

#### ABSTRACT

*Radiometric data and phylogenetic analysis of Cretaceous planktonic foraminifera suggest that the Cretaceous be divided into three epochs rather than two. Primitive globigerines occur in the Lower Cretaceous, single-keeled Rotalipora faunas characterize the Middle Cretaceous, and single-keeled and double-keeled Globotruncana faunas typify the Upper Cretaceous. Keels arose in three independent generic lines of development in the Upper Cretaceous. Long-ranging tropical species are restricted to very short stratigraphic ranges toward the tropical boundaries defined by Globotruncana-Rotalipora lines.*

## Cretaceous planktonic foraminiferal zonation

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#### INTRODUCTION

In recent years, much information has accumulated regarding environmental and evolutionary relationships of planktonic foraminifera in geologic time. Principles developed by studies of modern planktonic foraminifera have been applied mostly to Cenozoic populations with relatively little application to the interpretation of Cretaceous assemblages. This study is intended to evaluate important planktonic foraminiferal lineages of the Cretaceous in the light of both environmental and evolutionary factors. Ranges of important Cretaceous faunal indices are related to the standard European time scale as adjusted by radiometric data. The Cretaceous stage names of the European section are already widely used in many parts of the world by numerous investigators.

Cosmopolitanism of modern planktonic foraminifera is rather well established and is being corroborated by current studies of the Indian Ocean, Atlantic Ocean and Pacific Ocean cores and bottom grabs. All prominent planktonic foraminifera occur in each of the three oceans, but they are not distributed equally throughout all tropical waters of the oceans of the world. Not all the species in the Atlantic Ocean occur at any one place, due in large part to the movement of the different water masses. Prominent currents, such as the Kuroshio Current off Asia, the California Current off the western United States, and the Peru Current off the western coast of South America, extend more or less north-south along many continental margins. Thus, pronounced modifications of planktonic foraminiferal abundances and character (*i. e.*, cold-water and warm-water groups) characterize different currents in east-west cross sections in these cases, producing a pseudo-

longitudinal variation. This type of trend is likely to have been responsible for the longitudinal variation mentioned by Olsson (1965) for the Paleocene-Eocene. Evaluation of modern planktonic foraminiferal relationships and principles offers much toward the understanding of differences between planktonic foraminiferal zonation in different Cretaceous basins. Methods of cross correlation employed may be made more precise in the light of this expanded understanding.

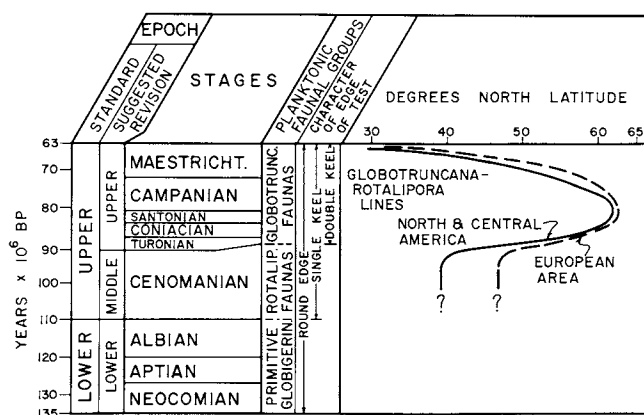
#### ACKNOWLEDGEMENTS

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#### ENVIRONMENTAL RELATIONSHIPS

##### General

Planktonic foraminifera today show marked population changes with latitude, with water depth, with changes in salinity, and from one type of water mass to another (Bandy, 1960a, 1960b, 1964a; Phleger, 1960). It is logical to assume that distribution patterns of Cretaceous planktonic foraminifera were subject to similar types of controls, and that these relationships should be carefully considered in evaluating problems of planktonic foraminiferal correlations in Cretaceous sections.



TEXT-FIGURE 1

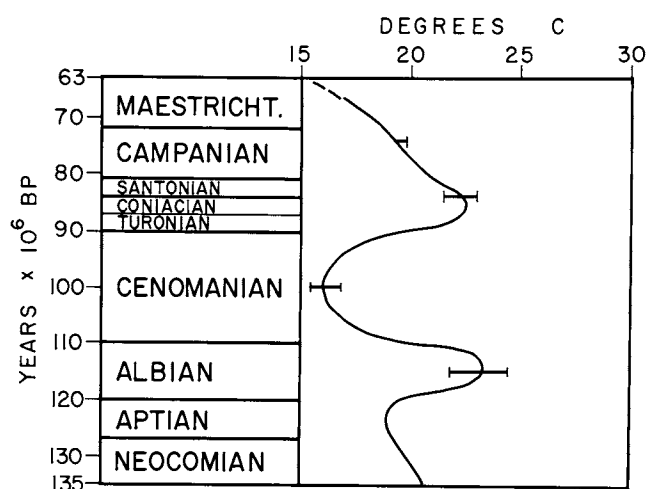
*Globotruncana-Rotalipora* lines, representing the general northern limits of keeled Cretaceous planktonic foraminifera (adapted from Bandy, 1960a).

#### Effects of latitude

In modern oceans, the northern and southern boundaries of modern diversified tropical planktonic foraminifera, especially the keeled types, are approximately defined by the two 17-degree isotherms (Bandy, 1964a), which fall generally between 20 and 40 degrees of latitude, depending upon local oceanographic conditions. Northern and southern polar areas may have great abundances of two or three species of relatively simple globigerinids, whereas tropical faunas are composed of more than 18 species. In addition, specimen abundance may be very great in both tropic and subarctic waters, whereas low values occur generally throughout most warm-temperate areas of the Pacific (Bradshaw, 1959).

It is possible to approximate the variations in the boundaries of tropical areas of the geologic past by plotting the limits of tropical planktonic foraminifera (Bandy, 1960a). Using this method, one finds that there were two major cycles of warming in which the limits of the tropical faunas extended significantly beyond the 40-degree parallel. The first general cycle was that of the Upper Cretaceous (text-figure 1) and the second was that of the Paleocene - Middle Eocene interval.

With reference to the Cretaceous cycle, the upper boundary of planktonic globotruncanids or keeled forms represents a surface that coincides with the upper limit of the marine Cretaceous within tropical areas but descends stratigraphically below the upper boundary of the Cretaceous toward the polar regions. A reverse trend is the stratigraphic rise of the lower boundary toward the polar areas. Thus, the expansion and retreat of the tropical planktonic faunas is seen in geologic section as a crudely wedge-shaped extension toward the polar regions, never reaching as far as the Arctic coastal plain of Alaska (Tappan, 1960) at a latitude of about 70 degrees, but extending to about 62 degrees (southern Alaska), according to data by Bergquist (1961).



TEXT-FIGURE 2

Paleotemperature curve for the Cretaceous of western Europe based upon  $O^{18}$  isotope analyses of belemnoids (adapted from the work of Urey, Lowenstam, Epstein, and McKinney, 1951; Lowenstam and Epstein, 1954; Bowen, 1961).

In northern California the maximum development of diverse globotruncanids is restricted to the Upper Turonian-Coniacian-Santonian interval (Martin, 1964; Takayanagi, 1965), although some globotruncanids extend up to near the Maestrichtian-Campanian boundary (Martin, 1964). Cooling conditions in California are corroborated by the occurrence in the Campanian of the tintinnid genus *Parafavella*, which flourishes at freezing temperatures in modern seas (Campbell and Clark, 1944, p. 4). In general, sections in Europe illustrate the upper occurrence of diverse globotruncanids as a stratigraphically descending surface to the north (Wicher, 1953; Bettenstaedt and Wicher, 1955; Bandy, 1960a). Some deviation from this pattern may be expected due to ancient northward-flowing tropical oceanic currents like the modern Gulf Stream. One such deviation is indicated by the occurrence of globotruncanids in the upper Maestrichtian of Scandinavia, as mentioned by Berggren (1962a).

It should be recognized that, in principle, any standard planktonic foraminiferal zonation in deep-water sections of tropical areas will deteriorate toward and across the *Globotruncana* line, the boundary of the tropical region. Both the lower and the upper boundaries of the occurrence of critical indices will be progressively restricted poleward and will occur in somewhat different combinations due to local oceanographic variations. This differentiation within a given basin is seen today in the Gulf of California (Bandy, 1961), and may be noted in the Upper Cretaceous of northern California by comparing the work of Takayanagi (1965) and Trujillo (1960).

Corroboration of northward and southward shifting of tropical faunas, and the implied tropical 17-degree isotherm, may be seen in paleoclimatic data from the work of Urey, Lowenstam, Epstein and McKinney (1951), Lowenstam and Epstein (1954), and Bowen (1961). These data, based on  $O^{18}$  isotope analyses of belemnoids, reflect two warm intervals during the Albian and Senonian, and three cooler intervals in the Aptian, Cenomanian and Maestrichtian (text-figure 2). Although more complex keeled genera were only beginning to develop in the Albian, it is probable that abundant round-edged globigerinids were initially tropical in origin and adaptation, and that they are to be identified with the warmer-water masses in the Early Cretaceous. In deeper-water Lower Cretaceous facies, distributions of abundant globigerinids may reflect expanding and contracting tropical isotherms. A major expansion and contraction of *Globotruncana-Rotalipora* lines in the Late Cretaceous (Senonian) coincided with the development and waning of a major warm interval evidenced by isotope analyses.

#### Effects of bathymetry

Modern investigations reveal a useful zonation of living planktonic species, according to depth of water as reflected in bottom sediments where their tests come to rest (Bandy, 1956), and in the water column (Bé, 1960). Phleger (1960, p. 241) explained the apparent depth zonation shown in bottom sediments as a function of species frequency as related to the size of populations and not to stratification in the water column. However, plankton tows of Bé (1960) caught the most abundant populations of planktonic specimens in the euphotic zone, and these enormous populations lacked species such as *Globorotalia tumida* and "*Sphaeroidinella dehiscens*". If the relationship were one of species frequency and population size, these forms should be found in association with the larger populations of the euphotic zone, but they are not. Bé also found that plankton tows from below the euphotic zone trapped specimens of a number of species with thickened walls or a cortex. Thus, a thickened wall or crystalline crust is essentially characteristic of mesopelagic depths of about 300 to 1000 meters or greater (Bé, 1960; Bé and Ericson, 1963). Off southern California, Casey (1963) has discovered that *Globigerina pachyderma*, a very thick-walled species, likewise characterizes depths greater than about 100 meters; thin-walled variants may occur at shallower depths.

Cretaceous planktonic foraminifera similarly display considerable modification of the wall thickness (e. g., *Praeglobotruncana stephani*), and in some cases there is a papillate ornamentation that may be possibly analogous to the sugary texture of the modern crystalline crust of some deep-water forms of living planktonic species. Furthermore, variation in diversity and abundance of planktonic Cretaceous species is apparent in some basins within the *Globotruncana* line. It is highly desirable, in paleoecological analyses of Cretaceous plank-

tonic species, to evaluate species diversity and character as a valuable and useful adjunct to analyses of environmental conditions based upon benthic faunas. An interesting example is the parallel that can be drawn between an offshore profile in modern tropical carbonate deposition areas, as off the southern coast of Cuba, and the facies variations in the Upper Cretaceous of Italy (Bandy, 1964b). A prominent change in biofacies occurs, in both cases within just a few kilometers, from benthic populations of larger discoidal shallow-water forms across a structural trend into deep-water assemblages which are more than 90 per cent planktonic specimens.

Often there is a change from small planktonic/benthic ratios of less than one on the outer shelf to more than one in the upper bathyal zone and to much greater values in deeper waters, but it should be noted that a reversal of this general trend may occur (Bandy and Arnal, 1960; Bandy and Rodolfo, 1964). In the eastern Pacific, the greatest abundance of planktonic specimens occurs in the outer shelf and upper bathyal zones, while deeper bathyal waters are characterized by decreasing ratios. Along with the decrease in planktonic foraminiferal specimens in deeper bathyal waters there is an increase in radiolarians, which are more abundant than foraminifera at depths below  $1200 \pm 200$  meters and are many times as abundant as foraminifera in the bottom sediments of the lower bathyal and abyssal zones.

#### Effects of salinity

Planktonic foraminifera are abundant in many open ocean areas of the world where the surface salinity values fall generally within the range of 34 to 37 parts per thousand (Sverdrup, Johnson and Fleming, 1942). Brackish-water areas are essentially devoid of planktonic foraminifera, and large river debouchments displace planktonic foraminiferal abundances away from shore lines considerably farther than along other portions of coast lines. The Baltic Sea, an important brackish-water body, lacks planktonic foraminifera (Segerstråle, 1957); the planktonic foraminifera of Hudson Bay are restricted to the deeper and more saline waters (Leslie, MS.); and in the Gulf of Mexico the abundances of planktonic foraminifera are much attenuated off the Mississippi River delta (Phleger, 1951; Parker, 1954; Walton, 1964).

On the basis of the above and much additional observational data, planktonic foraminifera may be considered to be stenohaline. Faunal and geologic relationships of the Cenozoic and Cretaceous are consistent with this concept. Foraminifera are typically marine organisms, and relatively few species, all benthic forms, have adapted to brackish-water habitats (Bandy and Arnal, 1960; Phleger, 1960). Thus, it is suggested that Cretaceous planktonic foraminifera define normal marine salinities within the range of about 34 to 37 parts per thousand. It should be noted that it is possible for less saline and less dense water to override deeper

saline waters, producing in this way a depositional mixture of two kinds of planktonic groups on the sea floor beneath such areas.

#### Relationships to water masses and currents

In open oceanic areas, water masses may be defined by such factors as temperature and salinity. Other characteristics serve to differentiate them also. As demonstrated by Arrhenius (1950), the boundaries between divergently flowing water masses of the tropical Pacific are zones of upwelling and overturning, an increased supply of nutrients, increased productivity of phytoplankton, and an increased volume of zooplankton, chiefly planktonic foraminifera. The increased numbers of planktonic foraminifera result in a concentration of globigerinid oozes beneath the major current convergences. Other planktonic foraminiferal abundances are known beneath the Kuroshio Current off the Asiatic coast (Polski, 1959) and the Gulf Stream off the southern part of the Atlantic coast of the United States (Wilcoxon, 1964).

That organic life is efficient in identifying different water masses is illustrated by many reports. Lubny-Gertsyk (1955) pointed out that the warmer waters of the Bering Sea flow into the Arctic Ocean, and that within a short distance their temperature is lowered to such a degree that this factor no longer serves as an indicator. Planktonic organisms continue to be carried by the Bering Sea water, thus indicating the true distribution of the Bering Sea water for a long distance. Boltovskoy (1959) discovered that the most abundant planktonic foraminiferal faunas off northern Argentina are associated with either the northward-flowing Malvinas Current (cold-water fauna) or the southward-moving Brazilian Current (warm-water fauna).

In reference to large, relatively shallow basins, Hudson Bay presents itself as an ideal body of water for illustrating relationships of planktonic foraminifera to water masses. Leslie (MS.) has found that planktonic foraminifera occur only in the central of three channels between Hudson Bay and Hudson Strait, an observation indicating that saline water from Hudson Strait enters the bay primarily through this central channel.

Coiling characteristics of planktonic foraminiferal species have provided useful means of defining water masses and currents. Most tropical populations of *Globorotalia* (*Truncorotalia*) *truncatulinoides* are dextral (right-coiling), whereas temperate zones usually have mostly sinistral (left-coiling) populations, as is evidenced in the work of Ericson *et al.* (1954). As noted later (Bandy, 1960b), dextral populations of this species are carried northward by the Gulf Stream and across the North Atlantic by the North Atlantic Current into the huge gyral off western Europe. Shifting positions of the current result in a change in the coiling direction of populations raining down on a particular position on the sea floor. Similarly, *Globigerina pachyderma* is mostly sinistral in polar regions today and dextral in

temperate regions (Bandy, 1959, 1960b; Ericson, 1959). These coiling characteristics have been of extreme value in increasing the precision of cross-correlating between geologic sections, in identifying types of water masses, and in contributing to an understanding of paleoclimates. Coiling characteristics of Cretaceous planktonic foraminifera may be used as well for assistance in correlations (Bolli, 1950, 1951a, 1957a), for the identification of water masses, and perhaps for developing a better understanding of paleoclimatic conditions.

#### Relationships of structure to environments and life cycle

Although there is a good foundation of evidence for assuming that many similar types of foraminifera had different origins, and that they are unrelated isomorphs (Bandy, 1960c), it is also abundantly clear that many structural relationships are now recognized as simple ecophenotypic adjustments (Lutze, 1962, 1964). In his studies of *Bolivina spissa* Cushman, *Bolivina pseudobeyrichi* Cushman and *Bolivina argentea* Cushman, benthic species living off the coast of southern California, Lutze demonstrated that within one species there may be great variation in width-length ratios, in the development of costae, in the length of an apical spine, in the amount of sutural limbation, in the proportion of pore-free areas on chambers, in the imbrication of the chambers, and in the development of keeled edges. He considered one of the primary controlling factors to be the level of oxygen concentration in the bottom waters of basins. High oxygen levels are associated with the secretion of more surface sculpture, such as more spines, more costae or larger keels, whereas very low oxygen concentrations result in the marked reduction or absence of many kinds of surface sculpture. The controlling factor is very likely the level of calcium carbonate saturation because of the relationship between oxygen and carbon dioxide (Sverdrup, Johnson and Fleming, 1942). Consumption of the free oxygen in the water and its consequent decrease result in higher levels of carbon dioxide, thus favoring the solution of calcium carbonate and making it difficult for foraminifera to obtain the excess calcium carbonate needed to form surface sculpture (spines, costae, apicules, *etc.*).

