extending into aperture face from basal suture or terminal and rounded; Jur. – Rec.
- Brizalina*  
(nos. 2/3) biserial often carinate, chambers wide and low; apertural slit runs into apertural face from basal suture; toothplate trough-like; Jur. – Rec. (with retral processes and sutures crenulate = *Bolivina* (no. 1), U. Cret. – Rec.; rhomboidal with strong longitudinal costae = *Bolivinoides* (nos. 4/5), U. Cret.; planispiral initial part = *Spirobolovina*, Pal. – Eoc.).
- Bolivinita*  
(nos. 6/7) biserial, much compressed with flat or concave sides and truncate periphery; Mio. – Rec.

- Rectobolivina*  
(no. 8)  
EOUVIGERINIDAE  
biserial to uniserial and only slightly compressed; aperture terminal and rounded; M. Eoc. – Rec.  
biserial to uniserial; aperture terminal, produced with neck and lip; L. Cret. – Rec.
- Eouvigerina*  
(no. 9)  
*Siphogenerinoides*  
(nos. 10/11)  
biserial, final chamber central; aperture with crenulate inner margin; Alb. – Eoc.  
biserial to uniserial and round in section; aperture oval or reniform (with toothplate visible at side); U. Cret. – Pal.
- Siphonodosaria*  
(no. 12)  
ISLANDIELLIDAE  
enrolled biserial to uncoiled; aperture in median line or subterminal with cornet-shaped toothplate; Cen. close-coiled with rounded periphery; toothplate with triangular free tip; Cen. (uncoiled in adult with subterminal aperture = *Cassidulinoides* (no. 15), U. Eoc. – Rec.; uncoiled, round in section with irregular chambers = *Orthoplecta*, Rec.).
- Islandiella*  
(nos. 13/14)  
*Ehrenbergina*  
(nos. 16–18)  
CASSIDULININACEA  
compressed carinate, enrolled biserial to uncoiled triangular; Eoc. – Rec.  
triserial to biserial and uniserial or enrolled biserial to uncoiled; aperture subterminal or near periphery in plane of compression usually with dentate lower or outer margin; toothplate a free siphon, reduced or lost in advanced forms, most genera hyaline oblique; L. Cret. – Rec. Key figure 10.7.
- PLEUROS TOMELLIDAE  
triserial to biserial and uniserial or unilocular, chambers embracing; aperture subterminal to terminal, crescentic or chevron-shaped, characteristically with dentate lower border; internal siphon connects upper border with previous foramen; L. Cret. – Rec.
- Wheelerella*  
(nos. 19/20)  
compressed triserial to biserial and uniserial; aperture subterminal, crescentic with broad tooth; U. Cret. (rounded and aperture subterminal beneath hood with two triangular teeth = *Bandyella*).
- Pleurostomella*  
(nos. 21/22)  
biserial to uniserial in the adult, elongate and round in section; aperture subterminal beneath hood with two triangular teeth; ?L. Cret. – Rec. (aperture crescentic with broad tooth = *Ellipsoidella*; aperture cribrate = *Criboleurostomella* Owen 1971, U. Cret.; uniserial throughout = *Nodosarella* (nos. 25/26), Cen.).
- Ellipsopolymorphina*  
(no. 27)  
biserial to uniserial, chambers strongly inflated and embracing; aperture chevron-shaped with spatulate tooth; Neo. (chambers completely overlapping = *Ellipsobulimina*).
- Ellipsoglandulina*  
(nos. 23/24)  
uniserial, chambers inflated and strongly overlapping, round in section; aperture crescentic with broadly spatulate tooth; Eoc. – Rec. (chambers completely overlapping, aperture terminal = *Ellipsolingulina* (nos. 28/29), Palaeogene).
- Parafissurina*  
(nos. 30/31)  
unilocular; aperture subterminal beneath hood, crescentic with broad tooth; siphon attached to rear wall;

- hyaline radial; M. Eoc. – Rec. (aperture a terminal slit without tooth; siphon usually projecting freely into interior = *Fissurina*).
- CASSIDULINIDAE enrolled biserial to uncoiled or streptospiral; aperture a curved slit parallel to the periphery with broad, low tooth on outer border; toothplate reduced to short plate projecting in from inner border, or absent; Eoc. – Rec.
- Cassidulina*  
(nos. 32/33) enrolled biserial, compressed carinate; Eoc. – Rec. (honeycomb ornament = *Favocassidulina*, Rec.; rounded periphery = *Globocassidulina*).
- Sphaeroidina*  
(no. 34) streptospiral and sub-globular; aperture crescentic and almost closed off by broad rounded tooth, near basal suture; toothplate absent; hyaline radial; U. Eoc. – Rec.



