

A Monographic Study and Atlas of Late
Cretaceous Planktic Foraminifera,
Part I

A Monographic Study and Atlas of Late Cretaceous Planktic Foraminifera, Part I:

Globotruncanids

By

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PREFACE

Globotruncanids are some of the most useful representatives of the foraminiferal group in the stratigraphy of the sediments and rocks of Late Cretaceous age accumulated in seas and oceans from the middle shelf to the abyssal plain. Their importance in economic studies is paralleled in the Late Cretaceous times only by the large-sized benthics with complex internal structures found in the shallow water paleoenvironments of warm climates, and to a lesser extent by the agglutinant benthics in deep oceanic conditions below lysocline. The high accuracy of the group in sediment dating and paleobathymetry estimations make the globotruncanids one of the most important foraminiferal groups in studies related to sequence stratigraphy on the middle and outer shelf, rarely shallower. These show that the globotruncanid group is one of the most important amongst those used in the prospection and exploration for hydrocarbons and this is further supported by the fact that all the data they yield in biostratigraphy, paleobathymetry and sequence stratigraphy can be readily integrated into basin analysis.

Fundamental and applied foraminiferal studies require a reliable classification framework in order to provide accurate results and this is particularly important in the case of widely used fossil groups, globotruncanids amongst them. The accuracy is partly achieved through a continuous study of newly collected material and re-study of the older specimens kept in collections. In addition, the taxonomic principles are challenged when new data becomes available and the previously published data is revised; this ultimately results in a refinement of our knowledge and interpretation of the fossil and microfossil groups. Needless to mention, concepts and interpretations that are no longer supported by data are abandoned and replaced by others that provide a better interpretation of the natural reality. In short, this describes the common scientific practice that is thoroughly used in the study of globotruncanids.

A new review of the globotruncanid group is presented herein. Its goal is to provide a classification framework that can be successfully used in fundamental and applied studies. The conceptual fundamentals are represented by the considerable influx of new data pertaining to high-detail test architecture and ultrastructures from the last decade. It is a current in Cretaceous planktic foraminiferal studies that I call the “ultrastructure revolution”. In this new methodology, the scanning electron microscopy is a major provider of data through the investigation of each species throughout its stratigraphical range. As a result, a considerable advance in understanding the globotruncanid evolution could be realized, which would result in the realization of a necessary shift from the classical Linnaean classification towards a more elaborate evolutionary classification. An evolutionary classification framework is not developed herein partly because globotruncanids represent end members of the larger group of coiled planktic foraminifera and additional studies are necessary in order to recognize the evolution at the scale of this whole group. Therefore, an evolutionary classification will be developed in the future as a distinct work and after the entire group of the coiled planktics is revised in the light of the “ultrastructure revolution”.

Personally I hope the readers will understand that the evolution process as considered in this work is entirely Darwinian. I find it hard to understand why, but the history of publications on globotruncanids shows that evolution in a Darwinian sense was not completely accepted by some specialists in the field. I would like to conclude this preface by mentioning that the whole effort I put into the “ultrastructure revolution”, including the present work, is circumscribed to Darwinian evolution; it is the only way through which the study of the fossil record can advance as part of science.

Calgary, March 15, 2020

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INTRODUCTION

Foraminifera are heterotrophic protists that often protect the cytoplasm and nucleus (nuclei) with a protective structure of organic or mineral nature known as test. A small number of living species do not have a test and for this reason they do not occur in the fossil record. This protective structure with a diverse composition and mineralogy can be relatively easily fossilized. Organic tests are chitinous, pseudochitinous or proteinaceous, whereas the mineralized ones can consist of agglutinated particles or secreted calcite, aragonite, etc. The mineralized tests form the vast majority of the foraminifera that are encountered as fossils. Foraminiferal tests are in general of microscopical sizes, with an average dimension of 0.100–1.000 mm. Tests can consist of one chamber up to several hundred and the oldest foraminifera are single-chambered. Foraminifera occur abundantly in the modern seas and oceans, with only a smaller number of taxa encountered in fresh and brackish water conditions. An even smaller number is adapted for terrestrial environments in which there is only a certain amount of moisture. Marine foraminifera are adapted for benthic and planktic habitat, whereas the non-marine ones are entirely benthic.

The foraminiferal group, which is formalized in the Linnaean classification as class Foraminifera of the phylum Sarcodina, evolved early in the Phanerozoic and the earliest fossil taxon with evident foraminiferal test morphology is the *Leukatiella* that was described from rocks of the Early Cambrian (Tommotian) age from Russia. Throughout the Cambrian times the foraminifers present an agglutinated test that can be free or attached to the different particles or structures on the sea floor. The evolution of the attached mode of life represented only the beginning of a long and sophisticated process of diversification at first of the test architecture followed by the wall mineralogy. During the Paleozoic, the fossil record holds compelling evidence for the evolution of test with multichambered architecture and different patterns of chamber addition in the course of the life cycle of a foraminiferal individual. Wall mineralogy became more diverse with the evolution of completely organic and calcitic walls. Foraminifera remained benthics throughout the Paleozoic and this setting remained almost unchanged at the beginning of the Mesozoic. But in the Mesozoic times is recorded one of the most important achievements in the history of foraminifera: evolution of the planktic mode of life.