With reference to the Cretaceous, it is not apparent that reduced oxygen levels then existed in the upper part of the water column, unless one selects rather localized instances. However, variation series are still needed for proper recognition of species. Variation phenomena in planktonic foraminifera are not so simple that they can be explained by one factor, the degree of calcium carbonate saturation. On the other hand, the principle expressed by Lutze applies in developing an understanding of the species and genera of planktonic foraminifera. That the erection of species and genera has gone far beyond the understanding of ecophenotypes and life cycles is exemplified by the discovery in studies of Cenozoic planktonic species that 1) some specimens of "*Sphaeroidinella dehiscens*" are simply a deep-water growth manifestation of *Globige-*

*rinoides triloba sacculifera* (Brady) (Bé, 1965), while other specimens of "*Sphaeroidinella dehiscens*" are produced as a deep-water growth form of *Globigerinoides conglobata* (Brady) (Bandy, Ingle and Frerichs, 1965); and 2) the middle and later Cenozoic genus "*Orbulina*" has now been found to be nothing more than a reproductive chamber associated with several different species and even different genera of planktonic forms (Bandy, 1965, 1966). Thus, Cretaceous planktonic species require continuous critical reappraisals in the light of rapidly advancing discoveries and the resultant better understanding.

#### PREVIOUS WORK

Thalmann first emphasized the significance of planktonic foraminifera for worldwide correlation in 1932. Following this, a number of studies on Cretaceous planktonic foraminifera began to appear. Early studies devoted at least in part to planktonic foraminifera and their value in stratigraphic correlation include the works of Thalmann (1934), Glaessner (1937), Gandolfi (1942), Cita (1948), Mornod (1950), Reichel (1950), Bolli (1951*b*), Tilev (1952), Sigal (1952), Brönnimann (1952*a*), Nakkady and Osman (1954), Brönnimann and Brown (1953), Hamilton (1953), Subbotina (1953), Hagn and Zeil (1954), Ayala-Castañares (1954), and the classic by Brönnimann and Brown on the taxonomy of the Globotruncanidae (1955).

Beginning in 1955, many diverse studies were published, including the works of Gandolfi (1955), Dalbiez (1955), Küpper (1955, 1956), Hofker (1956), Bonet (1956), Edgell (1957), Hofker (1957), Reiss (1957), Bolli, Loeblich and Tappan (1957), Morozova (1957), Bolli (1957*a*), Sigal (1958), Bolli (1959), Banner and Blow (1959), and a highly detailed stratigraphic study of the Albian, Cenomanian and Turonian Globotruncanidae of Switzerland by Klaus (1960). Other important papers include those of Belford (1960), Bolli and Cita (1960), Olsson (1960), Pessagno (1960, 1962), the comprehensive taxonomic study by Loeblich and Tappan of the Cenomanian species (1961), and significant contributions by Herm (1962), Ayala-Castañares (1962), Takayanagi and Iwamoto (1962), Barr (1962), Berggren (1962*a*, 1962*b*), Renz, Luterbacher and Schneider (1963), van Hinte (1963), Cita (1963), Graham and Church (1963), Martin (1964), Olsson (1964), Berggren (1964), Loeblich and Tappan (1964), Cati (1964), Takayanagi (1965), and Neagu (1965).

Papers with comprehensive bibliographic listings include the compilation of Graham (1961) for California Cretaceous microfossils, and the works of Berggren, Takayanagi, Loeblich and Tappan, and Klaus, cited above.

#### GROSS PLANKTONIC FORAMINIFERAL ZONATION AND THE CRETACEOUS PERIOD

According to the radiometry-based time scale presented by Kulp (1961), it is evident that there is a significant

temporal disparity (text-figure 1) in the use of the standard Early and Late Cretaceous divisions of the Cretaceous. Of the approximately 72 million years of duration assigned to the Cretaceous Period, only about 25 million years are represented by the Early Cretaceous, and about 47 million years are left for the Late Cretaceous. Subsequent evaluations reviewed by Casey (1964) show many dates between 80 and 100 million years ago for the Cenomanian with one good one as old as 105 million years (p. 201). There is no valid basis in the new figures for restricting the Cenomanian to less than about 20 million years duration. The upper boundary of the Cenomanian may eventually be established at about 80 or 85 million years ago and the lower boundary at about 105 million years. This would make the post-Cenomanian Cretaceous interval about the same duration as the Cenomanian.

It is suggested that, on the basis of both the radiometric data of Kulp and planktonic foraminiferal evolution, a more natural and reasonable division is a threefold division into Early Cretaceous (Neocomian, Aptian, Albian), representing about 25 million years of time; Middle Cretaceous (Cenomanian), representing about 20 million years of time; and Late Cretaceous (Turonian, Coniacian, Santonian, Campanian and Maestrichtian), representing about 27 million years of time. A threefold division of this kind would have an initial interval of expanding primitive globigerinids (Early Cretaceous), a second interval identified with the appearance and development of the more highly evolved *Rotalipora* faunas (Middle Cretaceous), and a third interval in which the highly evolved *Globotruncana* faunas appeared and developed (Late Cretaceous).

Coiling characteristics, studied and considered to be evolutionary by Bolli (1950, 1951*a*, 1957*a*), provide a degree of zonation. The direction of coiling is essentially random in the Lower Cretaceous, the *Rotalipora* group is mostly dextral or right-coiling in the Cenomanian, although there are some reversals, and the keeled *Globotruncana* group of the Upper Cretaceous is almost entirely dextral. Bolli considered coiling trends to be evolutionary, and this is in large part probable. He considered the basic trend to be from initial random coiling to a predominance of either dextral or sinistral coiling later in time, and he used both Cretaceous and Cenozoic species and genera as examples. His assumption that reversals in coiling direction are abrupt evolutionary jumps is not supported by modern investigations of these phenomena in Recent species, such as *Globorotalia* (*Truncorotalia*) *truncatulinoides* and *Globigerina pachyderma* (Ericson *et al.*, 1954; Bandy, 1959, 1960*b*, 1964*a*). Such reversals are more easily explained by the development of both dextrally and sinistrally coiled populations and their gradual adaptation to separate water masses, probably due to temperature differences. Shifting boundaries between these water masses would then result in abrupt changes in the coiling direction of planktonic specimens accumulating in a given part of the basin. In time, one or the other of the two groups might become extinct, leaving only

one group in existence. In theory, future regional studies of Cenomanian planktonic foraminifera may provide more detailed data regarding coiling characteristics, and in this way aid in defining positions and movements of water masses. Zonation based upon coiling ratios alone must be interrelated with zonation based upon the distribution of taxa in geologic time.

Zones used in this study are concurrent-range zones as defined by the American Commission on Stratigraphic Nomenclature (1961, Article 23). These are based on the overlapping ranges of specified taxa, one or more of which are selected as the name for each zone. The concurrent-range zones here employed may perhaps be valid only when qualified in terms of applicability to 1) deep-water marine deposits, 2) deposits in basins with deep-water communication with the open sea, 3) deposits within lower latitudes than those represented by the *Globotruncana-Rotalipora* lines, and 4) deposits in which there was gradual and continuous deposition, without the confusion of telescoped zones in instances of nondeposition. These requirements, together with those of avoiding the usual complications of reworking and faulting, indicate the need for a good understanding of the geologic context of each problem or case.

#### PREDECESSORS OF CRETACEOUS PLANKTONIC FORAMINIFERA

Globigerinids, reported in the Triassic of Austria in recent years by Oberhauser (1960), were described as *Globigerina ladinica* Oberhauser and *Globigerina mesotriassica* Oberhauser. Kristan-Tollman (1964) has also recently reported Triassic globigerines, *Globigerina rhaetica* Kristan-Tollman and *G. cf. mesotriassica* Oberhauser. *Globigerina rhaetica*, from the Upper Triassic of Austria, is amazingly similar in gross appearance to the modern *Globigerina humilis* (Brady), but this similarity is clearly one of isomorphism. The Triassic representative may possibly be related to benthic genera such as *Valvulineria* or *Quadrinophina*. *Globigerina mesotriassica* Oberhauser resembles the modern *Globigerinita glutinata* (Egger), again a case of isomorphic similarity due to convergence. This Triassic form has the morphology of a more typical globigerinid. It is important to study the wall structure and the phenotypic variation of populations of this species.

Jurassic planktonic foraminifera are represented by the questionable forms *Globigerina liassica* Terquem and Berthelin, and *Globigerina helvetojurassica* Haeusler (size about 0.27 mm. in diameter). Recently, confirmation of the existence and character of Middle and Upper Jurassic planktonic foraminifera in Europe has been provided by the studies of Balakhmatova (1953), Colom (1955), AGIP Mineraria (1959), and Eugen and Ilse Seibold (1960). Balakhmatova described globigerines and globorotaliids from the upper Bajocian. Colom (1955, p. 112, pl. 1, fig. 6) reported recognizing the first traces of globigerines in the Dogger levels in thin sections of *Halobia*-bearing pelagic sediment. In the Dogger these occurrences are irregular and dispersed, but they become more important toward the end of

the Jurassic. The *Halobia* and globigerine elements were reported to increase in abundance as radiolarians decrease, a relationship which compares closely with those between planktonic foraminifera and radiolarians in modern basins, such as the Gulf of California (Bandy, 1961), the Peru-Chile Trench area (Bandy and Rodolfo, 1964), and the southwestern part of the Indian Ocean as observed in a study now in progress. In these areas, radiolarian-rich bottom sediments of deep bathyal and abyssal zones give way on slopes of the middle and upper bathyal zones to planktonic foraminiferal abundances in occasional combination with pteropods. It would appear that the earliest recognizable globigerines were already adapted to the oceanic realm. Fine-grained limestones of the Upper Jurassic (Tithonian) contain an occurrence of a lithified globigerine ooze (Colom, 1955, p. 116, pl. 5, fig. 13) associated with occasional deep-water ammonites. Globigerines figured for the Upper Jurassic occurrence may very well be the same as those studied by Eugen and Ilse Seibold (1960) from the boundary of the Dogger and Malm in southern Germany and Switzerland (*Globigerina helvetojurassica*). Globigerines are also apparent in the thin sections of Middle and Upper Jurassic pelagic facies of Italy (AGIP Mineraria, 1959). These Italian occurrences are reported as proto-*Globigerina*.

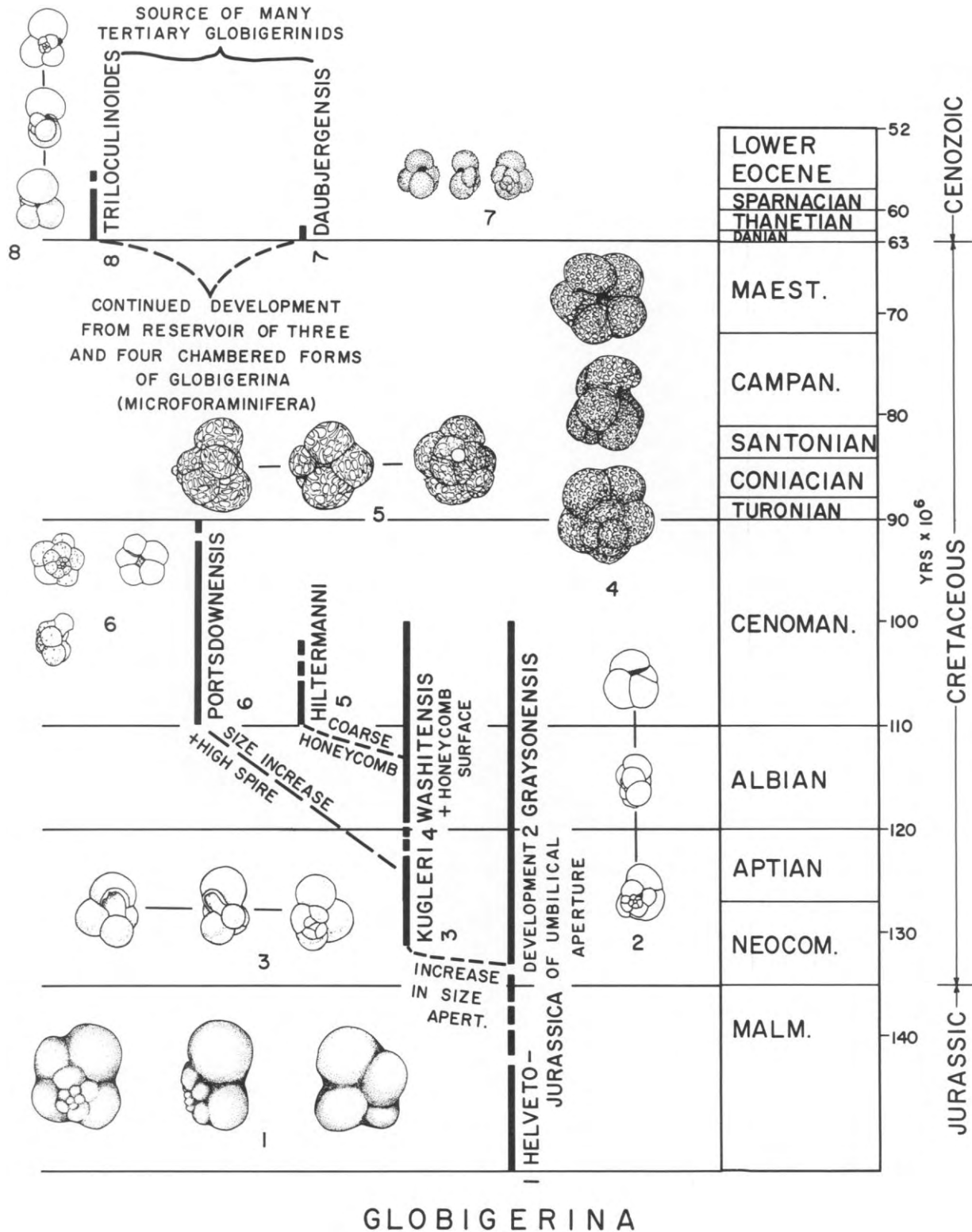
#### PHYLOGENY

##### Globigerina-like forms

Commencing with the globigerines of the Jura-Cretaceous (text-figure 3), it is plain that the major globigerine forms are species of the genus *Globigerina* itself in the Upper Jurassic, the Lower Cretaceous, the Cenomanian and the Cenozoic. A significant gap in the lineage occurs in the Upper Cretaceous. This may warrant using different generic categories for species above and below this gap, but it may also be possible that a connecting lineage does exist. First, it is suggested that, if these globigerinoid forms should be grouped into different supraspecific groups, such supraspecific groups should be maintained at the subgeneric level. Only trochospiral forms with an umbilical aperture are included here in *Globigerina*, which is considered as distinct from *Hedbergella* with its interiomarginal, extraumbilical aperture.

An important aspect of Cretaceous planktonic foraminiferal zonation is that of microforaminifera, a subject requiring further investigation. Its importance may be seen in the case of a modern example. Specimens of *Bolivina quadrata* Cushman and McCulloch are ordinarily benthic along the coast of southern California, and their length is about 0.30 mm. normally. However, in a study of live planktonic foraminifera off southern California, L. Lidz (personal communication) has found specimens of this species in the water column with about the same number of chambers as normal but with a length of about 0.06 mm. These microforaminiferal forms appear to represent the same species as the larger ones, hence it is entirely possible that this is a case of polymorphism.

# FORAMINIFERAL ZONATION



TEXT-FIGURE 3

Phylogeny of *Globigerina* species, Malm to Danian.

During the Cretaceous, evolving groups of planktonic species may possibly have been represented by different (polymorphic) forms, consisting of the microforaminiferal, normal megalospheric and normal microspheric forms of a species. It may then be possible that not all forms of a given species occurred together. In some environments or under adverse conditions, normal megalospheric forms may have been the only representatives in addition to the microforaminiferal forms. In other instances, it may be possible that only the microforaminiferal forms occurred, leaving no record of the normal megalospheric and microspheric generations. Thus, repopulation of an area may have arisen from an indigenous evolving microforaminiferal population, if the environment had changed to favor all polymorphic forms. An abundance of planktonic foraminifera in the Upper Cretaceous dictates that conditions must have been suitable for normal forms of planktonic species throughout the Late Cretaceous. Thus, this possibility cannot explain the absence of *Globigerina* in the Upper Cretaceous.