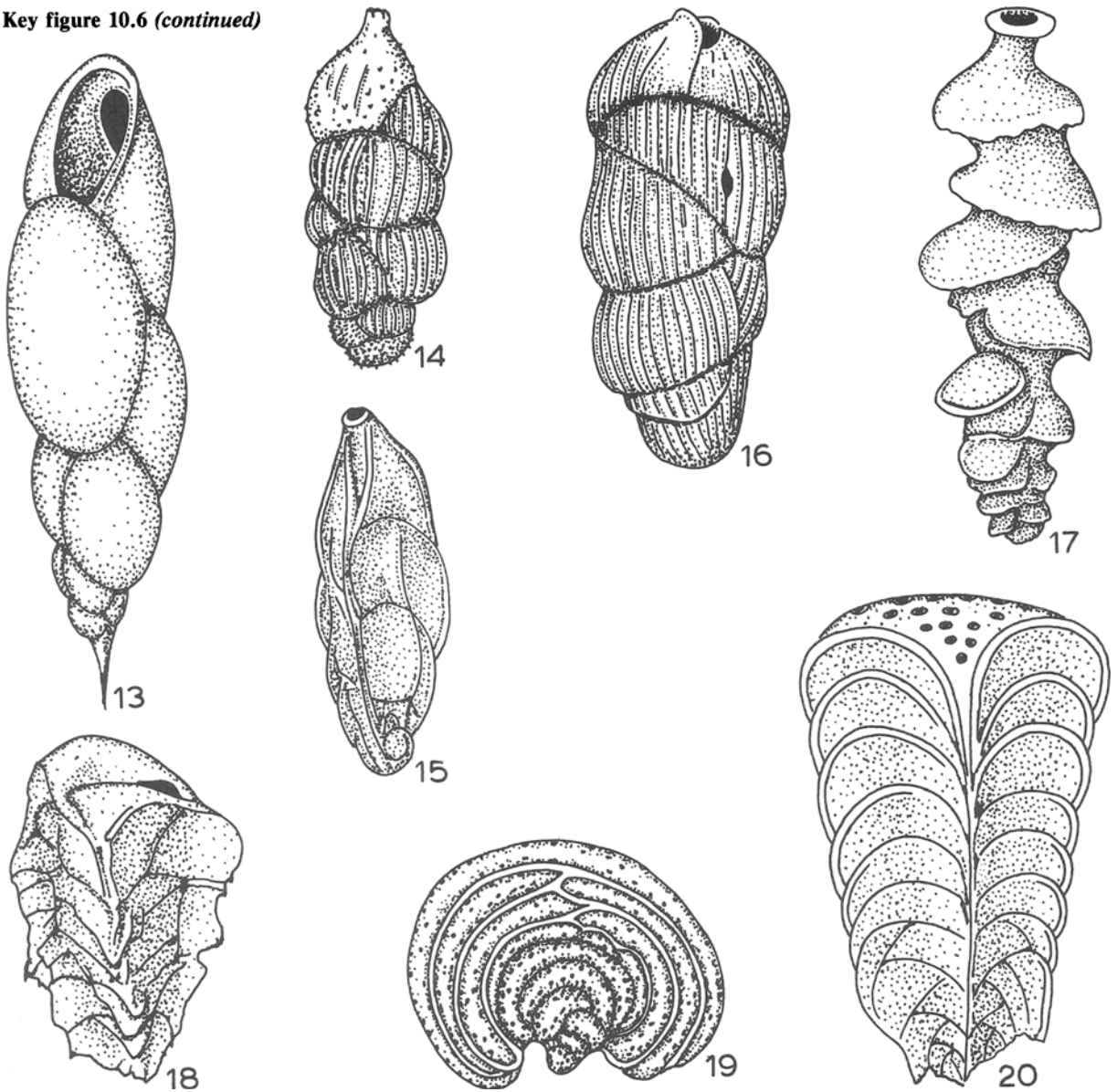
**Key figure 10.6 Buliminida, Buliminacea**