The timing of the beginning of the process of the planktic habitat evolution is in the late Triassic and starting in the late Early Jurassic times the planktic foraminifera became more frequent in the fossil record. The evolution of a planktic habitat evolved several times in the Mesozoic history of foraminifera and the newest data indicates that some species of the genera we traditionally considered benthics might have been in fact planktics. Cretaceous is the Mesozoic Period in which the planktic foraminifera diversified at a high rate and its record contrasts with the Late Triassic–Jurassic times when all the known taxa are globular-chambered. The diversification process is especially apparent in the Barremian–Maastrichtian interval and can be partly explained by the multiple originations of planktic taxa from benthic ancestors. A high rate of evolution, high diversity, high rate of dispersal and high frequency in the fossil record are all reasons why some of the representatives of the planktic foraminiferal group provide high-resolution data in Cretaceous biostratigraphy. Two iconic groups of planktics that were and still are extensively used in biostratigraphy are the rotaliporids of the upper Albian–Cenomanian stratigraphical interval and globotruncanids of the Turonian–Maastrichtian. Of them, the globotruncanids represent probably the epitome of the biostratigraphically significant Cretaceous foraminifera.

What are the globotruncanids? In the past and at the time when the Linnaean classification was the only methodology used for grouping taxa, there was in general an agreement amongst the specialists in the field that globotruncanids were planktic foraminifera with dorso-ventrally compressed chambers and one or two peripheral keels, but most of the species present two such structures. In the case of the species where only one keel occurs, the general test architecture is close to the double-keeled taxa. Additional studies showed that there are also globular-chambered taxa with double-keeled periphery. Furthermore, there were reported globular-chambered taxa that evolved only one peripheral keel resulting in tests that present strong resemblances with those of the globotruncanids. All these data come not only to demonstrate the group's morphological diversity, but at the same time they challenged our classical classification frameworks, which often took into consideration one or very few morphological characters in the definition of suprageneric units. As a result, the term globotruncanid could be used only in a general, informal sense, whereas in the formal classifications the taxa with globotruncanid aspect were included into different superfamilies.

The situation started to change with the development of the evolutionary classification in the globotruncanid group. The development of such high-resolution studies involved a different working methodology, in which the morphological data were collected through the extensive use of the scanning electron microscope throughout one species stratigraphical range. These data included high-detail morphological features of the test, including wall ultrastructure, ornamentation, porosity features and pore distribution pattern. By grouping species into lineages according with the demonstrated ancestor–descendant relationships as observed in the fossil record, it became possible to demonstrate that the group we informally call globotruncanids has multiple origins and the globotruncanid test architecture was achieved independently in several lineages. This perspective sharply contrasts with the previous concepts of globotruncanid evolution in which the group was considered as forming one single and unitary group that evolved in the Cenomanian.

Having new and more accurate data on the group evolution it became possible to recognize the globotruncanid test architecture as trochospiral Cretaceous planktics with truncated or rounded periphery and one or two peripheral keels. Six originations of lineages that evolved globotruncanid test architecture from non-globotruncanid ancestors are recognized herein. In some lineages the globotruncanid architecture was achieved in the terminal part, whereas the earlier species have non-globotruncanid architecture. In such cases, all the species are presented in this work, providing the most complete set of arguments in demonstrating the evolution of globotruncanid test morphology in the respective lineages. The considerable influx of high-resolution data generated during the development of evolutionary classification led to a major change in the presentation of globotruncanid classification. It is evident that the classical Linnaean classification can no longer provide species groupings that can accurately reflect the ancestor–descendant relationships. In these new conditions, the Linnaean classification must be changed to accommodate the new advances in recognizing the ancestor–descendant relationships between globotruncanid taxa, preparing the ground for a change of paradigm in species grouping.

LIST OF ABBREVIATIONS

DSDP	Deep Sea Drilling Project
HST	highstand systems tracts
LST	lowstand systems tracts
mbs	meters below surface
mbsf	meters below sea floor
ODP	Ocean Drilling Program
SEM	Scanning Electron Microscope and Scanning Electron Microscopy
TST	transgressive systems tracts

CHAPTER 1

MORPHOLOGY AND TERMINOLOGY

The globotruncanid test provides all the morphological features used in the group's classification. Therefore, a detailed presentation of these features is necessary. The importance of the test morphology and applied terminology has been recognized in every major work on globotruncanid taxonomy and classification (e.g., Pessagno 1967; Maslakova 1978; Robaszynski et al. 1979, 1984; Korchagin 2003, etc.). As a result, much of the terminology used in this work has its roots in that developed in the past. What differentiates the present terminology when compared with that used previously is the significant emphasis on the high-detail morphological features, wall ultrastructure and ornamentation, and porosity characteristics.