A second possibility, with ample support from studies of modern planktonic species, is that different forms of a species became extinct at different times. In the Cenozoic, there is evidence that dextral and sinistral forms of the same species have different geologic ranges. For example, sinistral forms of *Globorotalia menardii* (d'Orbigny) may be traced from the Miocene to the Recent, whereas dextral forms became extinct near the Pliocene-Pleistocene boundary. In the same way, perhaps the normal microspheric and megalospheric forms of a species may become extinct, whereas the microforaminiferal forms may continue to exist. Such a continuation of evolving microforaminiferal forms may bridge across the Late Cretaceous between the Early Cretaceous forms of *Globigerina* and those of the Early Tertiary. There appear to be microforaminiferal forms with three and four chambers in the final whorl in most pelagic deposits of the Upper Cretaceous. Many such forms can be seen also in thin sections of Upper Cretaceous pelagic facies, such as those of ACIP Mineraria (1959, pl. 96) and Bozorgnia (1964, p. 89). It is manifest that some of these very small simple forms are the young of *Hedbergella*, but it is equally probable that some of these are representatives of microforaminiferal forms of *Globigerina* in the Upper Cretaceous.

Commencing our phylogeny with *Globigerina helveti-jurassica* Haeusler of the Upper Jurassic, we observe that this species appears either to lack an aperture or to have one covered by the final chamber in a manner like a number of Cenozoic forms. *Globigerina graysonensis* Tappan, a Lower to Middle Cretaceous index, was placed in the genus *Gubkinella* by Loeblich and Tappan (1961). However, *Gubkinella* has a very high spire and a low interiomarginal extraumbilical aperture, while the holotype of *Globigerina graysonensis* has a low dorsal spire and its aperture is umbilical to extraumbilical, similar to those of many globigerines of the Cenozoic, such as *Globigerina pachyderma* (Ehrenberg).

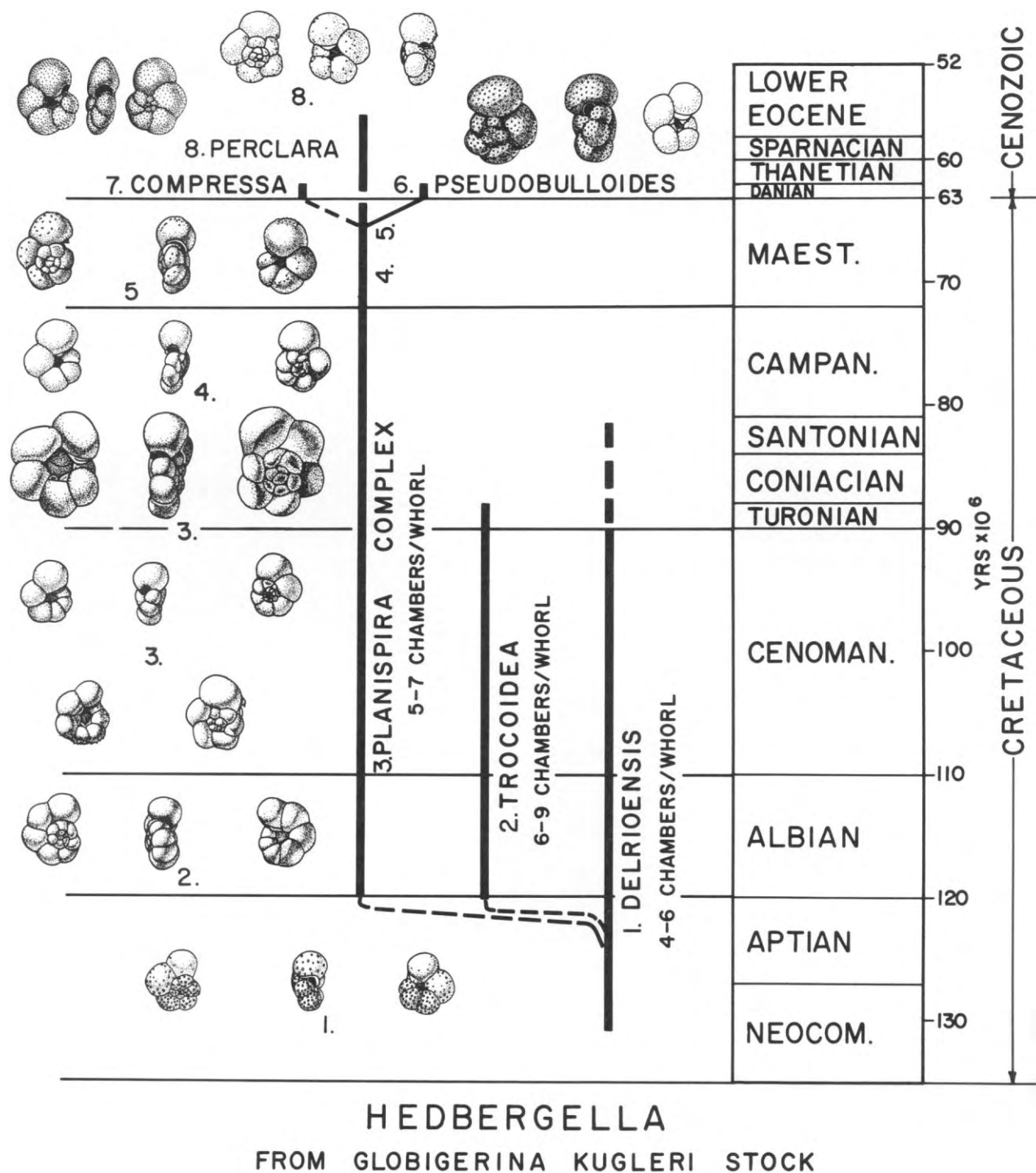
Furthermore, many specimens of *G. graysonensis* have low to flat dorsal spires and a diameter of about 0.21 mm. The species is more properly placed in *Globigerina* for the present.

*Globigerina kugleri* Bolli is another good index to the Lower Cretaceous, with a known range of Neocomian to Aptian. This species is rather variable as to the apertural character, for the height of the aperture is considerable in the types, but populations show variations from high to only moderately high apertures, umbilical in position. The maximum diameter is about 0.27 mm. This species or a similar form probably gave rise to *Globigerina washitensis* Carsey by developing a higher spire, adding one more chamber in the final whorl and a honeycomb surface sculpture, and increasing in size up to 0.54 mm. *G. washitensis* appears to range from Albian to about middle Cenomanian, and, near the boundary between these stages, it gave rise to a short-ranging (lower Cenomanian) more coarsely honeycomb-sculptured form, *G. washitensis hiltermanni* Loeblich and Tappan (maximum diameter about 0.52 mm.).

*Globigerina portsdownensis* Williams-Mitchell, 1948, as used in this study, includes *G. brittonensis* (Loeblich and Tappan) (= *Hedbergella brittonensis* Loeblich and Tappan, 1961), the latter being regarded as a junior synonym. Variation studies show that the aperture ranges from umbilical to umbilical and extraumbilical in position in both, the surface sculpture consists of papillae grading into spines and the areas covered vary markedly in both, and the size range is similar (maximum diameter about 0.36 mm.). Furthermore, the geologic age, Cenomanian, is the same. It is probable that some primitive forms occurred in the Albian, and the ancestor might have been *G. kugleri*, which might have given rise to this species by increasing the height of the spire, adding one more chamber in the final whorl, and developing spines and papillae on the surface.

Upper Cretaceous globigerines are not uncommon in the form of very small specimens with 3 or 4 chambers in the final whorl. However, it is difficult to distinguish between different types which are so extremely small. From this reservoir of evolving forms were derived many of the Tertiary globigerinids. *Globigerina triloculinoides* Plummer is one of these. This species was made the type of *Subbotina* by Brotzen and Pożaryska (1961). However, the pitted wall surface is transitional with the type found in a number of typical species of *Globigerina*. Apertural characteristics of position and the development of a lip are not sufficiently diagnostic to support the recognition of *Subbotina*. *Globigerina daubjergensis* Brönnimann is another important form to arise at the beginning of the Cenozoic. This species tends to develop secondary dorsal apertures, and it has served as the basis for the new genus *Globoconusa* Khalilov, 1956. However, it is suggested that *Globoconusa* be retained at the subgeneric level.

# FORAMINIFERAL ZONATION



TEXT-FIGURE 4

Phylogeny of *Hedbergella* and origin of Cenozoic species of *Globorotalia*. 3, the *Hedbergella planispira* complex with reproduction of illustrations of Cenomanian specimens by Loeblich and Tappan (1961); 4, *Hedbergella planispira holmdelensis* Olsson, reported to be restricted to the lower Maestrichtian (Olsson, 1964); 5, *Hedbergella planispira monmouthensis* (Olsson,) reported to be restricted to the upper Maestrichtian by Olsson (1964).

**Hedbergella**

A significant problem in the phylogeny of *Hedbergella* (text-figure 4) is its relationship to *Globorotalia* of the Cenozoic. It is quite evident that a plexus of *Hedbergella* gave rise to Paleocene species of *Globorotalia*. It is also evident that the distinction between the round-edged forms of the Cretaceous and the round-edged forms of the Paleocene is not completely clear at this time. As an illustration of this problem, note the comparison between *Hedbergella monmouthensis* (Olsson) of the Maestrichtian and *Globorotalia pseudobulloides* (Plummer) of the Paleocene (Berggren, 1962a, p. 40).

Upper Cretaceous, Maestrichtian  
*Hedbergella monmouthensis*

- 1) Asymmetrical portici
- 2) Imperforate portici
- 3) Finely perforate hispid wall
- 4) Final chamber inclined inwards
- 5) Small size, 0.15 mm. up to ?
- 6) Strongly depressed early chambers
- 7) Umbilicus very small
- 8) Test strongly involute

Cenozoic, Paleocene  
*Globorotalia pseudobulloides*

- Symmetrical portici
- Perforate portici
- Cancellate wall surface
- Final chamber not inclined inwards
- Large size, 0.18 mm. to 0.50 mm.
- More globose early chambers
- Umbilicus larger
- Test not strongly involute

Let us discuss the above differences in sequence. 1) Many specimens of *H. monmouthensis* have symmetrical portici. Some of these have been illustrated by Olsson (1964, pl. 1, fig. 3) and Berggren (1962a, text-fig. 5), and others have been found in topotype material supplied by Olsson. *G. pseudobulloides* usually has irregular or asymmetrical portici, as seen in many specimens and as recorded by Loeblich and Tappan (1957, pls. 40-46). 2) An examination of the perforate versus imperforate characteristics of portici shows that there are very fine perforations in the portici of a number of forms of *Hedbergella* and possibly also *Globotruncana*. The principal difference between the Cretaceous forms and those of the Paleocene in this respect may be size of perforations, the finer perforations occurring in the very small Upper Cretaceous species and the coarser ones being found in the larger Paleocene species. This difference in the size of the perforations may thus be a function of the size of the specimens. 3) The Upper Cretaceous species (*H. monmouthensis*) has a finely perforate and hispid wall, whereas the Paleocene species (*G. pseudobulloides*) has a cancellate wall. However, other Paleocene species, such as *G. perclara* Loeblich and Tappan, have a finely perforate and hispid wall, evidence showing this character to be of specific importance only. 4) Inclination of the final chamber inwards in the Cretaceous species is not consistent, and the Paleocene species also illustrates much variation in this character. 5) Small size of the Cretaceous species and large size of the Paleocene species are not significant, for the smaller specimens of the Paleocene species are in about the size range of the Cretaceous form. Certainly, size is not of generic importance. 6) Strongly depressed early chambers in the Cretaceous species separate it from the Paleocene form, which has more globose chambers. However, other Paleocene species, such as *G. compressa* (Plummer), have compressed early chambers, so that this character is of only specific importance. 7) Both small and large umbilical depressions may be

observed in the different Paleocene species, hence umbilical size is not of importance in distinguishing genera. 8) The involute character of the test shows much variation in both the Cretaceous and the Paleocene species under comparison, and this feature appears to have about the same degree of development in the two species figured by various authors (compare *H. monmouthensis* of Berggren, 1962a, text-fig. 5, and *G. pseudobulloides* of Loeblich and Tappan, 1957, pls. 40-46) and in specimens observed by this writer. Thus, the differences between *H. monmouthensis* and *G. pseudobulloides* are no greater than those differences separating many Paleocene species of *Globorotalia* from one another, with the possible exception of the perforation characteristics of the portici. The later Cretaceous species are clearly transitional between typical forms of *Hedbergella* and the derived species of *Globorotalia*.

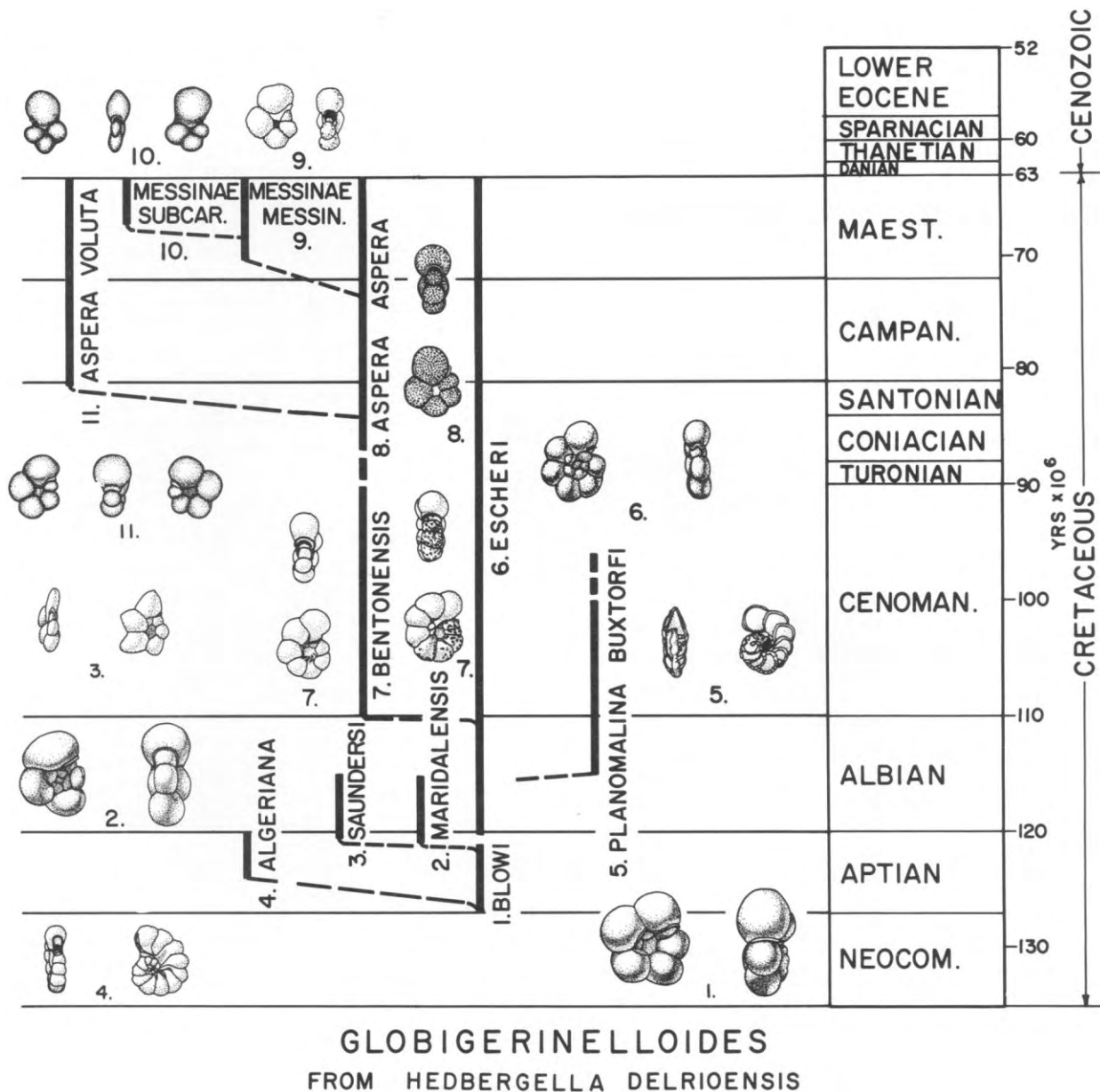
In regard to the principal species of *Hedbergella* (text-figure 4), it is possible that the most primitive and earliest species, *Hedbergella delrioensis* (Carsey), evolved from *Globigerina kugleri* stock by the development of an extraumbilical aperture and the addition of another chamber in the final whorl. The dorsal side of the test is usually flat, although it may become slightly convex in some specimens. The surface of the test is papillate to finely spinose, but poor preservation of the test contributes much to the modification of the ornamentation, eliminating papillae and spines entirely in some cases. Although there are usually 5 chambers in the final whorl, some specimens may have as many as 6 or as few as 4. The size range is about 0.20 to 0.60 mm. in diameter. This species is evidently restricted to the Neocomian - Santonian interval (Takayanagi, 1965).

*Hedbergella trocoidea* (Gandolfi) was derived from *H. delrioensis* by the addition of about two chambers in the final whorl to make a total of 6 to 9 chambers, and by the development of a roughened or rugose surface. The diameter ranges from about 0.20 to 0.40 mm. This species is identified with the Albian to Turonian interval.

One of the common long-ranging species of the Cretaceous (Albian to Maestrichtian) is *Hedbergella planispira* (Tappan). The illustrations of this species given in text-figure 4 are from the Cenomanian study by Loeblich and Tappan (1961). Examination of populations of this species reveals probable microspheric and megalospheric individuals with a size range in diameter of about 0.10 to 0.30 mm. The surface of this species appears to vary from almost smooth to finely hispid, and the umbilical area varies considerably in size. It is a very thin species in edge view, and the dorsal side is quite flat. The apertural portici are highly variable, some being more extended than others. There appear to be perforations in the portici of some specimens of this species.

