

## PRIMARY GLOBIGERINID STOCK IN PLANKTONIC FORAMINIFERAL EVOLUTION AND RADIATION

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### ABSTRACT

The foraminifera have started adopting the planktonic habitat in oceanic waters since the Middle Jurassic times. During this period, the morphotypes similar to the *Globigerina* appeared which were possibly evolved from some benthonic Discorbid forms. Throughout the history of evolution of the planktonic foraminifera, simple primitive looking Globigerine forms have given rise to more complex plexus at different periods in the geological history. Some of these progenies were highly specialised and therefore disappeared with the slightest ecological imbalances. It is emphasised that the planktonic foraminifera survive till today through the Globigerinid stock. The present paper draws the conclusion that the complex, ornate and specialised periodic adaptations have maintained the morphological linkages with the primary stock of the simple Globigerine forms throughout the period of their evolution.

### INTRODUCTION

Since the beginning of the Jurassic period, progressively large number of foraminiferal types have attained the planktonic habitat. The adaptation of this new mode of life induced greater degree of intra-specific variability in terms of morphology of their tests which was necessary to develop the floating habit in different water masses. Though there has been a constant increase in specific diversity through time, the planktonic foraminifera have undergone through several stages of repeated fluctuations from high to extremely low diversity and yet persisted to diverge. The fluctuations in the diversity of the planktonic foraminifera have resulted primarily due to the extinction of the morphologically complex but ecologically sensitive species while the morphologically simpler forms seem to have been persisting and dominating periodically in the geological column representing the time span since the Late Mesozoic.

The central doctrine of the most acceptable theory of evolution is the concept of a consistent change with descent resulting in progressive modifications of the forms with time. Several new groups of life have been able to establish themselves by taking the advantage of a decreased competitive pressure at times of low diversity. The mass extinction of any biota generally follows the attainment of its highest degree of freedom to evolve into more complex morphological variants. Such a concept is utilized in recognising synchronous events on a regional scale in the geological history which is the basis for a geological correlation. Such an useful hypothesis, on the other hand, fails to account for the modern and several past planktonic foraminiferal distribution patterns, their

selective growth and diversity, due to the continued appearance of more simple and apparently primitive forms in the geological column. The concept of progress as involving continued improvements in the adaptation is rather obvious and apparently promising, it fails to account for the cause of simultaneous maintenance and preservation of more simple forms of the original stock while resulting into the extinction of evolved and more complex progenies. The morphology of the present day Globigerines such as represented by *Globigerina bulloides* D'Orbigny is considered to be simple and therefore "primitive" among the planktonic foraminifera. The forms having the Globigerinid characters were the earliest to adopt the planktonic habitat in the Mesozoic and later experienced several adaptive modifications. The purpose of this paper is to record the early evolutionary history of the Globigerinid stock, to examine the continuation of the simple morphostructural patterns in the later progenies and to explain the repetitions in diversification and selective extinctions of the planktonic foraminiferal species in the geological past.

### PLANKTONIC HABITAT IN THE GEOLOGICAL PAST

It is now generally accepted that the planktonic habitat was possibly in existence since the Late Precambrian times and several types of planktonic life progressively appeared in different periods. A fairly large number of forms have failed to preserve in rocks and thus their continuous records are largely missing. One of the oldest records of the possible planktonic life represented by "acritarchs" are from the rocks of 1 billion years old (Tappan, 1968) and these forms have remained profusely common throughout the Palaeozoic. Some of

the authorities (Downie 1967, Roblot 1964) claim the existence of the planktonic habitat as old as 3 billion years ago. A large number of microplanktons which appeared in the Early Palaeozoic includes Radiolaria and Dinoflagellates. These forms continued to attain higher degree of diversification throughout the Palaeozoic and covered the entire oceanic regime. It is a great mystery why the foraminifera, which is now almost universally present in the oceanic water, could not evolve themselves to acquire the planktonic habitat which has been almost infinite in existence and available to a large number of similar groups of micro-organisms for the last several hundred million years. As will be discussed later in this paper, it was during the Middle Jurassic, that the foraminifera could enter into the planktonic regime of the ancient environments. The planktonic habitat has since been, more and more, favoured by a large number of foraminiferal species throughout the Cenozoic and Quaternary.