- 1 *Turrilina brevispira*, Dam, after Hansen,  $\times 312$
- 2/3 *Buliminella elegantissima* (d'Orbigny); 2 after L. & T.,  $\times 200$   
3 toothplate after Hofker,  $\times 500$
- 4/5 *Baggatella inconspicua* Howe; 4 side view, 5 ventral view,  $\times 300$
- 6 *Buliminoides williamsonianus* (Brady), after Hofker,  $\times 450$
- 7-9 *Epistominella vitrea* Parker, after Haynes; 7 ventral view, 8 dorsal view,  
9 side view, all  $\times 320$
- 10 *Bulimina thanetensis* Cushman & Parker, after Haynes,  $\times 120$
- 11 *Praeglobobulimina ovata* (d'Orbigny), after Haynes,  $\times 120$
- 12 *Virgulinella pertusa* (Reuss), after L. & T.,  $\times 64$

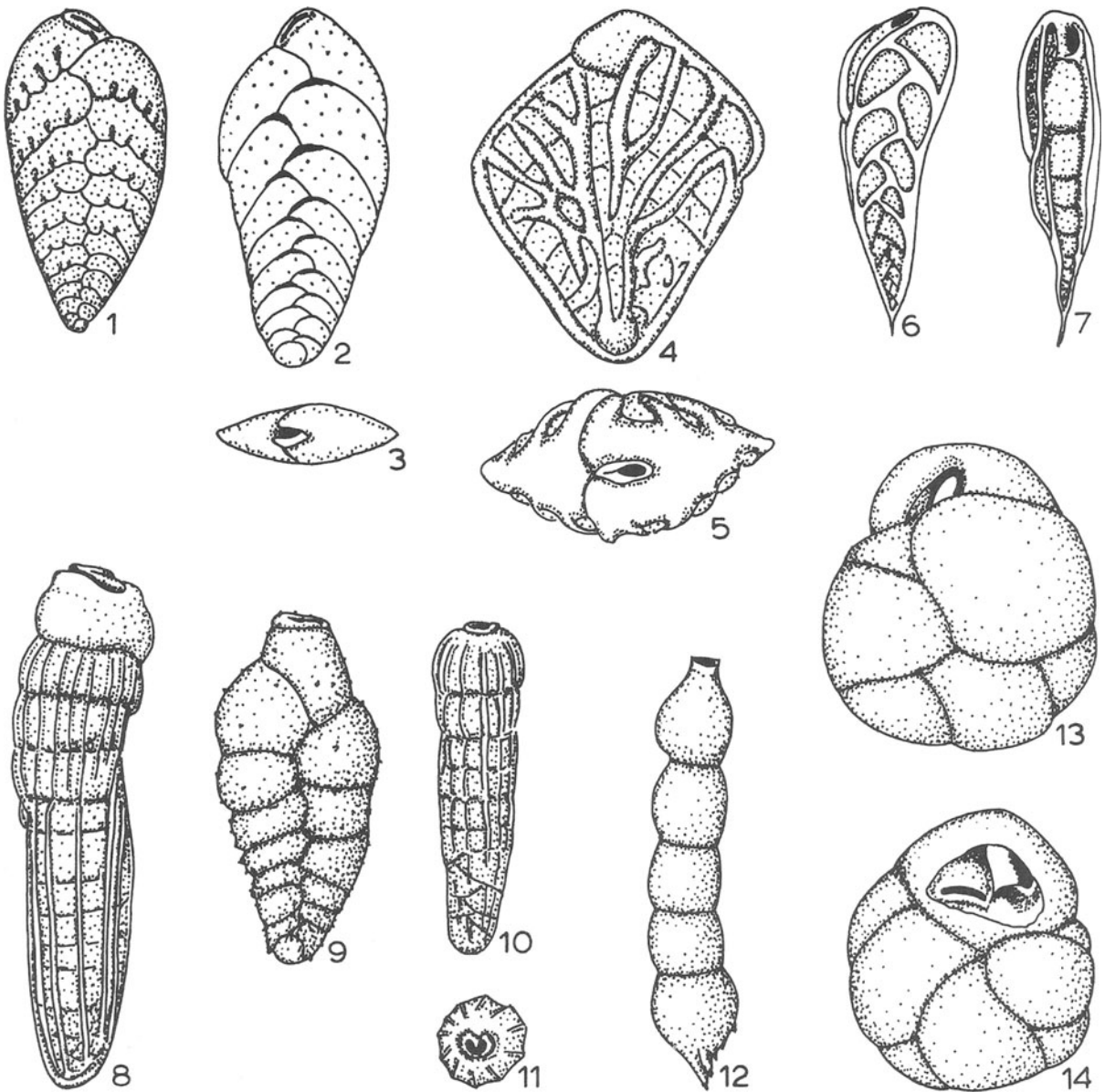
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Key figure 10.6 (continued)