Shown in text-figure 4 are two forms taken from Olsson (1964) and representing (4) *Hedbergella planispira holmdelensis* Olsson of the lower Maestrichtian and (5)

# FORAMINIFERAL ZONATION



TEXT-FIGURE 5

Phylogeny of *Globigerinelloides* and *Planomalina*, Aptian to Paleocene.

*Hedbergella planispira monmouthensis* (Olsson) of the upper Maestrichtian. Populations of these are difficult to separate from megalospheric forms of *H. planispira sensu stricto*. Many specimens of *H. planispira s. s.* have only 5 chambers in the final whorl, just as these two forms have; the supposedly more rapid increase in chamber size in the new forms is no more rapid than that in many megalospheric forms of *H. planispira* from the Cenomanian; and the supposedly more elongated chambers in the direction of coiling in the new forms are not shown by the figured holotypes and hypotypes (Olsson, 1964). Specimens of *H. planispira* from the Middle Cretaceous include forms amazingly similar to

the subspecies of Olsson. Compare the size increase of chambers and number of chambers in the Cenomanian specimen of Loeblich and Tappan (1961, pl. 5, fig. 4) with those of Olsson's specimens. Forms of *H. planispira* with about 5 chambers in the final whorl are probably megalospheric forms, whereas those with about 7 chambers in the final whorl are thought to be microspheric forms. It is interesting to note that different ratios of these dimorphic forms are encountered from horizon to horizon in the stratigraphic sequence of the Middle and Upper Cretaceous. It is suggested that the megalospheric form endured longer in time, becoming the dominant form in the Maestrichtian. Certainly, on

comparing the figures of *H. planispira* and the two Maestrichtian forms of Olsson (1964, pl. 1, figs. 1-4), it is manifest that the approach of Lutze (1962, 1964) in using variation statistics is needed here.

Paleocene derivatives of the *planispira* complex include *Globorotalia pseudobulloides* (0.16 to 0.50 mm. in diameter) with a cancellated surface, *Globorotalia compressa* (0.16 to 0.38 mm. in diameter) with a compressed test and a finely perforate smooth surface, and *Globorotalia perclara* (0.26 mm. in diameter) with a finely perforate hispid surface. Variable portici occur, some symmetrical and others asymmetrical. The smaller sizes of these Paleocene forms is consistent with the sizes of many specimens of the *H. planispira* complex of the Maestrichtian.

#### Globigerinelloides and related genera

Several planispiral or nearly planispiral planktonic genera have appeared in geologic time and were mostly combined under one or two generic designations in early works. *Globigerinella* and *Hastigerina*, often combined under the earlier name *Hastigerina*, appear to have arisen independently in the middle or later Cenozoic and represent two of these genera. A third is *Pseudohastigerina* or *Globanomalina* of the Eocene, derived from *Globorotalia elongata chapmani* (Glaessner) in the latest Paleocene, and a fourth is *Globigerinelloides* of the Cretaceous, which arose from *Hedbergella delrioensis* of the Lower Cretaceous (text-figure 5). These are good examples of nonsynchronous isomorphism, resulting from evolutionary convergence. *Globigerinelloides* usually has relict apertures showing around the umbilical depressions.

One of the earliest species of *Globigerinelloides* (text-figure 5) is *G. blowi* (Bolli), reported to be restricted to the Aptian of Trinidad (Bolli, 1959). It may have been derived from *Hedbergella delrioensis* stock by a trend toward bilateral symmetry and by the migration of the aperture onto the edge of the test. Some variation in this direction is noted in populations of *H. delrioensis*. *Globigerinelloides maridalensis* (Bolli), a lower Albian index, is a derivative of *G. blowi* by elongation of the chambers in the direction of coiling. Otherwise they are alike. *G. saundersi* (Bolli), also restricted to the lower Albian, was probably derived from *G. blowi* by the development of radially elongate chambers. All three of these species are usually between 0.30 and 0.35 mm. in diameter.

*Globigerinelloides algeriana* Cushman and ten Dam, an index to the Aptian of North Africa and perhaps elsewhere, may possibly have been derived from *G. blowi*, which occurs slightly earlier in geologic time. This requires an increase in the number of chambers per whorl and a doubling of the size of the test. The occurrence of double apertures in some specimens is considered to be an abnormal condition, the appearance of rare recessive traits.

*Globigerinelloides escheri* (Kaufmann), ranging throughout the Albian - Maestrichtian, was probably derived

directly from *G. blowi*. Populations of this species show considerable variation in the degree of exposure of the earlier chambers in the umbilical regions, in the size increase of the chambers, and in the number of chambers per whorl. The species was originally described as ranging from 0.055 to 0.12 mm. in diameter, but specimens often attain a diameter of about 0.25 mm. These are still very small, and they are often slightly more involute on one side than on the other. *Hedbergella planispira* (Tappan) and this species are easily confused in making frequency counts unless almost every specimen is turned over. *G. escheri* (Kaufmann, 1865) is a senior subjective synonym of *G. caseyi* (Bolli, Loeblich and Tappan, 1957).

*Planomalina buxtorfi* (Gandolfi), an index to the upper Albian and lower Cenomanian, was an offshoot of *G. escheri* which developed more numerous chambers, a peripheral keel, raised limbate sutures, and a triangular apertural face.

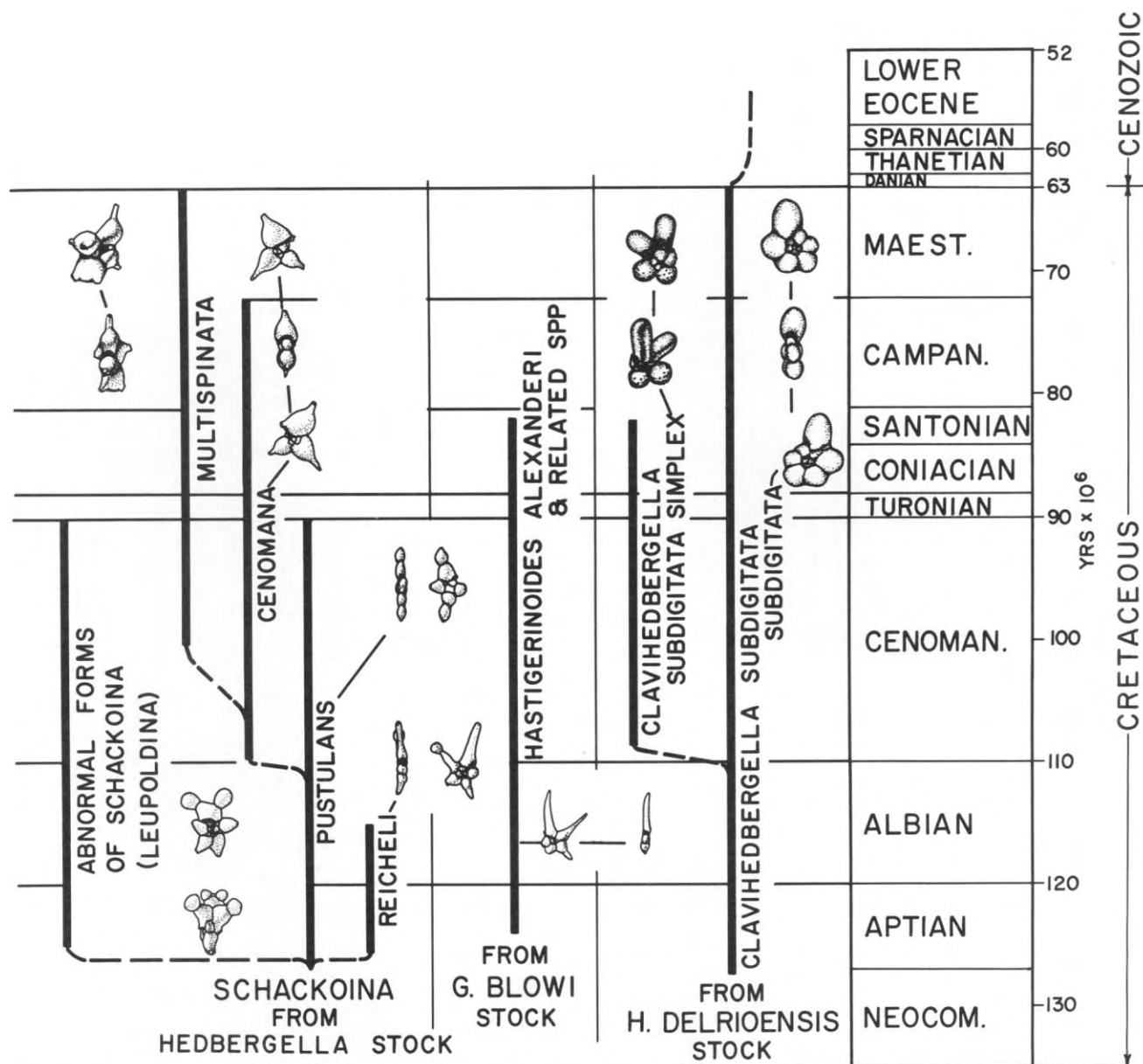
*Globigerinelloides bentonensis* (Morrow), apparently restricted to the Cenomanian, was derived from *G. escheri* by increasing in size to a diameter ranging between 0.20 and 0.40 mm., by becoming more involute than the usual forms of *G. escheri*, and by developing more closely appressed chambers. Primitive populations of *G. escheri* show gradations in the degree of the exposure of the earlier chambers, and so the *G. bentonensis* line was probably derived from the more involute forms of *G. escheri*. Surface sculpture consists of fine spines in the earlier portion of the test, but some specimens are almost barren of this hispid ornamentation.

*Globigerinelloides aspera aspera* (Ehrenberg), restricted to the Upper Cretaceous, was derived from the *G. bentonensis* group by decreasing the number of chambers per whorl, enlarging the chambers more rapidly in the final whorl, and developing the spinose surface so characteristic of this species. The size range is about the same as that of *G. bentonensis*, about 0.20 to 0.40 mm. in diameter.

*Globigerinelloides messinae messinae* (Brönnimann), restricted to the Maestrichtian for the most part, although with possible occurrences and derivation in the Campanian, evolved from *G. aspera* by decreasing to about 4 or 4½ the number of chambers in the final whorl and by reduction of the surface sculpture to minute papillae. This species also typically has a higher-arched apertural opening than *G. aspera*, and it is about the same size, ranging from 0.31 to 0.40 mm. in diameter.

*Globigerinelloides messinae subcarinata* (Brönnimann), as illustrated in text-figure 5, is restricted to the upper Maestrichtian. It was derived from *G. messinae messinae* by the development of a compressed test with an abruptly rounded to almost angular edge. The size is the same, and there are intergradational forms between these two subspecies. The last chamber is often not quite as large as that shown in text-figure 5.

# FORAMINIFERAL ZONATION



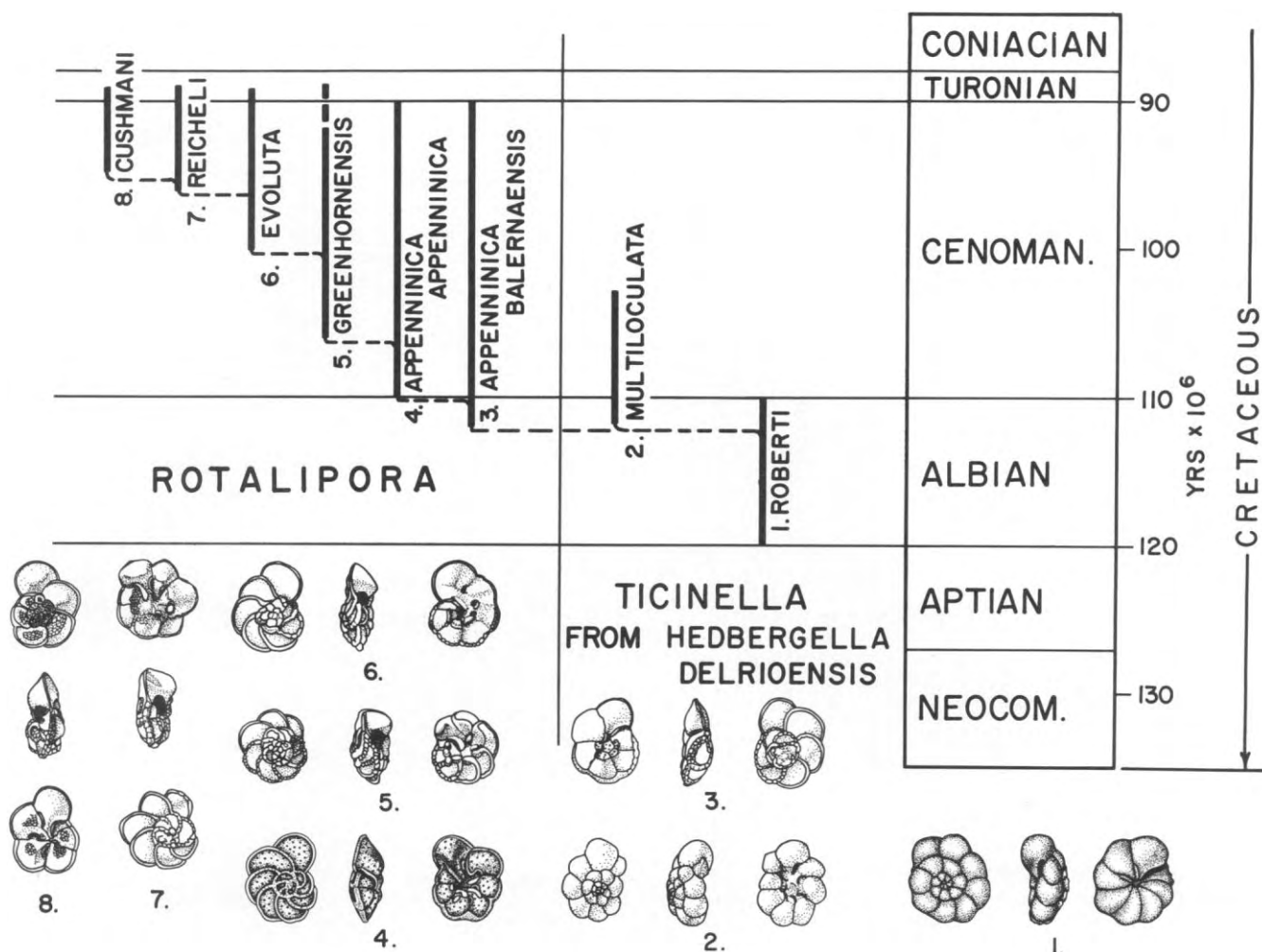
TEXT-FIGURE 6

Phylogeny of *Clavhedbergella*, *Hastigerinoides* and *Schackoina*.

*Globigerinelloides aspera voluta* (White), restricted to the Campanian and Maestrichtian as presently understood, was derived from *G. aspera aspera* by the development of a completely smooth test. Although the aperture is often characterized by a projecting lip, this feature is quite variable. In many of the more nearly involute species of *Globigerinelloides*, relict earlier apertures are detected with considerable difficulty, even on very well-preserved specimens.

## Clavhedbergella, Hastigerinoides, and Schackoina

*Clavhedbergella subdigitata subdigitata* (Carman, 1929) arose near the Neocomian-Aptian boundary and lasted throughout the remainder of the Cretaceous (text-figure 6). It was derived from *Hedbergella delrioensis* stock represented by transitional forms such as "*Hedbergella amabilis*". Transitional forms of this kind occur with many of the populations of *C. subdigitata* in numerous horizons of the Cretaceous and are considered as



TEXT-FIGURE 7

Phylogeny of *Ticinella* and *Rotalipora*.

junior synonyms of this species. *C. subcretacea* (Tappan, 1943) is also a junior synonym of *C. subdigitata* (Carman, 1929). It is likely that this form gave rise to the populations of *C. (?) eocanica* (Nuttall) of the Eocene.

*Clavahedbergella subdigitata simplex* (Morrow), ranging from Cenomanian to Santonian, is a more trochoid variation with the chambers radially elongate. *C. subdigitata subdigitata* also develops much more radially elongate chambers, and there are many gradational forms between these two subspecies. Juvenile growth stages of the modern *Hastigerina pelagica* (d'Orbigny, 1839) develop into adult forms referred to as *Hastigerinella digitata* (Rumbler, 1911); the latter is now considered to be a junior synonym of the former (see analysis by Bé, 1965). Somewhat similar types of variation from nearly planispiral to trochoid forms, and with respect to radial elongation of the chambers, are noted in these Cretaceous species and also in the Eocene.

*Hastigerinoides alexanderi* (Cushman) is typically planispiral and appears to have evolved from *Globigerinelloides blowi* stock by the development of radially elongate chambers. This species is common in the Turonian, and it is similar to a group of species that range more extensively in the Cretaceous from the Aptian to the Santonian. Relict apertures around the umbilical areas and planispiral coiling separate *Hastigerinoides* from *Schackoina*, although some of the species of *Hastigerinoides* might have arisen from *Schackoina* by becoming planispiral and eliminating the relict apertures.