The planktonic habitat is unique as it comprises the vast open interlinked oceans of almost infinite dimensions and having practically no bounds for a relatively homogenous medium, yet it is enclosed in a closed system. Within this broad, closed continuous system, an environment may rarely be divided and separate niches for the planktonic assemblages are thus not theoretically possible. The study of modern oceanic environments (Bradshaw 1959, Banerji, Schafer and Vine 1971, Banerji, 1974) has however, established the variable degree of patchiness in the distribution of several planktonic species at different latitudes and depths and there is a possibility that different organic constituents can live in isolation as if occupying different niches. The total diversity, when accounted for the evolution of planktonic foraminifera, is not inclusive of these separate niches which may have localised profound effects. The present discussion will therefore be based on the consideration of the entire planktonic habitat as one broad continuous closed system, keeping in view that the system may behave differently at various trophic levels.

While considering the distribution of all kinds of ancient life, it is worthwhile to record that the Palaeozoic and early Mesozoic life was more widespread and having a wide geographic distribution, the fauna since the Middle Jurassic seems to be more diversified and somewhat endemic. During this period, Pacific, Tethyan, Boreal and several other environmental elements started differentiating. This resulted in the geographic isolation of populations and in the genetic discontinuity. Several new life adaptations started encroaching new habitats. A part of the original benthonic populations of foraminifera entered the planktonic habitat. It is however emphasised that the geographical separation alone was

not sufficient for the adaptation of new habitat. Factors such as cosmic radiation, nutrient depletion at the sea bottom, nutrient concentration within the photic zone, change of sea water composition, cooling of waters, density stratification and biological interaction of the bottom dwelling organisms had played dynamic role.

#### PRIMITIVE GLOBIGERINES

The earliest forms of foraminifera which acquired the planktonic habitat had a simple Globigerine morphology. The origin of the Globigerinid stock is of anybody's guess, however, in all probability it was linked with more globular, rotaliid and discorbid forms dominating in the Triassic-Jurassic waters. El-Naggar (1971) considers the Middle Jurassic helicospiral forms such as *Gubkinella* Suleymanov (Bajocian-Callovian) as forming the ancestral stock from which other genera of globigerinid characters have evolved in the later period. Others (Oberhauser 1960, Kristan-Tollmann 1964) have reported the presence of Globigerine forms in still older sediments such as *Globigerina ladinica* Oberhauser, *G. mesotriassica* Oberhauser, and *G. rhaetica* Kristan-Tollmann in the Triassic sequence of Austria. Bandy (1967) has been rather critical to suggest the genetic relationship of these forms with some well known benthonic genera such as *Valvulineria* and *Quadriformina*. The surface wall of the majority of these reported Globigerine forms are agglutinated which indicates their non-planktonic affinity. Fuchs (1967) has therefore rightly reassigned these forms to new genera *Oberhauserella* (*O. mesotriassica* and *O. rhaetica*) and *Kallmanita* (*K. ladinica*) belonging to a new benthonic family Oberhauserellidae. These forms have a greater resemblance with the forms of the subfamily Discorbinæ Ehrenberg (as suggested in case of *Gubkinella* by Bykova *et al.*, in Rauzer-Chernousova and Fursenko, 1959). It is now generally agreed, as suggested by Galloway (1933) and Cushman (1948) that the Discorbid forms were the real ancestors of the planktonic Globigerine species.

Although more than a dozen species belonging to the genus *Globigerina* have been reported from the Jurassic, the Globigerine forms which have been found in association of the pelagic sediments are not likely to be from the horizons older than the Middle to Late Jurassic (Balakhmatova 1953, AGIP Mineraria 1959). The true Globigerine forms with the calcareous tests were extremely rare till the Late Jurassic (viz. *Globigerina bathoniana* Pazdrowa, *G. conica*, Ioveceva and Trifonova and *G. jurassica* (Hofman) and became rather common since the Aptian Stage of the Early Cretaceous. The Aptian-Albian was a period of general sea level rise resulting in the transgression of the sea over the vast continental areas which provided high energy agitated conditions to the emerging coastal and shallow water