1.1 Test orientation and gross architecture

All globotruncanid planktic foraminifera have trochospirally coiled tests. Therefore, the terminology and test orientation is that applied to all foraminiferal tests with such a coiling mode (Fig. 1). The test side on which all the chambers are visible is referred to as spiral or dorsal. The opposite side on which only the chambers of the last-formed whorl and umbilicus are visible is referred to as ventral or umbilical. The lateral or edge view is perpendicular to the test periphery and has the aperture of the last-formed chamber visible; opposed to it is the antiapertural side. Lateral and antiapertural sides can be also referred to as lateral and antiapertural views respectively. All the other views of the test are termed oblique.

Proloculus is the first chamber of the test and occurs in the middle part of the spiral side. Chambers are added successively during the ontogenetic development and no taxa with more than one chamber added in a growth step are known. The successively added chambers form whorls. The last or final whorl occupies a peripheral position and consists of the last-formed chambers during ontogeny. All the other whorls between the proloculus and the last whorl are referred to as inner whorls. The terminology used for the inner whorls is according to their position with respect to the proloculus: first whorl, second whorl, etc. Chambers are counted and labelled wherever necessary from the proloculus and in the order of addition.

The junction line between two adjacent chambers is termed a suture. The term is used in the globotruncanid foraminifera mostly for the junction line between two chambers that are successively added during ontogeny, but this cannot be considered a rule. For example, the junction lines between the chambers of the last whorl and those from the inner whorls are also termed sutures. Sutures can be observed in every view of the test: dorsal, lateral, ventral and antiapertural. The sutures can be simple and depressed or lined with sutural ridges, in which case they have a raised, in-relief aspect.

The most apparent feature on the umbilical side is a central depression, which is termed an umbilicus. The aperture is that of the last-formed chamber, which occurs within the umbilicus and can extend outside the umbilical region over a short distance. The aperture is bordered by a calcitic plate, which is referred to as a periapertural structure. The apertures of the successive chambers can remain connected within the umbilical region. In well-preserved tests, where the delicate periapertural structures are fossilized, the umbilicus can be partly covered by the periapertural structures resulting in a closed aspect to this feature.

Edge views are paramount in evaluating the trochospire height. Other morphological features that are extensively used in the taxonomy and classification of groups are included in the more general category of peripheral structures (agglomerations of pustules, imperforated peripheral bands and keels).

Test growth axis is defined by the centers of the successively added chambers during the ontogenetic development; in all the globotruncanid taxa this feature is a three-dimensional coil. The growth direction is recognized by the position in which the new chambers are added: anterior direction is given by the free margin of the last-formed chamber and its intersection with the test growth axis, whereas the posterior direction is towards the proloculus and along the growth axis. Test coiling axis is the imaginary line that passes through the proloculus and the center of the umbilical region as defined after the test last chamber was added; it is the axis around which the three-dimensional coiling develops. The imaginary axis that passes through the center of one chamber's dorsal and ventral faces is referred to as chamber's dorso-ventral axis.