*Schackoina* embraces trochospiral to planispiral species with tubulospines and with an interiomarginal equatorial aperture possessing a very narrow to broad spatulate lip. This genus evolved either directly from *Hedbergella delrioensis* stock or possibly from primitive forms of *Globigerinelloides blowi* which were in turn derived from *Hedbergella delrioensis*. Modern studies of Recent planktonic foraminifera, together with growth sequence

studies of *Schackoina*, indicate that *Leupoldina* Bolli, 1957, consists of abnormal growth forms of *Schackoina*. Although these abnormal forms are only known to range from Aptian to Cenomanian (Bolli, 1959), it is possible that rare abnormal forms will be found in the Senonian as well.

*Schackoina reicheli* Bolli, ranging from the Aptian to the Albian, is similar to *Hastigerinoides*, excepting that it is slightly trochospiral. It is more than possible that species of *Hastigerinoides* and forms such as *S. reicheli* are dimorphic forms of the same species. The type is about 0.52 mm. in diameter.

*Schackoina pustulans* Bolli, ranging from Aptian to Cenomanian, has bulb-shaped extensions of the chambers of the last whorl, and the chambers are globular in contrast to the radially elongate chambers of *S. reicheli*. The type is about 0.41 mm. in diameter.

*Schackoina cenomana cenomana* Schacko, ranging from Cenomanian to Campanian, has subglobular chambers with 3 or 4 in the final whorl, each produced into a long, centrally placed tubulospine. *S. gandolfi* Reichel and several other forms are included in this species, as discussed by Loeblich and Tappan (1961). Takayanagi (1965), following this concept, included *S. tappanae* Montanaro Gallitelli in *S. cenomana*, with an upper reported range of Campanian. The diameters range from about 0.13 to 0.25 mm.

*Schackoina cenomana multispinata* (Cushman and Wicken-den), ranging from the Cenomanian to the Maestrichtian, is simply *S. cenomana* with the addition of more spines and is considered to be a subspecies of *S. cenomana* in this study. The diameter varies from 0.15 to about 0.25 mm.

#### Ticinella and Rotalipora

*Ticinella roberti roberti* (Gandolfi), restricted to the Albian as presently understood, is the most primitive forerunner of a lineage (text-figure 7) leading to *Rotalipora*, the dominant planktonic genus of the Cenomanian. It appears to have been derived from *Hedbergella delrioensis* stock by the development of small sutural apertures on the ventral side and the addition of more chambers per whorl.

*Ticinella roberti multiloculata* (Morrow), ranging from the upper part of the Albian to the middle of the Cenomanian, is a variable form intermediate between typical *Ticinella* and *Rotalipora*. This subspecies includes a range of variation from specimens with globose chambers and no keel to those with globose chambers and the beginning of a keel (Klaus, 1960). Also, the secondary apertures on the ventral side occur between all the chambers and have better-developed lips. It is probable that statistical variation studies would make it desirable for *Ticinella* to be reduced to a subgenus under *Rotalipora*.

*Rotalipora* includes species with keels, a smooth surface, and well-developed secondary apertures along the sutures on the umbilical slopes. Such forms appeared in the uppermost Albian and disappeared within the Turonian. *R. appenninica balernaensis* Gandolfi appeared in the uppermost Albian and disappeared near the top of the Cenomanian. It has poorly developed secondary apertures and seems to be mostly dextral, especially in the middle and upper Cenomanian. Many specimens attain a diameter of 0.40 mm.

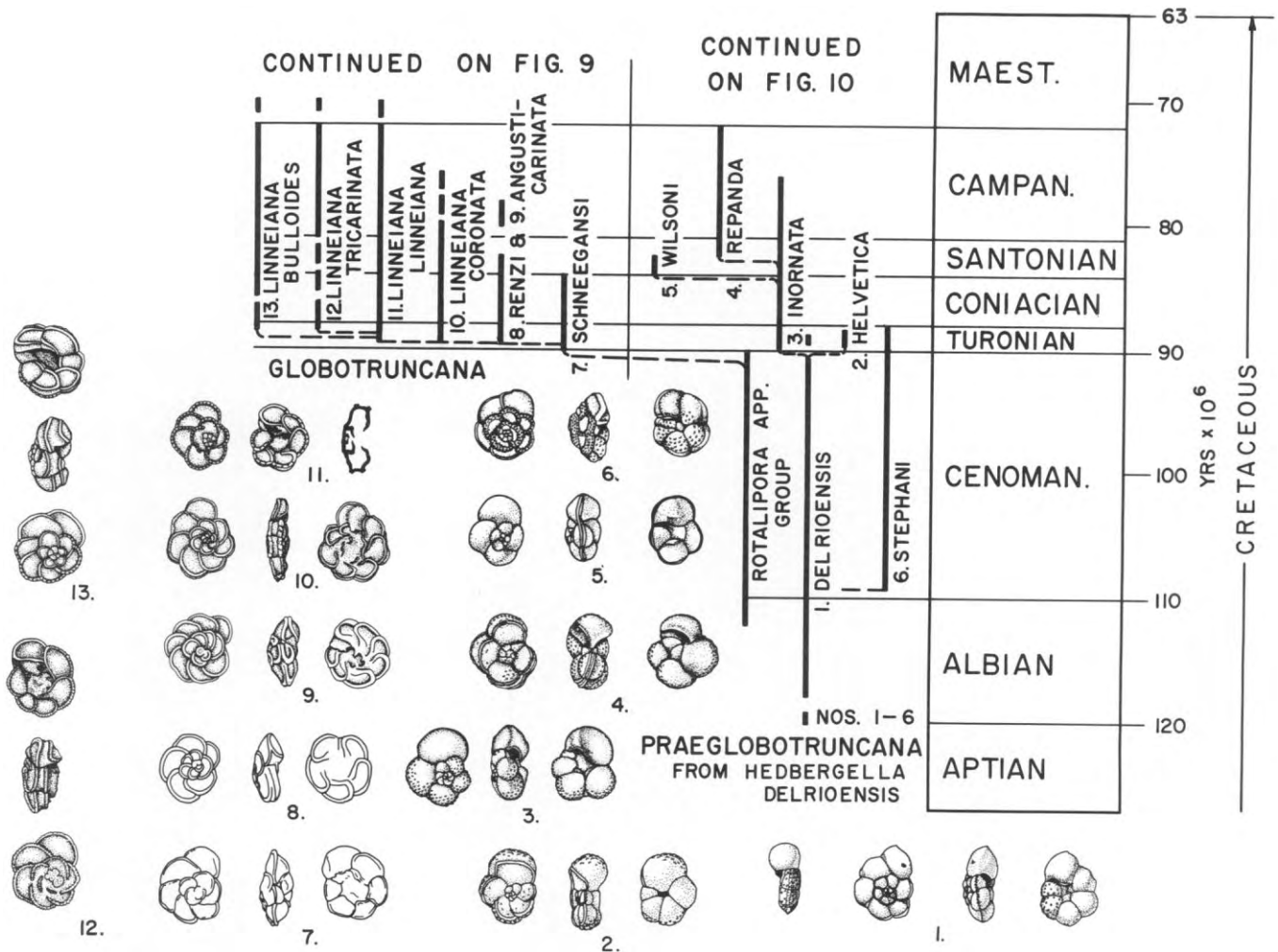
*Rotalipora appenninica appenninica* (O. Renz) is essentially restricted to the Cenomanian. It usually has a smooth surface and rather well-developed secondary apertures. Coiling is mostly dextral, especially in the middle and upper Cenomanian. Populations of this species range from about 0.15 to more than 0.90 mm. in diameter.

*Rotalipora greenhornensis* (Morrow, 1934), ranging through the middle and upper Cenomanian and into the Turonian, represents a group of forms with chambers inflated on the ventral side, a distinct umbilical shoulder, and about 6 or 7 chambers in the final whorl. The surface of the test is commonly roughened in the early portion, but populations show a considerable variation in the degree of development of this characteristic. Many of these variations have been given different specific names by authors, and the long synonymy of most of these has been discussed and presented by Loeblich and Tappan (1961). These junior synonyms include *Rotalipora globotruncanoides* Sigal, 1948, *Thalmaninella brotzeni* Sigal, 1948, *Globorotalia decorata* Cushman and Todd, 1948, and others. Coiling is mostly dextral in the middle and upper Cenomanian and Turonian. The maximum size noted is about 0.55 mm.

*Rotalipora reicheli* Mornod, upper Cenomanian to lower Turonian, is perhaps better ranked as a subspecies of *R. greenhornensis* because of its similar chambers inflated on the ventral side and well-developed umbilical shoulder. It has rather highly nodose and thickened sutures on the dorsal side and a typical keel along the edge of the test. The last few chambers are quite inflated, producing a more lobate periphery. Specimens are usually dextrally coiled. The diameters noted range up to more than 0.75 mm.

*Rotalipora cushmani* (Morrow), an index of the uppermost Cenomanian and lower Turonian, has 5 or 6 chambers in the final whorl, rarely 7. This species is deeply umbilicate. It was derived from and may belong to the *R. greenhornensis* group. The earlier part of the test is spinose or rugose. *R. cushmani* (Morrow, 1934) is an earlier name for the junior synonyms *R. turonica* Brotzen, 1942, and *R. montsalvensis* Mornod, 1950. This species shows both dextral and sinistral coiling. Diameters range up to about 0.75 mm.

The genus *Rotalipora* and its important species define a middle section of the Cretaceous Period which forms almost one third of the time of the Cretaceous (text-figure 7), as discussed earlier in this report. The range



TEXT-FIGURE 8

Phylogeny of *Praeglobotruncana* and *Globotruncana* (part).

of this planktonic genus is almost synonymous, then, with the middle one of three subequal parts of the Cretaceous, while *Globotruncana* is the important index to the third or last of these three parts, the Upper Cretaceous.

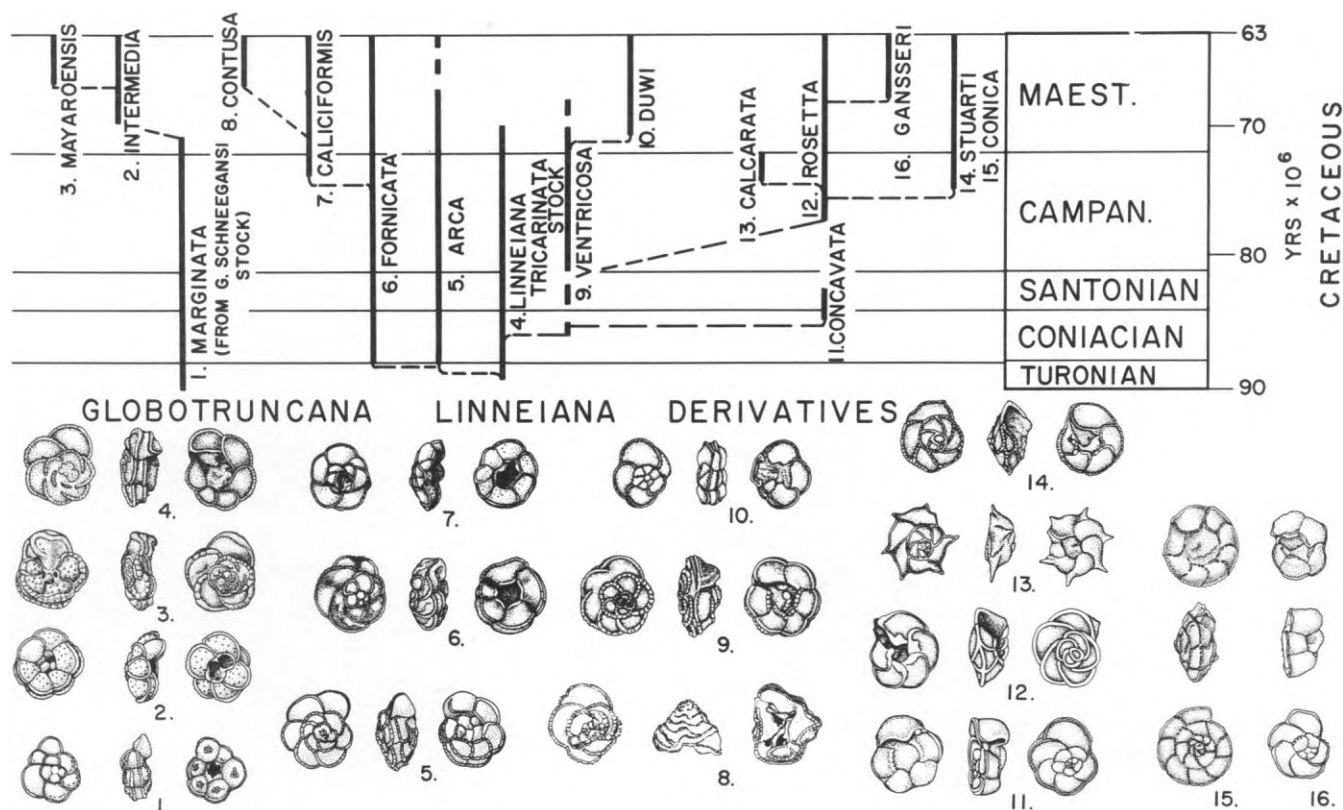
#### *Praeglobotruncana*

*Praeglobotruncana* (text-figures 8 and 10) precedes *Globotruncana*, and, although they are similar, the two arose independently from *Hedbergella delrioensis* stock. This stock produced a branch, the genus *Ticinella*, by the development of secondary apertural openings on the umbilical slopes of the ventral sutures; *Ticinella* evolved into *Rotalipora* by the development of improved umbilical plates, larger secondary apertures and lips, and a keel; *Rotalipora*, in turn, gave rise to *Globotruncana* by the elimination of the secondary apertures and division into one-keeled and two-keeled lines. A second branch arose from *Hedbergella delrioensis* stock with the ap-

pearance of *Praeglobotruncana delrioensis*, which shows an interesting transition from a round to a sharp or angled edge within the populations of this species. *P. delrioensis* also develops a granular or papillate ornamentation which parallels surface sculpture in the *Rotalipora-Globotruncana* sequence. In the branch leading to *Praeglobotruncana*, there is an apertural lip but no umbilical tegilla at first as in the globotruncanids. *Praeglobotruncana* is a Cretaceous isomorph of *Globorotalia* of the Cenozoic, and both show variations from round-edged to keeled forms in different species groups. Furthermore, globotruncanoid keels develop on some Upper Cretaceous species of *Praeglobotruncana*, an example of parallelism between the latter and *Globotruncana*.

*Praeglobotruncana delrioensis delrioensis* (Plummer), ranging from the Aptian-Albian border into the Upper Cretaceous (Turonian), consists of round-edged, sharp-edged and intergradational forms in the populations of this subspecies. Granular surface sculpture develops

# FORAMINIFERAL ZONATION



TEXT-FIGURE 9

Phylogeny of *Globotruncana* (continued).

along the spiral and radial sutures, and covers variable areas of the surface, usually the early part of the test. This subspecies is low-spined, the thickness being about one-third of the diameter. Diameters of specimens are between 0.40 and 0.50 mm. Most specimens are about 0.40 mm. in diameter or slightly more.