environments and rendered them less habitable for the microfauna. More and more forms became free-floating and acquired the new vast environmental opportunities of the planktonic habitat present away from the coastal regions. The fixation of greater concentration of the atmospheric CO<sub>2</sub> in the ocean (by the phytoplanktons), resulted due to the large scale enundation of the land forest, had provided a better opportunity for the newly evolving planktonic foraminiferal group to adopt CaCO<sub>3</sub> as their sole skeletal building material. The transformation of the agglutinated test to a calcareous type was thus achieved in Aptian-Albian times. This is evident from the fact that several new genera such as *Hedbergella* (represented by *H. delrioensis* (Carsey), *H. graysonensis* (Tappan), *H. simplicissima* (Magne and Sigal), *H. trocoidea* (Gandolfi) and *H. washitensis* (Carsey), *Ticinella* (*T. roberti* (Gandolfi), *T. primula* (Luterbacher), *Globigerinelloides* (*G. algeriana* Cushman and ten Dam *G. blowi* (Bolli), *G. cushmani* (Tappan), *G. saundersi* (Bolli), *G. ultramicra* (Subbotina) and *Clavihedbergella* (*C. bizonae* (Chevalier) appeared in Aptian times (Fig. 1).

The early Globigerine forms had a simple morphology which consisted of a few rounded chambers arranged in a spiral coil (Fig. 2). While all the chambers could be seen on one side (the spiral/dorsal side), the last whorl covered all the preceding ones on the other side (ventral/umbilical side). The apertural character was rather simple and was located in the umbilical arch. The fundamental structural morphology as seen in case of certain very early forms including those of questionable planktonic nature such as *Oberhauserella mesotriassica* and *O. rhaetica* from the Triassic sequence has remained largely conservative and the similar morphology can be observed in several modern planktonic forms such as *Globigerina glutinata* Egger and *G. humilis* (Brady). All those forms which acquired a somewhat variable apertural adaptations as in case of *G. helvetojurassica* Heusler from the Late Jurassic have essentially maintained the basic framework of the Globigerine structure. The truly umbilical apertures are sometimes covered by the final chamber as seen in several modern forms—*G. quinqueloba* Natland and *G. glutinata* Egger. These observations indicate that the Globigerine morphology has not undergone any appreciable modifications since its first arrival though several new adaptations have periodically come and disappeared.

#### RADIATION OF PLANKTONIC FORAMINIFERA

##### (A) IN CRETACEOUS

The radiation of planktonic foraminifera increased considerably during the Cretaceous times. Several new forms which appeared during this period had maintained the basic Globigerine morphology. Typical Early Cre-

taceous species such as *G. graysonensis* Tappan and the Late Cretaceous (Cenomanian) form—*G. portsdownensis* William-Mitchell have umbilical to extra-umbilical apertures. In the Late Cretaceous, the typical Globigerine shape of the test with an extra-umbilical aperture is distinguished as *Hedbergella* Brönnimann and Brown. Bandy (1967) considers that the most primitive and earliest species of this genus—*H. delrioensis* (Carsey) has evolved from *Globigerina kugleri* Bolli by the development of extra-umbilical aperture and by the addition of one more chamber in the final whorl. Masters (1977) has assigned *Globigerina portsdownensis* as a junior synonym of *H. delrioensis* and *G. kugleri* to *G. hoterivica* Subbotina; the latter has evolved from *G. jurassica* by the gradual reduction in the spire height. Along with the rich and varied *Hedbergella* assemblage in the Late Cretaceous sequence, a large number of micro-foraminiferal forms of ?*Globigerina* are always present.

Certain other forms which are nearly planispiral including (*Globigerinelloides* have also appeared in the Early Cretaceous. *G. blowi* (Bolli), a typical Aptian species appears to have been developed from *Hedbergella delrioensis* through the development of a bilateral symmetry, marginal basal aperture and spinose surface. Masters (1977) suggests that another species of this genus *G. ultramicra* (Subbotina) has descended from another well known species of *Hedbergella*—*H. planispira* (Tappan). At the same time, another specific trend leading into a more involute form can be seen in *Globigerinelloides bentonensis* (Morrow). The genus in the later part of the Cretaceous reduces its number of chambers in the final whorl and lacked the surface sculpturings.