- 13 *Stainforthia concava* (Höglund),  $\times 200$   
 14 *Uvigerina pygmaea* d'Orbigny, after L. & T.,  $\times 94$   
 15 *Trifarina angulosa* (Williamson), after L. & T.,  $\times 83$   
 16 *Uvigerinella oveyi* Haynes,  $\times 200$   
 17 *Siphouvigerina fimbriata* (Sidebottom), after L. & T.,  $\times 185$   
 18 *Reussella spinulosa* (Reuss), after L. & T.,  $\times 100$   
 19 *Pavonina flabelliformis* d'Orbigny, after Brady,  $\times 60$   
 20 *Chrysalidinella dimorpha* (Brady), after L. & T.,  $\times 140$

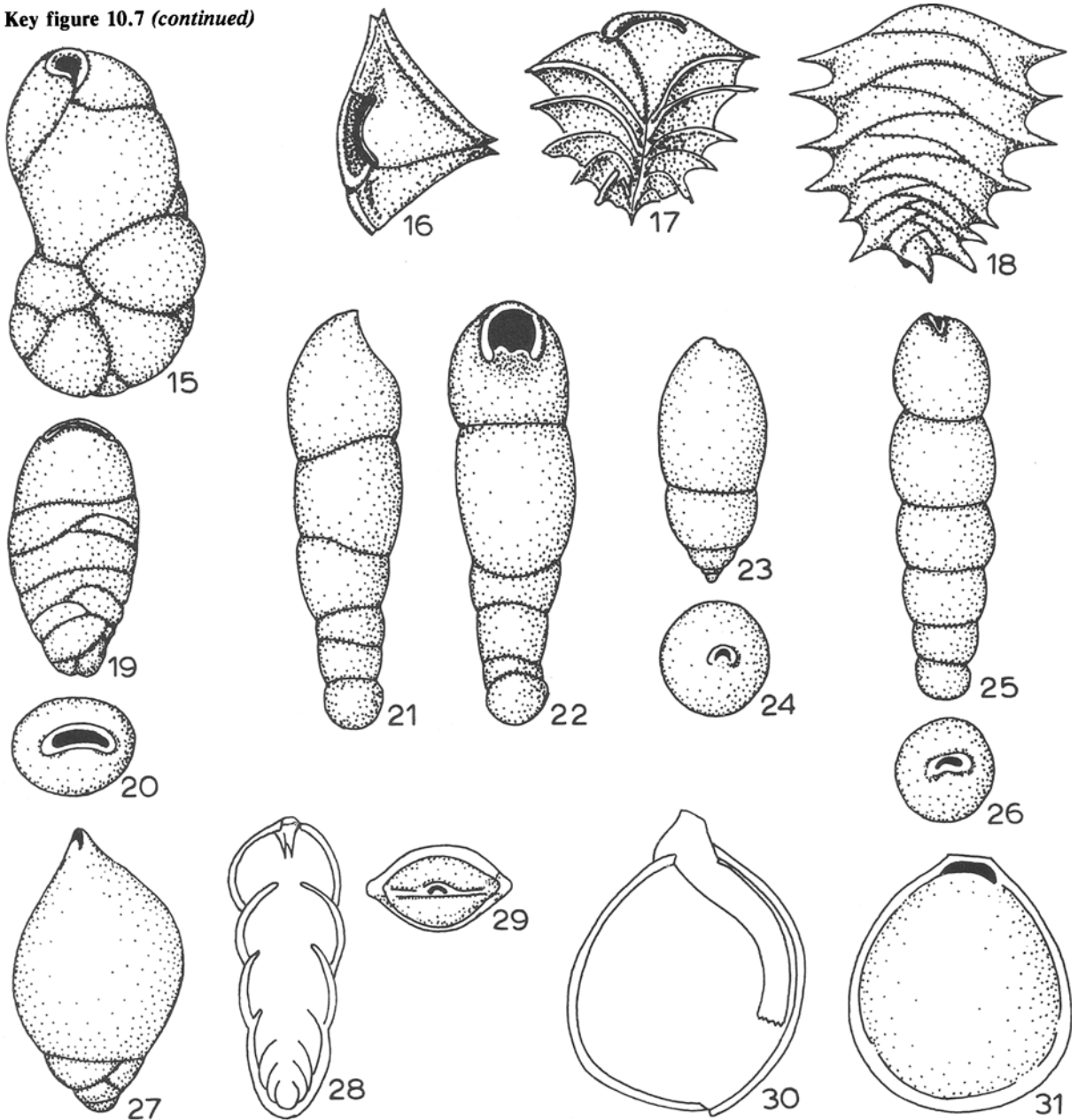


**Key figure 10.7 Buliminida, Bolivinitacea**

- 1 *Bolivina robusta* Brady,  $\times 100$
- 2/3 *Brizalina spatulata* (Williamson), side and apertural views, after Haynes,  $\times 100$
- 4/5 *Bolivinoidea draco* (Marsson), side and apertural views, after Montanaro Gallitelli,  $\times 100$
- 6/7 *Bolivinita quadrilatera* (Schwager), side and edge views, after Brady,  $\times 35$
- 8 *Rectobolivina raphana* (Parker & Jones), after L. & T.,  $\times 55$
- 9 *Eouvigerina zelandica* (Finlay), after Montanaro Gallitelli,  $\times 180$
- 10/11 *Siphogenerinoides plummeri* (Cushman), side and apertural views, after Montanaro Gallitelli,  $\times 66$
- 12 *Siphonodosaria abyssorum* (Brady), after L. & T.,  $\times 22$