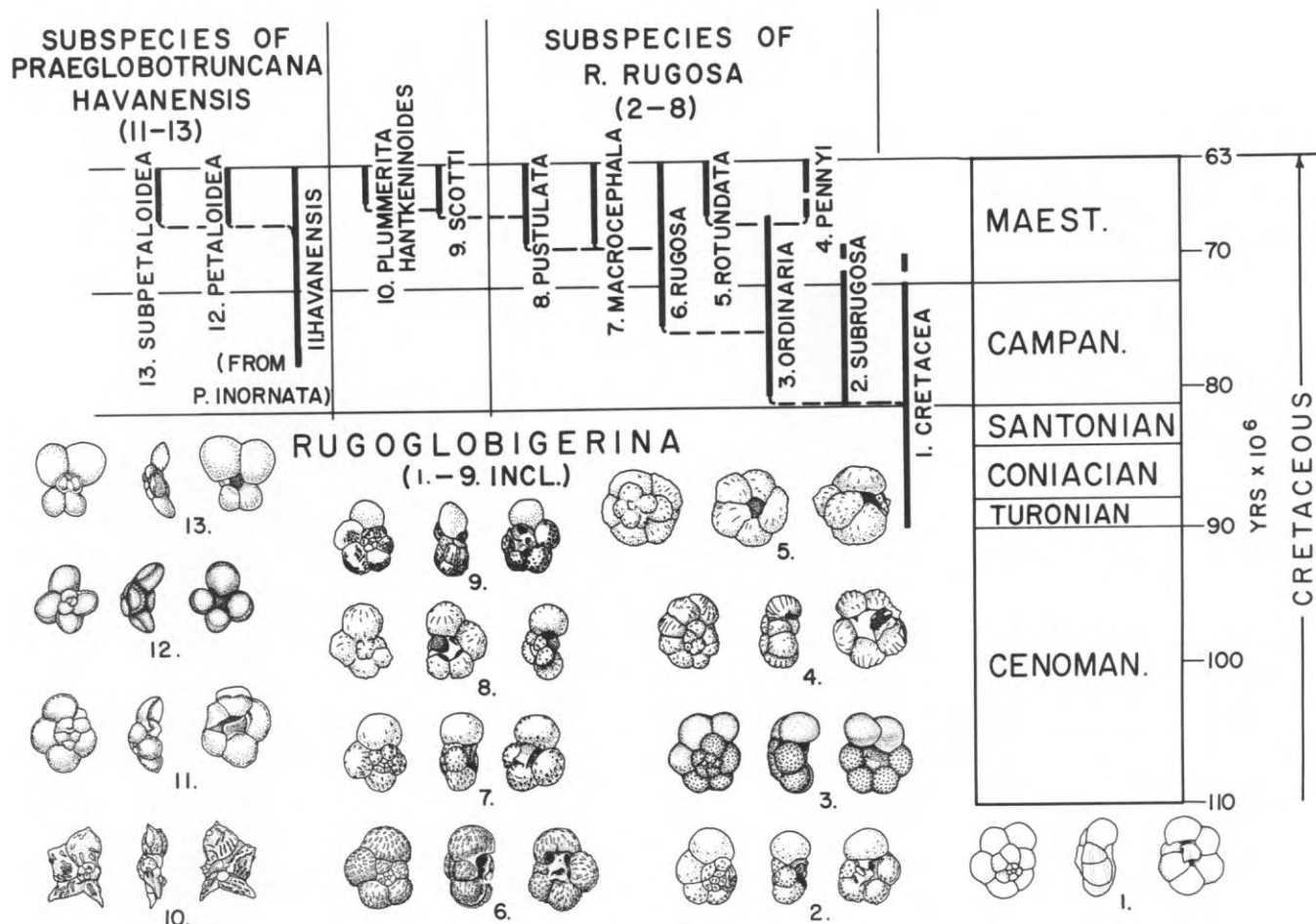
*Praeglobotruncana delrioensis stephani* (Gandolfi) was derived from *P. delrioensis delrioensis* in the basal Cenomanian and lasted into the Turonian. This subspecies is relatively thick and high-spined, the thickness being about one half or more of the diameter. Specimens of typical populations are strongly papillate along the thickened keel and sutures, and on the ventral surface, the dorsal surface varying from strongly papillate to almost smooth. It is included as a subspecies of *P. delrioensis* because of the intergradation of typical *delrioensis* and *stephani* populations in the lower and middle Cenomanian. The maximum diameter is about 0.40 mm.

*Praeglobotruncana helvetica* (Bolli), an index of the Turonian, was derived from *Praeglobotruncana delrioensis delrioensis* stock by the development of a flat dorsal surface and a slight keel along the peripheral edge of the dorsal surface. The chambers are strongly inflated ventrally, and the umbilicus appears to have no tegilla.

This species is contemporaneous with the beginning of the typical *Globotruncana* group, which developed as biconvex keeled forms from the *Rotalipora* group. Bolli (1957a) reported *helvetica* as 98 per cent dextral. Thus, *P. helvetica* is an isomorph of some of the later single-keeled globotruncanids. Diameters noted are between 0.40 and 0.50 mm.

*Praeglobotruncana inornata* (Bolli), ranging from the Turonian into the Campanian, was derived from *P. delrioensis* stock by reduction in the number of chambers per whorl and a more rapid increase in the size of chambers in the final whorl. The tegilla are not well developed, and the final chamber usually becomes compressed with a more abruptly angled peripheral edge. Surface sculpture is pustulose or papillate, similar to that of *P. delrioensis*. Coiling is predominantly dextral. Diameters noted are about 0.45 mm.

*Praeglobotruncana wilsoni* Bolli, apparently restricted to the lower part of the Santonian, is characteristically smooth and biconvex. It has four chambers in the final whorl and a faint double keel that appears as a single keel in poorly preserved specimens. Umbilical tegilla are poorly developed, if present. The species is predominantly dextral in coiling habit. Diameters noted are about 0.50 mm. or slightly less.



TEXT-FIGURE 10

Phylogeny of *Rugoglobigerina* and *Praeglobotruncana* (part).

*Praeglobotruncana repanda* (Bolli), ranging from the Santonian to the uppermost Campanian as presently understood, was derived from *P. inornata* by the addition of two narrow keels near the dorsal side of the peripheral margin. The surface is ornamented with papillae or rugose areas, especially on the ventral side. Keels and papillae may be absent on the last of the four chambers comprising the final whorl. Coiling is predominantly dextral. Diameters are about 0.40 mm.

*Praeglobotruncana havanensis havanensis* (Voorwijk, 1937), restricted to the upper Campanian and Maestrichtian (text-figure 10), was derived from *P. inornata* stock by the development of petaloid chambers and a faint marginal keel. The convex dorsal side and concave ventral surface are quite characteristic. It is an earlier name for *P. pschadae* (Keller, 1946), *P. citae* (Bolli, 1951), and *P. coarctata* Bolli, 1957. This species probably gave rise to the Paleocene species *Globorotalia praemendii* Bolli (Subbotina, 1960). The imperforate peripheral band and slight keel may be quite variable. The umbilical region apparently has a complete cover-

plate of tegilla. Coiling is predominantly dextral. Maximum diameter is nearly 0.50 mm. Small specimens tend to be less convex dorsally and were the basis for *P. coarctata* Bolli, 1957. Removal of the last chamber of *P. havanensis havanensis* produces the general symmetry of *P. coarctata*.

*Praeglobotruncana havanensis petaloidea* (Gandolfi, 1955), apparently restricted to the upper Maestrichtian, represents the most pronounced development of petaloid chambers. It has an extremely lobate edge and four chambers in the final whorl. This form is placed in *P. havanensis* as a subspecies because of the intergradational sequence between the two. The maximum diameter of specimens is about 0.30 mm. Coiling is overwhelmingly dextral.

*Praeglobotruncana havanensis subpetaloidea* (Gandolfi, 1955), also restricted to the upper Maestrichtian, is almost identical with *P. havanensis petaloidea*. It seems to be merely a more irregular form with somewhat more rugose ornamentation. It coils dextrally and has a

maximum diameter of about 0.30 mm. These two subspecies (*petaloidea* and *subpetaloidea*) show a degeneration or elimination of the imperforate band and slight keel of *P. havanensis havanensis*.

The *P. havanensis* group is illustrated in text-figure 10 for ease of comparison with typical forms of *Rugoglobigerina*.

#### *Globotruncana*

*Globotruncana*, the most characteristic planktonic foraminiferal index of the Upper Cretaceous, spanning the interval from 90 million to about 63 million years before the present, was derived from the *Rotalipora appenninica* group near the end of the Cenomanian or the beginning of the Turonian (see text-figure 8).

*Globotruncana schneegansi* Sigal, Turonian and Coniacian, is the earliest representative of the genus. It is a primitive globotruncanid with a form similar to that of members of the *Rotalipora appenninica* group, but it lacks the secondary apertures along the sutures on the umbilical slopes. *G. schneegansi* has only a single keel, and the umbilical tegilla are not well defined. These features are to be expected in a primitive form transitional between *Rotalipora* and *Globotruncana*. Takayanagi (1965) discussed the characteristics of this species at length. He placed it in *Globotruncana*, and his usage is followed in this study. The coiling is mostly dextral. The maximum diameter noted is about 0.60 mm.

*Globotruncana renzi renzi* Gandolfi, Turonian to Santonian or possibly Campanian in range, has about 5 chambers in the final whorl. It was derived from *G. schneegansi*. It is biconvex and has two keels which are spaced close together in the early part of the last whorl and merge to become a single keel in the last chamber. The sutures are granular, but otherwise the surface is mostly smooth. Coiling is mostly dextral in all observed populations. The maximum diameter is about 0.60 mm.

*Globotruncana renzi angusticarinata* Gandolfi, ranging from the Turonian to the Santonian or possibly to the Campanian, differs from *G. renzi renzi* primarily in having about 7 chambers in the final whorl. The double keel is very closely spaced and usually does not become fused into a single keel excepting in the last chamber. It is derived from *G. renzi* or perhaps directly from *G. schneegansi*. Coiling is mostly dextral. The maximum diameter is about 0.60 mm.

*Globotruncana linneiana coronata* Bolli, 1945, one of the subspecies of the important two-keeled *linneiana* group, appeared in the Turonian and disappeared in the Campanian. It is a large form (in which the maximum diameter may be as much as 0.70 mm.) with a very low spire, compressed, and typically with about 7 or 8 chambers in the final whorl. The sutures are granular or papillate, and the coiling is dominantly dextral. This subspecies was derived either from *G. renzi angusticarinata* or directly from *G. linneiana linneiana*.

*Globotruncana linneiana linneiana* (d'Orbigny), ranging from the Turonian to the Maestrichtian, is considered to be conspecific with *G. lapparenti* Brotzen in this study (see discussion by Takayanagi, 1965, p. 217). It was probably derived from *G. renzi* stock directly. There are usually about 5 or 6 chambers in the final whorl, and the test is thicker than in *G. linneiana coronata*. The sutures are granular or papillate, and the coiling is characteristically dextral. The maximum diameter is about 0.60 mm., but many specimens are less than 0.50 mm. in diameter.

*Globotruncana linneiana tricarinata* (Quereau), ranging from the Turonian to the Maestrichtian, was derived from *G. linneiana linneiana* by the development of chambers inflated on the ventral side and a periumbilical keel. Otherwise, this subspecies is similar to *G. linneiana linneiana*. Coiling is characteristically dextral. The maximum diameter is about 0.66 mm.

*Globotruncana linneiana bulloides* Vogler, ranging from the upper Turonian to the Maestrichtian, was derived from *G. linneiana linneiana* by the development of inflated chambers. The raised horseshoe-shaped sutures of the ventral side serve to separate this subspecies from *G. marginata*, which has essentially radial sutures ventrally. This is another dextrally coiled form. The maximum diameter noted is 0.55 mm.

*Globotruncana marginata marginata* (Reuss) (text-figure 9), ranging from the Turonian to the Campanian-Maestrichtian boundary and probably into the lower part of the Maestrichtian, is an important double-keeled globotruncanid subspecies of the Upper Cretaceous. It arose from *G. schneegansi* stock in the lowermost Turonian, parallel with the rise of the *G. renzi*-*G. angusticarinata*-*G. linneiana* lineage. The latter developed characteristic horseshoe-shaped ventral sutures and retained them throughout the development of the group. The *G. marginata* group developed a double keel and retained the nearly straight radial ventral sutures of *G. schneegansi*. *G. marginata marginata* gave rise to an irregular variation, *G. marginata imbricata* Mornod, that may be restricted to the Turonian-Coniacian (Takayanagi, 1965). Another derivative is *G. marginata subcircumnodifer* (Gandolfi), which may be a Campanian index. Coiling in *G. marginata marginata* is essentially dextral. The maximum diameter noted is about 0.45 mm. It should be added that *G. marginata canaliculata* (Reuss) is closely related to the typical *G. marginata*, having one or two more chambers per whorl and the typical straight radial ventral sutures. This form is no more than a subspecies of *G. marginata* and appears to occur throughout the Senonian. However, its confusion with *G. linneiana* in the past renders the reported ranges of little value.

*Globotruncana intermedia* Bolli, restricted to the Maestrichtian (text-figure 9), arose from *G. marginata* stock by the development of a slightly convex test, more compressed than that of *G. marginata*, and with the keels

somewhat closer together. It is dextral in coiling, the umbilicus is small, and the maximum diameter is about 0.6 mm. Bolli (1951b) preferred a derivation from *Praeglobotruncana havanensis* (= *G. citae*), representing *G. intermedia* as an intermediate form between *G. havanensis* and *G. mayaroensis*. For this reason, Berggren (1962a) placed these species (*havanensis*, *intermedia* and *mayaroensis*) in *Praeglobotruncana*. At this time, it would appear that the transition from *marginata* to *intermedia* to *mayaroensis* is to be favored (text-figure 9).

*Globotruncana mayaroensis* Bolli, identified with the upper Maestrichtian (text-figure 9), is one of the most characteristic planktonic foraminifera of the latest Cretaceous. This species represents the trend toward a smaller umbilicus among the globotruncanids, also seen in incipient form in *G. marginata* in many cases (see Takayanagi, 1965; Edgell, 1957). The coiling is mostly dextral. The diameters noted are between 0.6 and 0.8 mm.

*Globotruncana arca* (Cushman), arising near the Turonian-Coniacian boundary or slightly earlier (Klaus, 1960; van Hinte, 1963), is characteristically biconvex and has rather horseshoe-shaped ventral sutures which show its derivation from *Globotruncana linneiana tricarinata* (text-figure 9). It appears to be right-coiling throughout its range of occurrence. In this study it is considered to have arisen from the *tricarinata* stock very early in the Coniacian or in the latest Turonian. In California it has been reported in the Santonian and Campanian by Takayanagi (1965), in the Campanian by Bandy (1951), and in the basal Maestrichtian by Martin (1964). The maximum diameter noted is about 0.55 mm.

*Globotruncana fornicata* Plummer, ranging from the Coniacian to the end of the Maestrichtian (text-figure 9), was derived from *G. arca* by the development of a concavity in the central area of the dorsal side of each of the last three or four chambers, a feature leading toward the *caliciformis-contusa* group. There are still traces of a horseshoe shape of the ventral sutures, although this characteristic is not as marked in some individuals as in others. The ventral side tends to become concave. In peripheral view, the double keels on the edge are oblique to the plane of coiling. The coiling is mostly dextral and the maximum diameter is about 0.55 mm.

*Globotruncana contusa caliciformis* (de Lapparent), ranging from the upper Campanian through the Maestrichtian (text-figure 9), developed from *G. fornicata* by becoming slightly more convex dorsally and flat to slightly convex ventrally, and also by a weakening of the lower of the two keels, which may disappear in the last chamber or two. Vogler (1941) figured a typical specimen of *G. contusa contusa* (Cushman, 1926) (described by Cushman on p. 23), using the name *G. linnei caliciformis*. Herm (1962) figured forms similar to the subspecies *caliciformis* under the name of *contusa* and erected new subspecific names for the high-crowned forms similar to the holotype of *contusa*. The low-crowned subspecies

*caliciformis* is longer ranging than the high-crowned typical *contusa* (text-figure 9). The coiling is almost entirely dextral. The diameters noted are between 0.45 and 0.75 mm.

*Globotruncana contusa contusa* (Cushman) was described by Cushman (1926, p. 23) as a variety of *G. arca*. It is restricted to the Maestrichtian and to the upper Maestrichtian for the most part (text-figure 9). It is derived from the *fornicata-caliciformis* trend and forms a highly complicated (specialized?) end product. The coiling is mostly dextral, and the diameters noted are between 0.50 and 0.90 mm.

*Globotruncana ventricosa* White, ranging from the Coniacian into the Maestrichtian, is a derivative of *G. linneiana tricarinata* (text-figure 9). The primary change was that of the peripheral keels drawing closer together, while the ventral chamber surfaces remained inflated. Populations are essentially all dextrally coiled. The diameters noted are about 0.60 to 0.75 mm.

*Globotruncana duwi* Nakkady (introduced as *G. aegyptica* subsp. *duwi* Nakkady, 1950) is an earlier name for the same form described later as *G. gagnebini* Tilev (1952). The stratigraphic range appears to be restricted to the upper Maestrichtian and possibly the upper part of the lower Maestrichtian (text-figure 9). The species is characterized by two closely spaced keels, as in *G. ventricosa*, which may be reduced to one keel in the final chamber. The chamber number is reduced to about 4 or 5 in the final whorl, the surface is nearly smooth to somewhat beaded in topotype specimens, and the sutures are beaded. Coiling is predominantly dextral. The maximum diameter noted is about 0.50 mm.

*Globotruncana concavata* (Brotzen), in a restricted sense ranging from upper Coniacian to lower Santonian (text-figure 9), was derived from *G. ventricosa* White by developing a flat to concave spiral side with the two keels becoming spaced very close together at the periphery of this flattened surface. The ventral sides of the chambers are more inflated and rounded than in *G. ventricosa*. Populations are mostly dextral. The maximum diameter is about 0.70 mm.

*Globotruncana rosetta rosetta* (Carsey), ranging from the Campanian to the end of the Maestrichtian (text-figure 9), was derived from *G. ventricosa* by the elimination of one of the two keels, excepting for faint traces of a small second keel in the earlier portion of the final whorl of occasional specimens, and by the flattening of the dorsal or spiral side. The holotype of Carsey has a single keel and the population of type material contains many other similar forms. *G. ventricosa*, which also occurs in the type material, has been confused with *G. rosetta* by Olsson (1964), van Hinte (1963), and others. In some populations there is considerable variation from a smooth to a somewhat papillate surface, the latter perhaps characterizing a different subspecies. Populations are mostly dextral in coiling. Diameters are between 0.50 and 0.60 mm.

*Globotruncana calcarata* Cushman, restricted to the uppermost Campanian (text-figure 9), is of the *G. rosetta* group but differs from *G. rosetta* in having tubulospines on the periphery and coarse spines on the ventral surface. This species is considered to be a highly specialized offshoot of *G. rosetta*. Coiling is entirely dextral, so far as now known. Diameters noted are between about 0.40 and 0.60 mm. Specimens of this form occur in the upper part of the Holz Shale of southern California.