It is interesting to record that the simple trochoid globigerine features have largely persisted through the diverse forms such as *Clavihedbergella*, *Rotalipora*, *Schackoina* and *Ticinella*, whereas the typical planispiral characters as of *Hedbergella* are retained in *Hastingerinoides*. One of the oldest species—*Clavihedbergella bizonae* (Chevalier) from the Aptian, has chamber shape similar to those of *H. planispira*. The genus *Schackoina* may be considered to have derived either from *H. delrioensis* or *Globigerinelloides ultramicra* in Aptian-Albian times and it exhibits an initial trochospiral chamber characteristic of *Globigerina*. The genus *Ticinella* being trochospiral with accessory apertures, has evolved from *Hedbergella* (Sigal, 1966) and differs from *Rotalipora* and *Praeglobotruncana* by having a perforate peripheral margin.

*Hedbergina*, originally described by Brönnimann and Brown (1956) as a globigerine form (type species *Globigerina seminolensis* Harlton) has been placed by Bolli *et al.*, (1957) as a junior synonym of *Praeglobotruncana*. The globigerine morphology of *Praeglobotruncana* includes both the ovate and spherical chamber shape and more umbi-

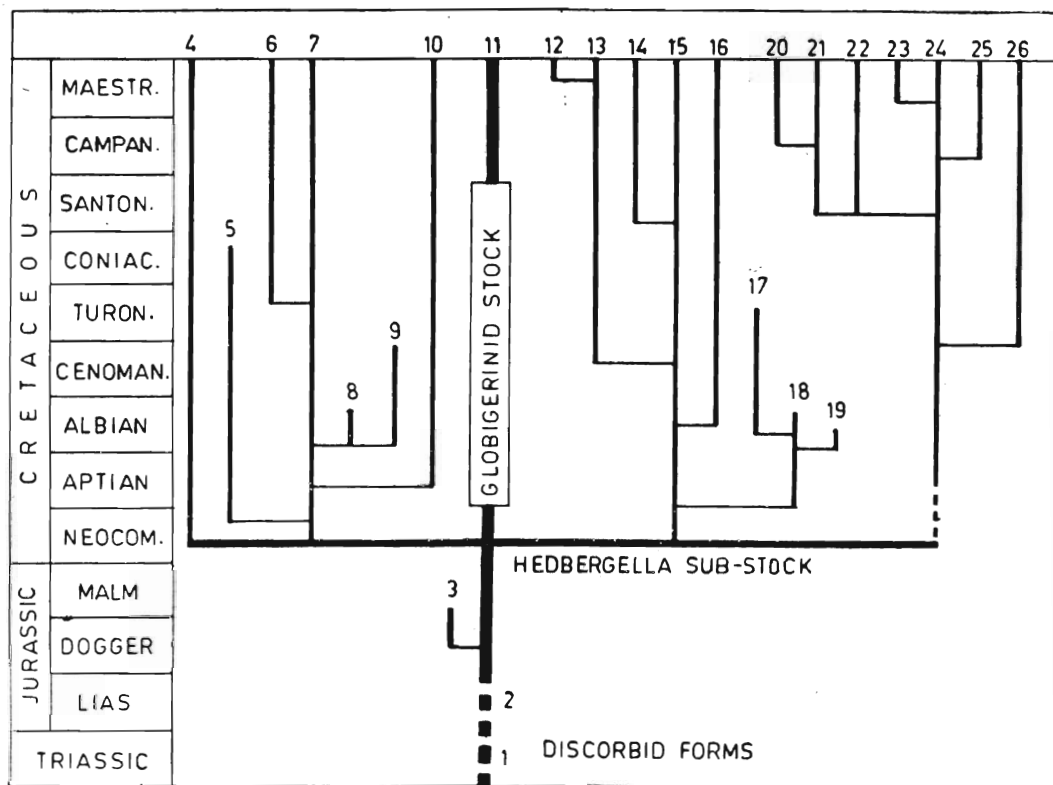


Fig. 1. Phylogeny of important planktonic foraminifera in Mesozoic (forms designated by following numbers).