- 13/14 *Islandiella islandica* (Nørvang); 13 side view, 14 internal view to show toothplate,  $\times 50$

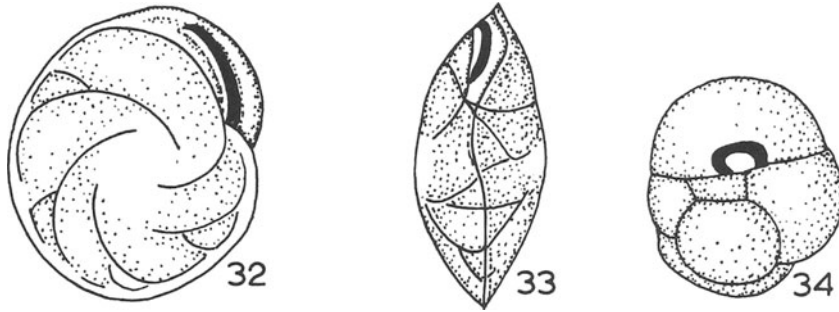
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Key figure 10.7 (continued)



- 15 *Cassidulinoides parkerianus* (Brady), after L. & T.,  $\times 150$   
 16–18 *Ehrenbergina pacifica* Cushman, apertural, front and rear views, after Brady,  $\times 60$   
 19/20 *Wheelerella magdalensis* Petters, side and front views, after L. & T.,  $\times 100$   
 21/22 *Pleurostomella subnodosa* (Reuss), side and front views, after L. & T.,  $\times 75$   
 23/24 *Ellipsoglandulina laevigata* Silvestri; side and apertural views,  $\times 44$   
 25/26 *Nodosarella rotundata* (d'Orbigny), side and apertural views, after L. & T.,  $\times 36$   
 27 *Ellipsopolymorphina schlichti* (Silvestri),  $\times 50$   
 28/29 *Ellipsolingulina silvestri* Galloway, side and apertural views,  $\times 150$   
 30/31 *Parafissurina ventricosa* (Silvestri), internal and apertural views,  $\times 55$

## Key figure 10.7 (continued)



- 32/33 *Cassidulina laevigata* d'Orbigny, side and edge views, after L. & T.,  $\times 78$   
34 *Sphaeroidina bulloides* d'Orbigny, apertural view, after Vášíček,  $\times 44$