*Globotruncana stuarti stuarti* (de Lapparent), ranging from the upper Campanian to the top of the Maestrichtian (text-figure 9), is a biconvex form with about 5 or 6 chambers which is otherwise rather similar to *G. rosetta*. It arose either from *G. rosetta* or directly from the *G. ventricosa* stock, probably the latter in view of the almost simultaneous appearance of both forms. It varies from almost smooth to slightly papillate. The coiling is dextral and the maximum diameter is about 0.70 mm.

*Globotruncana stuarti conica* White, with about the same range as *G. stuarti stuarti* (upper Campanian and Maestrichtian), is like *G. stuarti stuarti* except that it has 8 chambers in the final whorl and may become somewhat less convex ventrally. Coiling is dextral, and the maximum diameter noted is about 0.6 mm.

*Globotruncana gansseri* Bolli (text-figure 9), mostly upper Maestrichtian in occurrence, was derived from *G. rosetta* stock by the development of chambers strongly inflated on the ventral side. This widely distributed species is reported in Australia (Edgell, 1957, pl. 2, figs. 7-9). However, many reports of this species, such as those of Brönnimann and Brown (1955), and Olsson (1964), show a form which is within the *rosetta* group but lacks the ventrally highly inflated chambers of *G. gansseri*. *G. gansseri* typically has a strongly papillate ventral surface and a nearly smooth dorsal surface. The *G. rosetta* group includes variations from smooth to rather papillate forms to which a number of different specific names have been given.

Proper statistical variation studies of the species groups of *Globotruncana* are needed. It may be possible that the development of spinosity on the surface of some planktonic species is an ecophenotypic phenomenon, dependent upon depth-temperature-oxygen relationships or upon the level of carbonate saturation in the particular marine waters of each slightly different variant.

#### Rugoglobigerina

*Rugoglobigerina cretacea* (d'Orbigny), originally described as *Globigerina cretacea*, ranges from the lowermost Turonian to the Campanian-Maestrichtian boundary or just above (text-figure 10). The two very faint lines along the periphery are like keels, although they are only very slightly developed in most specimens. This, together with an umbilical covering structure composed

of tegilla, has led a number of investigators (Banner and Blow, 1960; Takayanagi, 1965) to refer this species to *Globotruncana*. It is here suggested that the thinner wall structure, rugose surface, character of the umbilical plate, aperture, shape of the chambers, and geologic range combine to indicate a stronger affinity with *Rugoglobigerina* than with *Globotruncana*. There are a number of ways in which this species might have arisen. It might have arisen from other rugoglobigerines, but its first appearance far precedes those of the other species. It might have arisen from *Globotruncana linneiana bulboides*; however, *cretacea* arose as early or before the first occurrences of that species, the wall of *cretacea* is considerably thinner, and its surface is rugose or spinose rather than smooth. It might have arisen from *Praeglobotruncana delrioensis*, but this species shows a strong tendency to develop an angled edge which would lead to more of a keeled form. The origin favored here is the *Hedbergella trocoidea* stock by the development of a larger umbilicus covered with tegilla and the appearance of two faint peripheral keels. *H. trocoidea* shows a tendency to expand its portici which could lead to the development of tegilla to form a cover plate, and this species overlaps the range of *R. cretacea* in the Turonian. *Rugoglobigerina cretacea* (d'Orbigny, 1840) is a senior synonym of "*Globotruncana*" *globigerinoides* Brotzen, 1936. In this interpretation, the development of faint keels is an example of parallelism to the development of keels in globotruncanids. Populations show mostly dextral coiling. The maximum diameter is about 0.50 mm.

*R. bulbosa* Belford, 1960, in the Santonian and *R. kingi* Trujillo, 1960, from the upper Coniacian might be regarded as primitive offshoots of *R. cretacea*. Takayanagi (1965) reported these species together with *R. rugosa* in the lower Senonian and upper Turonian of California. However, his figures do not show the umbilical structure of *Rugoglobigerina*. Instead, they show the restricted umbilicus and interiomarginal umbilical to extraumbilical apertures which are characteristic of *Hedbergella*.

*Rugoglobigerina rugosa subrugosa* (Gandolfi, 1955), originally described as *Globotruncana* (*Rugoglobigerina*), is intermediate between *R. cretacea* and *R. rugosa ordinaria* (Subbotina, 1953). It has only very weakly developed keels together with meridionally arranged coarse spines, pustules and rugosities. It appears to have evolved from *R. cretacea* in the latest Santonian or earliest Campanian by the development of more rugose ornamentation with a tendency toward meridionally arranged papillae and spines, and by showing a more rapid increase in chamber size. Populations are mostly dextrally coiled. The maximum diameter noted is about 0.50 mm.

*Rugoglobigerina rugosa ordinaria* (Subbotina, 1953), described originally as *Rotundina*, was derived directly from *R. cretacea* by the development of more rugose ornamentation with a tendency to show some meridionally arranged papillae and spines, while retaining

about the same number and size of chambers in the final whorl. Berggren (1962a) placed this subspecies in synonymy with *R. rugosa rugosa*. However, there is no striking development of meridionally arranged ornamentation in the specimens illustrated by Subbotina, and there is a very faint suggestion of peripheral keels in a few cases in both the original illustrations and in populations studied by the writer. This subspecies appears to have arisen in the earliest Campanian, and it became extinct in about the middle of the Maestrichtian. Populations are dextrally coiled, for the most part, and the maximum diameter noted is about 0.60 mm.

*Rugoglobigerina rugosa pennyi* Brönnimann, 1952, apparently confined to the upper part of the Maestrichtian, was derived from *R. rugosa ordinaria* by the development of a flattened dorsal side, closely appressed chambers, and more striking meridional ornamentation. Populations are dextrally coiled, and the maximum diameter is about 0.38 mm.

*Rugoglobigerina rugosa rotundata* Brönnimann, 1952, restricted to the upper Maestrichtian, appears to have been derived from *R. rugosa ordinaria* stock within the Maestrichtian by becoming high-spired with a dorsal-ventral elongation of chambers and by the development of meridional ornamentation. Populations are dextrally coiled, and the maximum diameter is about 0.30 mm.

*Rugoglobigerina rugosa rugosa* (Plummer), ranging from the upper Campanian to the top of the Maestrichtian, has 5 or 6 globular chambers with meridionally arranged spines, papillae and rugosities. This typical subspecies was probably derived from *R. rugosa ordinaria* by the development of prominent radially oriented ornamentation. Populations are dextrally coiled, and the maximum diameter is about 0.45 mm.

*Rugoglobigerina rugosa macrocephala* Brönnimann, 1952, mostly upper Maestrichtian in occurrence, appears to have been derived from *R. rugosa rugosa* by a more rapid size increase of the chambers and a decrease to about four chambers in the final whorl instead of the five or six in the typical *R. rugosa rugosa*. This tendency resulted in the very large size of the ultimate chamber. Surface ornamentation is generally not as well developed in this subspecies as in the typical subspecies, but there is a patent intergradation between the two. Populations are dextrally coiled, and diameters are between 0.35 and 0.45 mm.

*Rugoglobigerina rugosa pustulata* Brönnimann, 1952, restricted to the middle and upper portions of the Maestrichtian, was derived from *R. rugosa rugosa* by the development of very globular chambers and a nearly planispiral test. Populations coil dextrally, and diameters are about 0.35 to 0.45 mm.

*Rugoglobigerina scotti* (Brönnimann, 1952), upper Maestrichtian in range, was derived from *R. rugosa pustulata* by the development of somewhat compressed chambers

and an imperforate peripheral band that may become a keel in the last chamber or two, especially in the uppermost part of the Maestrichtian. Although this species is the type of the genus *Trinitella* Brönnimann, 1952, it is not generically distinct and should be included in *Rugoglobigerina*. Populations coil dextrally, and the maximum diameter is about 0.40 mm.

*Plummerita hantkeninoides* (Brönnimann, 1952), upper Maestrichtian in range, developed more closely appressed chambers and peripheral spinelike chamber extensions. This species, the type of *Plummerita* Brönnimann, 1952, shows intergradations from chambers with rounded peripheral angles to those with spine-like extensions. Populations appear to be dextrally coiled, and the maximum diameter is about 0.30 mm., perhaps more.

#### Heterohelix and some related genera

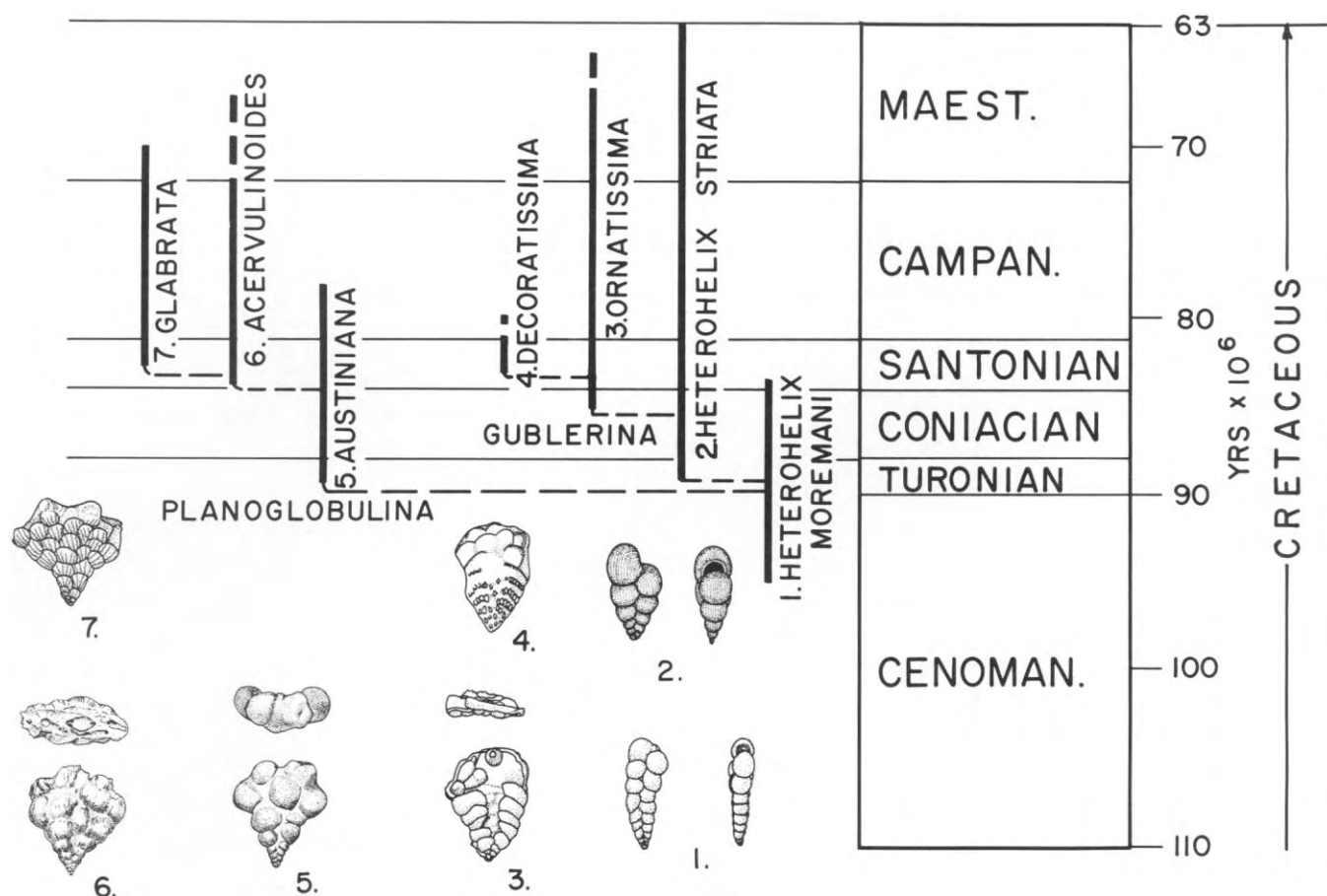
Studies of the Heterohelidae (text-figures 11 and 12) in recent years have clarified possible phylogenetic relationships of the genera of this family. These studies include those of Loeblich (1951), Brönnimann and Brown (1953), Montanaro Gallitelli (1957), and Loeblich and Tappan (1964).

*Heterohelix*, as at present understood, may either be completely biserial or have a very small early planispiral stage followed by a biserial chamber arrangement. One of the oldest significant species of *Heterohelix* is *H. washitensis* (Tappan, 1940), which appears to range from about Aptian to Cenomanian. It has a maximum length of about 0.21 mm., differing from *H. globulosa* of the Upper Cretaceous in being about half as long and much thinner. It is ancestral to other species of *Heterohelix*, and it probably gave rise to *Guembelitra harrisi* Tappan and to *Guembelitriella graysonensis* Tappan, with which it is associated. *Guembelitriella graysonensis* and *Guembelitra harrisi* intergrade and may well belong to the same species. *Heterohelix washitensis* may contain individuals that have an early planispiral stage, but this possibility has not been properly confirmed.

*Heterohelix moremani* (Cushman), ranging from Cenomanian to Coniacian or later, is apparently a distinct species derived from *H. washitensis*. It may be possible that the two are dimorphic forms of the same species, but *H. washitensis* extends back farther in geologic time, and it is probably the small ancestral form which gave rise to *H. moremani* and the later species of *Heterohelix*. *H. moremani* has a maximum length of about 0.45 mm. It is slender with globular chambers that are often slightly irregular.

*Heterohelix reussi* (Cushman), ranging from Coniacian to Campanian, was probably derived from one of the variants of *H. moremani* or *H. globulosa* in the latest Turonian or earliest Coniacian. It should be noted that populations of *H. moremani* contain forms which are not quite as slender as the holotype, and it is thought that these variants represent the ancestral stock of *Heterohelix reussi* and *H. globulosa*. *H. reussi* has

# FORAMINIFERAL ZONATION



TEXT-FIGURE 11

Phylogeny of *Heterohelix* and some related genera.

a tapered test, and the chambers are globular with little tendency to overlap each other. The maximum length noted is about 0.50 mm.

*Heterohelix globocarinata* (Cushman), Santonian to lower Maestrichtian, is slightly carinate in the early portion and has rapidly expanding later chambers which are finely striate. The maximum length noted is about 0.50 mm.

*Heterohelix punctulata* (Cushman), Campanian to Maestrichtian in range, is longitudinally striate or costate in the early portion and punctate in the later portion. The early chambers expand rapidly in diameter, whereas the later chambers expand slowly. The maximum length of specimens is about 0.55 mm.

*Heterohelix globulosa* (Ehrenberg), ranging from the Turonian to the top of the Maestrichtian or above, was derived from *H. moremani* by the development of somewhat more rapidly expanding globular chambers. It is not as thick a species as *H. reussi*, often being comparatively thin. The maximum length of specimens of *H. globulosa* is about 0.50 mm. It is possible

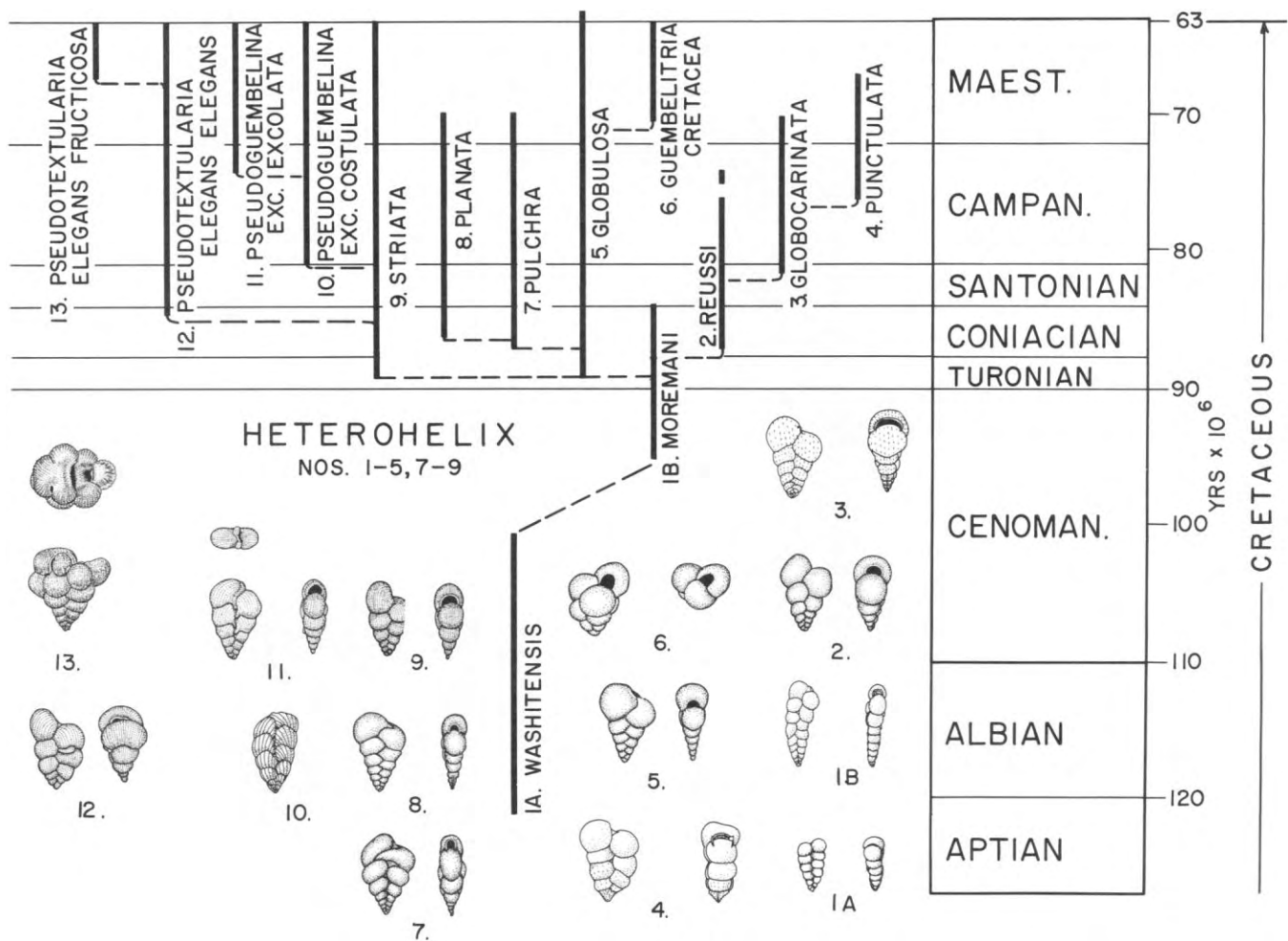
that *H. globulosa* and *H. reussi* may represent dimorphic forms of the same species.