1. Doubtful planktonic foraminifera, probably related to the subfamily Discorbidinae.
2. *Globigerina helvetojurassica* Heusler
3. *Globigerina jurassica* Hofman
4. *Globigerinelloides* Cushman and Ten Dam, 1948
5. *Clavahedbergella* Banner and Blow, 1959
6. *Hastigerinoides* Brönnimann, 1952
7. & 15. *Hedbergella* Brönnimann and Brown, 1958
8. *Planomalina* Loeblich and Tappan, 1946
9. *Praeglobotruncana* Bermudez, 1952
10. *Schackoina* Thalmann, 1932
11. Original Globigerinid stock
12. *Abathomphalus* Bolli, Loeblich and Tappan, 1957
13. *Globotruncana* Cushman, 1927
14. *Rugoglobigerina* Brönnimann, 1952
16. *Guembelitra* Cushman, 1937
17. *Rotalipora* Brotzen, 1942
18. *Ticinella* Reichel, 1950
19. *Biticinella* Sigal, 1956
20. *Platystaphyla* Masters, 1976
21. *Pseudotextularia* Rzehak, 1891
22. *Pseudoguembelina* Brönnimann and Brown, 1953
23. *Planoglobulina* Cushman, 1927
24. *Heterohelix* Ehrenberg, 1843
25. *Gublerina* Kikoin, 1948
26. *Ventilabrella* Cushman, 1928

lically directed apertures. The genus *Globotruncana* which dominated the Late Cretaceous waters almost throughout the world and *Rugoglobigerina* were possibly derived from *Hedbergella* at the end of Cenomanian and in Santonian respectively (Fig. 1).

The diversification during the Cenomanian-Senonian was perhaps of the highest order in the history of the planktonic foraminifera. Various new structural manifestations were introduced which included the biserial (*Heterohelix*) to pseudomultiserial (addition of supple-

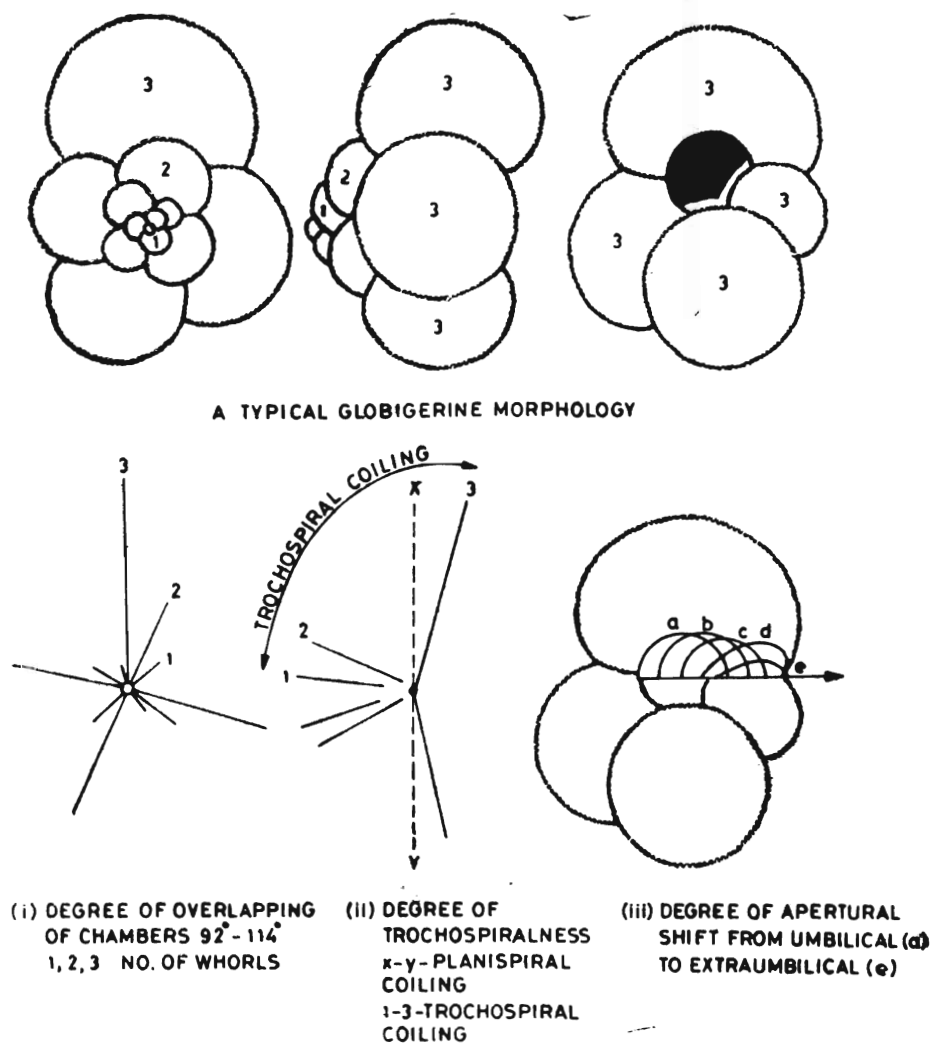


Fig. 2. Structural morphology of a typical Globigerinid planktonic foraminifera and their variations