*Guembelitria cretacea* Cushman, Maestrichtian in age, is probably a triserial derivative of *Heterohelix globulosa*. It is a smooth species and represents a second appearance of the triserial genus *Guembelitria*, the previous appearance being that of *G. harrisi* Tappan in the Albian. The maximum length noted is about 0.20 mm.

*Heterohelix pulchra* (Brotzen, 1936), Coniacian to Maestrichtian, was derived from *H. globulosa* by developing a compressed test with broad chambers and curved sutures in the last portion. The maximum length noted is about 0.50 mm.

*Heterohelix planata* (Cushman), apparently ranging from the Coniacian to the Maestrichtian, was derived from *H. pulchra* by developing fine perforations in longitudinal lines and, usually, a slight keel in the earliest part of the test. The maximum length is 0.45 mm.

*Heterohelix striata* (Ehrenberg), ranging from Turonian to Maestrichtian, was derived from *H. globulosa* by the addition of very fine striae on the surface. The maxi-



TEXT-FIGURE 12

Phylogeny of Gublerina and Planoglobulina.

imum length noted is about 0.60 mm., although lengths of about 0.40 mm. are more common. This species occasionally shows accessory lateral apertures at the base of the last chamber, but these are uncommon and occur on rare occasions in various other species of *Heterohelix*. Thus, *striata* is not transferred to *Pseudoguembelina* but is retained in *Heterohelix*, following Montanaro Gallitelli (1957) and Takayanagi (1965).

*Pseudoguembelina excolata costulata* (Cushman), apparently ranging at least from basal Campanian beds to the upper limit of the Maestrichtian, was derived from *Heterohelix striata* by the development of compressed chambers, secondary apertures at the basal margin of the later chambers, and longitudinal costae. The maximum length of this species is about 0.30 mm. Brönnimann and Brown (1953) erected the genus *Pseudoguembelina*.

*Pseudoguembelina excolata excolata* (Cushman), ranging from the upper part of the Campanian to the upper limit of the Maestrichtian, was derived from *P. excolata*

*costulata* by a simple size increase. Thus, both of these forms are considered to be subspecies within one species. They are recognized as subspecies because of the apparent stratigraphic implications, the larger form commencing later in time. The maximum length noted is about 0.50 mm.

*Pseudotextularia elegans elegans* (Rzehak), ranging from the uppermost Coniacian to the Maestrichtian, was derived from *Heterohelix striata* stock in the Coniacian by the development of cuneiform chambers with an inversion of the proportion of breadth to thickness, and a very broad aperture at the base of the last septal face. Montanaro Gallitelli (1957) discussed this genus in detail, comparing it with other closely related forms. Some specimens show the addition of aberrant chambers. The maximum length of the specimens noted is about 0.65 mm., but the true maximum length may possibly be much more.

*Pseudotextularia elegans fructicosa* (Egger), identified with the upper Maestrichtian, is an outgrowth of *P. elegans*

*elegans* by the proliferation of chambers at the summit of an otherwise biserial or planispiral to biserial test. This proliferation of chambers at the summit of the test is an incipient phenomenon in *P. elegans elegans* and a pronounced development in *P. elegans fructicosa*. The length of the specimens noted is in some cases nearly 1.50 mm. Populations of *P. elegans fructicosa* show variations from typical forms of *P. elegans elegans* to forms with proliferated chambers. The genus *Racemiguembelina* Montanaro Gallitelli, 1957, erected for the forms with proliferated chambers, is considered to be synonymous with *Pseudotextularia* Rzehak, 1891, in this study.

#### Gublerina and Planoglobulina

*Gublerina ornatissima* (Cushman and Church), ranging from Coniacian to Maestrichtian in California (text-figure 12), is restricted to the Maestrichtian in many other parts of the world (Takayanagi, 1965). Montanaro Gallitelli (1957) discussed the relationships of *Gublerina* at some length, clarifying much of the taxonomic confusion regarding this genus. *G. ornatissima* arose from *Heterohelix striata* stock in the latest Coniacian or earlier, retaining the planispiral to biserial chamber arrangement and the variable longitudinal striae and costae. It developed beyond *H. striata* by the addition of papillae or granules along the sutures, by the divergence of the later chambers, leaving a central cavity between these chambers, and thus by the production of a rather triangular test in side view. The maximum length of the specimens noted is about 0.65 mm., perhaps more. Many specimens in California are less than 0.50 mm. long, due in part to the breaking off of the last chamber or two in most cases.

*Gublerina decoratissima* (de Klsasz), Santonian and basal Campanian in distribution, was derived from *G. ornatissima* by the development of strongly granulated and raised sutures. It may be merely a variant or subspecies of *G. ornatissima*.

*Planoglobulina austiniana* (Cushman), apparently restricted to the Turonian - Campanian interval, was probably derived directly from *Heterohelix moremani* stock in the earlier Turonian. The characteristic early biserial stage is followed by a proliferated series of globular chambers spread out in the plane of biseriality so as to give a flabelliform shape to the test. This primitive species has a smooth wall and depressed sutures. The maximum length noted is about 0.55 mm.

*Planoglobulina acervulinoides acervulinoides* (Egger), ranging from the Santonian to well up in the Maestrichtian, was derived from *P. austiniana* by the development of longitudinal striae or costae. The maximum length of the specimens is about 0.75 mm.

*Planoglobulina acervulinoides glabrata* (Cushman), with about the same general geologic range as *P. acervulinoides acervulinoides* (Santonian-Maestrichtian), shows a degeneration of the striae or costae in the adult portion of the test or in the last chambers that are added. The maximum length of the specimens is about 0.60 mm.

#### DISCUSSION AND CONCLUSIONS

It is apparent, in terms of modern geochronometry, that the evolution of primitive globigerinids, ancestral to keeled planktonic genera, required about one third of the Cretaceous Period (Neocomian, Aptian and Albian). Furthermore, it is important to note that the development of the *Rotalipora* faunas spanned about 20 million years or almost a third of the Cretaceous (Cenomanian), and that the *Globotruncana* faunas developed and diversified in the final third of the Cretaceous (Turonian to Maestrichtian). Thus, it is suggested that, on the basis of foraminiferal evolution, a threefold division of the Cretaceous Period is logical.

Environmental analyses of modern planktonic faunas indicate by analogy that the most dependable stratigraphic zonation is that established between the equator and the *Globotruncana-Rotalipora* lines, representing the northern and southern limits of diversified and dependable indices. However, zonation appears to degenerate over a considerable distance, the degeneration affecting some species groups more severely than others. It is important to recognize that the best zonation will be developed in deep-water sediment sequences which were deposited in waters with rather stable normal salinity values between 34 and 37 parts per thousand. Currents and the divergences and convergences between water masses probably contributed materially to variations of planktonic abundances and to changes in coiling directions of populations during the Cretaceous much as at present. This would not refer to the decided predominance of dextral coiling among most species of *Rotalipora* and *Globotruncana*, a development that was undoubtedly evolutionary. It would refer to other species or to those that have both dextral and sinistral populations.

If one compares the suggested Cretaceous zonations in California of Takayanagi (1965), Martin (1964) and Trujillo (1960) with those of Bolli (1951*b*, 1957*a*, 1959), Barr (1962), Klaus (1960), Sigal (1952), Dalbiez (1955), Edgell (1957), and many others, it is plain that the concept of concurrent range zones has been difficult to apply from region to region and even within local basins. For example, Bolli (1959) erected a *Globotruncana fornicata* zone for the upper part of the Santonian, whereas Takayanagi (1965) erected a *Globotruncana fornicata*/*Globotruncana coronata* zone for the upper Turonian. In another paper of Bolli (1957*a*), *G. fornicata* was interpreted as ranging from the bottom of the Santonian to the lower part of the Maestrichtian; in the study of Takayanagi (1965), *G. fornicata* and *G. coronata* were recognized as ranging from the upper Turonian to the upper limits of the Coniacian. The ranges given for *Globotruncana arca* show equally great discrepancies. Thus, the species selected are not significant indices of the zones indicated in other sections of the same basins studied, nor of the indicated zones in other regions of the world. The zonal definition must be defined by elaborating upon overlapping ranges and other zonal indices. Much of this kind of

TABLE 1

## CRETACEOUS PLANKTONIC FORAMINIFERAL ZONATION

EPOCHS	Dominant Group	STAGES	ZONES
LATE CRETACEOUS (27 million years duration)	GLOBOTRUNCANA	Maestrichtian	1. <i>Globotruncana mayaroensis</i> - <i>G. gansseri</i> Zone 2. <i>Globotruncana ventricosa</i> - <i>Guembelitria cretacea</i> Zone
		Campanian	3. <i>Globotruncana calcarata</i> - <i>G. rosetta</i> Zone 4. <i>Praeglobotruncana inornata</i> - <i>Rugoglobigerina rugosa subrugosa</i> Zone
		Santonian	5. <i>Globotruncana renzi</i> - <i>Gublerina ornatissima</i> - <i>Praeglobotruncana wilsoni</i> Zone
		Coniacian	6. <i>Globotruncana concavata</i> - <i>G. renzi</i> - <i>G. schneegansi</i> Zone
		Turonian	7. <i>Praeglobotruncana helvetica</i> Zone
MIDDLE CRETACEOUS (20 million years duration)	ROTALIPORA	Cenomanian	8. <i>Rotalipora appenninica appenninica</i> - <i>R. cushmani</i> - <i>R. reicheli</i> Zone 9. <i>Ticinella multiloculata</i> - <i>Rotalipora appenninica balernaensis</i> - <i>Planomalina buxtorfi</i> Zone
EARLY CRETACEOUS (25 million years duration)	PRIMITIVE PLANKTONICS	Albian	10. <i>Ticinella roberti</i> - <i>Planomalina buxtorfi</i> - <i>Globigerina washitensis</i> Zone 11. <i>Ticinella roberti</i> - <i>Globigerinelloides maridalensis</i> Zone
		Aptian	12. <i>Globigerinelloides algeriana</i> - <i>Globigerina kugleri</i> Zone
		Neocomian	Globigerines with first appearance of <i>G. kugleri</i> and <i>G. graysonensis</i>

(See text-figures 3-12 for illustrated ranges of these faunal indices and the supporting overlapping ranges of other species.)

background support is usually more readily ascertained by examination of the particular range charts of each author. Takayanagi (1965) provided an excellent comparison by showing the ranges in his section of northern California and the extension of these as reported by other workers.

In this report, an attempt has been made to provide the total geologic range or geochron of each of a number of the more important planktonic species from a phylogenetic approach. This was done with the full realization that in any particular basin there will not be the complete development of this zonation unless open oceanic deeper-water conditions prevailed throughout the Cretaceous and unless the location is between the equator and the *Globotruncana-Rotalipora* lines, thereby avoiding the latitude effect which would seriously affect the zonation. Thus, the zonation here suggested is based upon important species with overlapping geochron ranges together with more restricted short-ranging species.

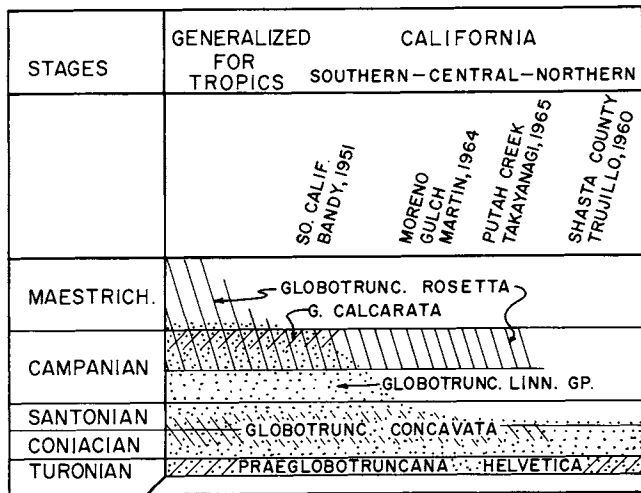
A zonation is proposed as indicated in Table 1. It is a zonation that should apply in typical tropical areas which have well-developed planktonic foraminiferal faunas throughout the Cretaceous. It is interesting to examine briefly the Cretaceous zonation in California with respect to the more general tropical zonation suggested in Table 1 and the ranges given in text-figures 3-12. Lower Cretaceous planktonic foraminifera of California are only now being studied in detail (Berry, 1965; Church, 1965), and globigerines have been found which suggest the *Globigerinelloides algeriana*-*Globigerina kugleri* zone, according to the oral reports presented by these and other workers.

Albian, Cenomanian and Turonian faunas are known in the Franciscan Formation of western California and have been studied by a number of workers, as reviewed in the extensive report by Bailey, Irwin and Jones (1964). *Rotalipora* faunas have been recorded from the Cenomanian, *Praeglobotruncana helvetica* has been noted in some limestone samples of Turonian age, and both have been observed by this writer in other samples. Trujillo (1960) reported on Upper Cretaceous foraminifera from the northern end of the Great Valley. In his study he found a rather typical Turonian fauna (*P. helvetica* Zone), but his Coniacian planktonic species are very long-ranging types when examined on a framework of total ranges.

A Coniacian fauna with *Globotruncana concavata* and *G. schneegansi* has been reported by Takayanagi (1965) to occur in the Putah Creek section on the western side of the Great Valley across from Sacramento. In his study there is not a good correlation of the post-Coniacian planktonic zones and ranges with those of tropical areas, since most of the species range up into the Maestrichtian in the tropical areas. Thus, the zonation is based upon teilchrons. A study by Martin (1964) of the Moreno Gulch section farther south along the western side of the southern Great Valley (San Joaquin Valley) showed much the same pattern, as Martin also reported mostly long-ranging forms of planktonic foraminifera.

It is interesting to note that in the area of the work of Takayanagi and Martin *Globotruncana linneiana linneiana* occurs only in the Coniacian and lower Santonian, whereas toward the tropics it is known to range from the Turonian to the Maestrichtian. Toward the tropics

# FORAMINIFERAL ZONATION



VARIATION OF GLOBOTRUNCANID RANGES WITH LATITUDE

TEXT-FIGURE 13

Time-transgressive nature of the *Globotruncana linneiana* and *G. rosetta* groups in relation to latitude. Note the more restricted occurrences of *G. calcarata*, *G. concavata* and *Praeglobotruncana helvetica*, which are therefore more dependable indices in tropical and temperate latitudes. The northern occurrence of *G. calcarata* is in the upper portion of the Holz Shale of Silverado Canyon, Santa Ana Mountains, southern California. *Globotruncana linneiana* is noted in the upper Campanian report of Bandy (1951) as *G. canaliculata*.

it occurs together with variations of *Globotruncana rosetta*, as in San Diego County, southern California (Bandy, 1951). Martin reported *G. rosetta* in the Campanian of Moreno Gulch, and a variation of the same species, *G. putahensis* Takayanagi, was reported in the Campanian of Putah Creek in the northern part of the Great Valley. A *Globotruncana calcarata* fauna, collected by the writer, occurs in the upper part of the Holz Shale at Silverado Canyon in the Santa Ana Mountains of southern California. This is evidence which would indicate that the upper boundary of this formation is near the upper boundary of the Campanian rather than within the middle of the Campanian, as reported by Popenoe, Imlay and Murphy (1960). Thus, it is rather clear that *Praeglobotruncana helvetica*, *Globotruncana concavata*, *G. rosetta* and *G. calcarata* are rather good zonal indices. It is equally clear that subspecies of *Globotruncana linneiana* demonstrate a remarkable wedge-shaped attenuation northward into northern California, being restricted there to the Coniacian and lower Santonian (text-figure 13). In principle, the stratigraphically long-ranging species of tropical areas are erratic and undependable zonal indices where they occur in temperate areas in restricted zones (teichrons), while the short-ranging or stratigraphically restricted species of tropical areas are dependable stratigraphic indices where they occur in temperate areas.

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