mentary chambers to the biserial form resulting in *Planoglobulina*, *Platystaphylla*, *Pseudoguembelina* and *Pseudotextularia*), planispiral (*Hastigerinoides*) to trochospiral forms (*Abathomphalus*, *Bilicella*, *Clavibergella*, *Globotruncana*, *Rotalipora*, *Rugoglobigerina* and *Ticinella*). The exclusive variations in apertural characters and positioning, wall ornamentation, modification and keeling added to the diversification list. The diversification during the Late Cretaceous was even based on the climatic factors distinguishing into forms belonging to the cold and warm water groups. According to Frerich (1971), there is a direct correspondence between the palaeo-temperatural variations of the surface waters of the oceans and in the diversity of the planktonic foraminifera. It is important to note that in all these variable morphotypes, the early stages invariably retain the earliest ontogeny of the Globigerinid stock. A simple Globigerine form is structurally most suitable for universal floating habitat in diverse

ecology. The adaptation of a complex morphology over the simple Globigerine structure has been either on account of new opportunities or restrictions in the environments and invariably it encouraged the suicidal tendency of self extinction.

#### (B) IN CENOZOIC

At the close of Cretaceous (Late Mastrichtian), there was a severe decline in the diversity of planktonic foraminifera and the extinction of virtually all the evolved complex forms. As a result, the trend of superimposing complex morphology over the simple globigerine shape as observed in the Late Cretaceous brought the extinctions much faster. The already diversified forms were not compatible with the change of time and environment. Thus there has been almost a complete replacement of these advanced forms during the early part of Cenozoic. Such a severe cut in the diversity is well evident in the

microfaunal assemblage of the Danian. During this period, there were hardly four or five species with relatively simple morphology that consisted of a series of unornamented spherical chambers arranged in a trochospiral coil. These simple forms were world wide in distribution and showed little endemism (Lipps, 1970). Such forms are—*Globoconusa daubjergensis* (Brönnimann), *Globigerina spiralis* Bolli, *Subbotina inconstans* (Subbotina) and *S. triloculinoides* (Plummer). According to Berggren (1968), only one *Globigerina* species is known from the earliest Danian and thus in all probability the entire Palaeogene and later planktonic foraminiferal fauna can be linked to this single species.

Cifelli (1969) believes that not only the Globigerines managed to persist through time of drastic reduction but they once again continued to diversify. Further diversification was achieved with the development of flattened spiral side and angular periphery (*Morozovella* and *Turborotalia*). The early globular Globigerines became relatively compressed after the Danian. Once again after the Cretaceous period, the appearance of the keeled and beaded sutures are seen with different species of *Globorotalia*. The Turborotalid characters superimposed on the Globigerinid structure have resulted into the development of Truncorotalids. All these diversities are recorded during the Late Palaeocene-Eocene interval. *Hastingerina*, which appeared in Eocene, has a planispiral morphology in the adult stage, however, it started its life with a typical Globigerine coil and later diversified into *Pseudohastingerina*, *Clavigerinella*, *Hantkenina* and *Cribohantkenina* (Fig. 3). Krashennikov (1969), while comparing the Crimean-Caucasus and Mediterranean regions suggested a progressive increase in provincialism of characters resulting into diversification during the Late Palaeocene and Early Eocene times.

The early forms of the Cenozoic displayed all the basic character of adaptations as observed in case of the Cretaceous planktons. The early Palaeocene Globigerines were characterised by the simplicity of structures and conservatism as observed in the forms belonging to Late Jurassic-Early Cretaceous times. The off-shoots derived from this stock during both the periods had high potentiality towards adapting new morpho-structures. A simple Globigerinid form is primary in character and has a unique tendency to radiate or diversify in different directions till the new form can survive with time. During the Cenozoic, the primary Globigerines have played their role in repeated radiations as exemplified by *Globigerinoides* and keeled *Globorotalia*. In ancestral Globigerines, a tendency has been seen to develop the supplementary apertures on the spiral side as in *Globoconusa* in Danian. This tendency was greatly enhanced during the Early Miocene (*Globigerinoides* group of species) and

is again observed in some of the simple Globigerines of today (e.g. *Globigerina bulloides* Parker, Jones and Brady). The tendency to develop conical keeled Globorotalid forms, which was first introduced during the later parts of the Early Palaeocene, became significant by the end of Palaeocene and was soon eliminated by the end of the Middle Eocene within 15 m. years. Similar keeled Globorotalids once again appeared in the Early Miocene (Fig. 3). It is emphasised that the intermediate period—the Oligocene, was dominated by simple to relatively less complex *Globigerina* (*G. angulicostata* Bolli, *G. ampliapertura* Bolli, *G. ciperoensis* Bolli, *G. praebulloides* Blow etc.) which bore close resemblance to those of Danian forms. The decrease in the number of *Globigerina* species at the end of Oligocene is related to the origin and radiation of several new genera including the keeled Globorotalids during the Early Miocene.

The rate of change for all types of the planktonic foraminifera was highest at the Late Oligocene.—Early Miocene period. The diversification during the Neogene is, according to Cifelli (1976), one of the two major evolutionary radiations that planktonic foraminifera have undergone. As much as 30 forms have appeared in the Early Miocene from the Globigerinid stock showing, almost similar morphological developments as witnessed during the early periods in planktonic evolution. This kind of radiation, where the conservative ancestral stock gives rise to descendants following an earlier witnessed trend is described as “iterative radiation”. Though unusual, this type of evolution is rather common for the Mesozoic ammonite and several other marine invertebrates. The Neogene planktonic foraminifera such as *Catapsydrax*, *Globigerapsis*, *Globigerinatella*, *Globigerinoides*, *Globoquadrina* and *Orbulina* etc. have essentially primary Globigerine structures with some modifications due to the development of bulla, secondary sutural apertures, enlargement of the last chamber or change in shape. On account of these modifications, the complex forms have been evolved at different stages which are, however, interrelated through their ancestry. Some of the very specialised forms are supposed to be conspecific variants. Bé (1965) has presented the evidences that the forms like *Globigerinoides sacculifer* (Brady) and *Sphaeroidinella dehiscens* (Parker and Jones) are such variants and these two forms are separated mainly on secondary thickening of wall and presence of spines.

During the Neogene period, the evolutionary sequence leading to *Globorotalia fohsi* group of subspecies is well known. This evolutionary lineage may be considered to be the repetitions of similar sequences observed in the earlier periods. The development of new forms is well evident till the Late Miocene and there is no appreciable change afterwards except at population levels. The cli-

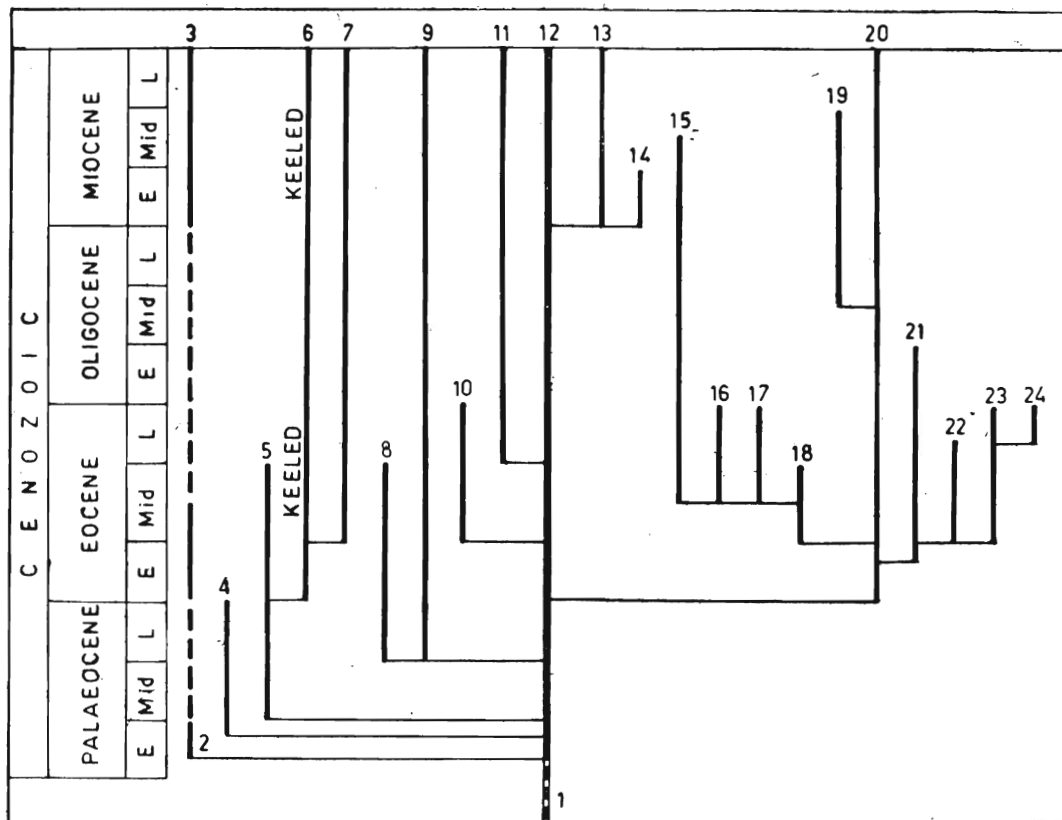


Fig. 3. Phylogeny of important planktonic foraminifera in Cenozoic (forms designated by the following numbers)

1. Original stock of Globigerinid form—*Hedbergella* in Late Cretaceous
2. *Globoconusa* Khalilov, 1956
3. *Globigerinoides* Cushman, 1927
4. *Subbotina* Brotzen and Pozaryska, 1961
5. *Morozovella* McGowran and Luterbacher, 1964
6. *Globorotalia* Cushman, 1927
7. *Turborotalia* Cushman and Bermudez, 1949
8. *Acarinina* Subbotina, 1953
9. *Globigerina* D'Orbigny, 1826 (*s. str.*)
10. *Truncorotaloides* Brönnimann and Bermudez, 1953
11. *Globoquadrina* Finlay, 1947
12. Primary Globigerinid stock
13. *Orbulina* D'Orbigny, in De la Sagra, 1839
14. *Globigerinatella* Cushman and Stainforth, 1945
15. *Catapsydrax* Bolli, Loeblich and Tappan, 1957
16. *Globigerapsis* Bolli, Loeblich and Tappan, 1957
17. *Globigerinathea* Brönnimann, 1952
18. *Orbulinoides* Blow and Saito, 1968
19. *Cassigerinella* Pokorný, 1955
20. *Hastigerina* Thomson in Murray, 1876
21. *Pseudohastigerina* Banner and Blow, 1959
22. *Clavigerinella* Bolli, Loeblich and Tappan, 1957
23. *Hantkenina* Cushman, 1934
24. *Cribrohantkenina* Thalman, 1942

matic changes during the Pleistocene had a very little effect on the planktonic foraminifera in terms of their evolution except on their temporal shift in global distribution and in coiling direction (Bolli 1957).

The present day planktonic foraminiferal assem-

blage comprises of several species of *Globigerina* and related forms which have the ancestral link with the original Globigerinid stock. The widely distributed form in the present waters is *Globigerina bulloides* which maintains the most fundamental and basic skeleton of *Globigerina*



(Fig. 2), yet some of the specimens of this species have tendency to develop supplementary apertures on the spiral side (compare with *Globoconusa daubjergensis* in Palaeocene and *Globigerinoides* in Miocene). It is thus suggested that the primary Globigerine structure has continued to remain as the most conservative as well as the fundamental framework of the structural morphology of the planktonic forms since the Middle Jurassic. It is probable that the progressive progenies of the present day planktonic species may follow the trends shown by their ancestral assemblages in the geological past, whereas the fundamental Globigerinid stock will continue to survive, flourish and radiate.

#### ACKNOWLEDGEMENT

The authors are grateful to the Director, Indian Institute of Technology, Bombay for providing facilities to work in the Microbiostratigraphy Laboratory in the Department of Earth Sciences, I. I. T., Bombay.

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