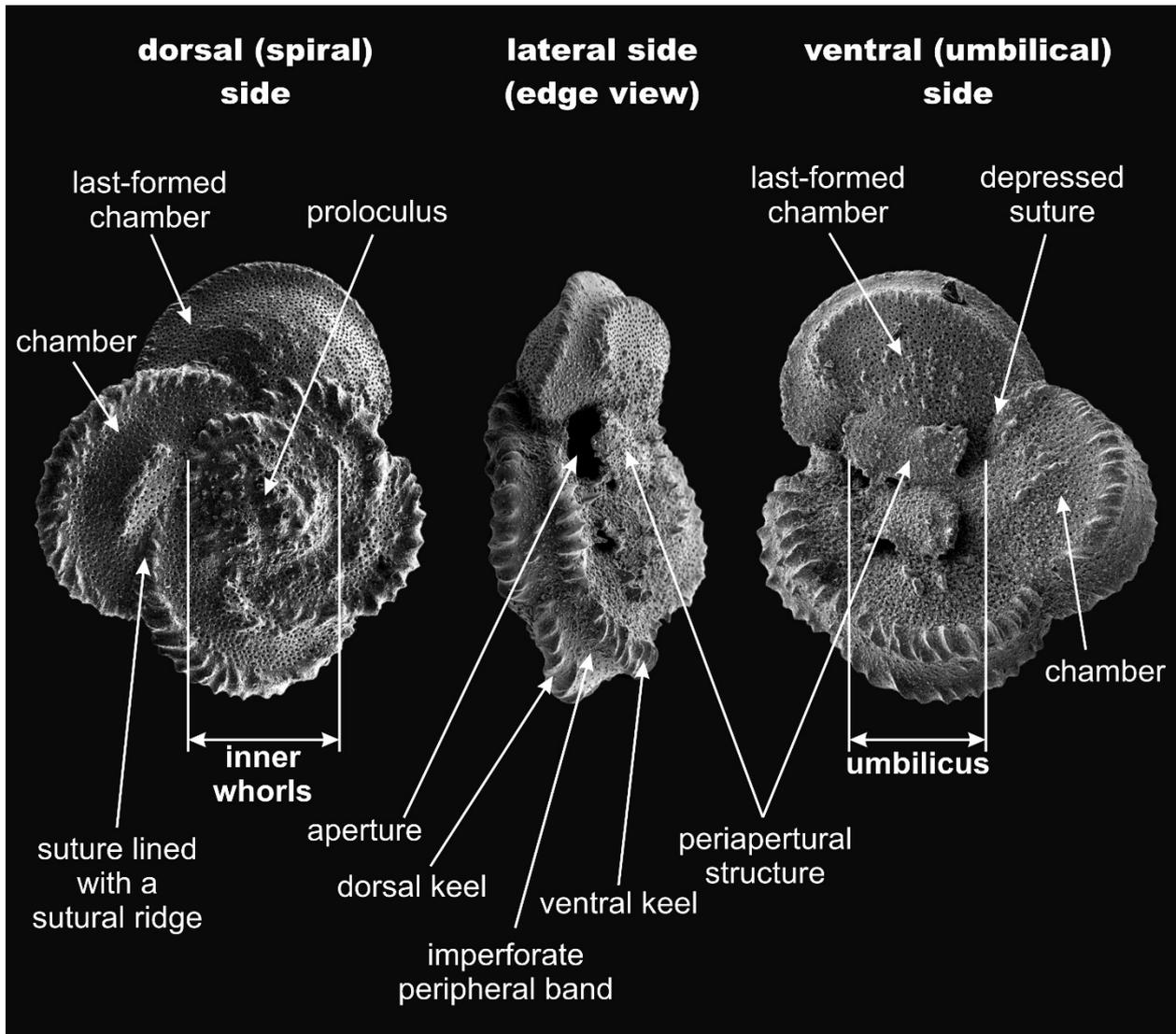


Fig. 1. Globotruncanid test orientation and gross architecture features. No scale is implied.

1.2 Test outline

This feature can be observed in dorsal and ventral views. It is relatively important in the taxonomy and classification of most of the globotruncanid taxa, and in some plays a crucial role. The four different types of test outline are recognized according to the following features: periphery indentation at the peripheral extremity of the sutures, development of a straight chamber margin and development of chamber backward projections (Fig. 2).

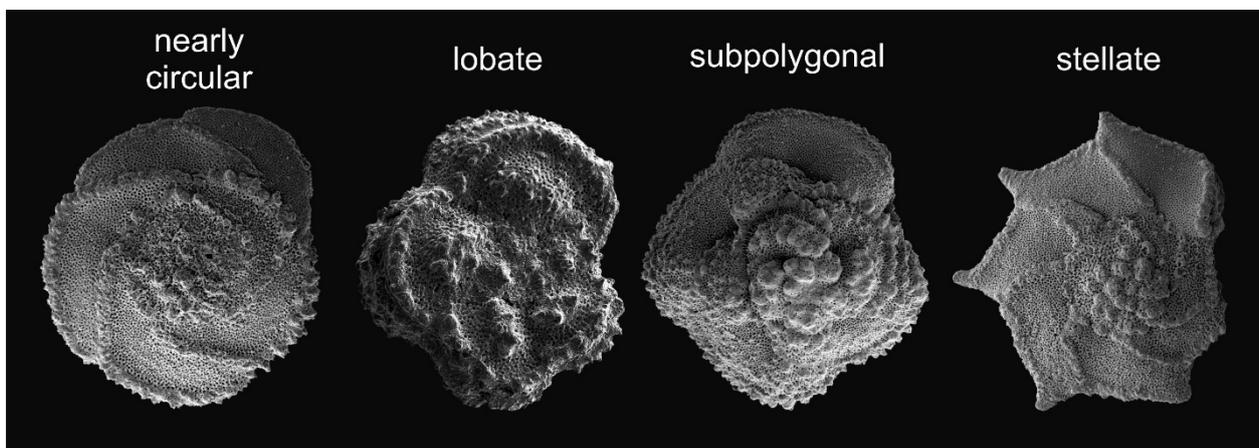


Fig. 2. Main types of test outline illustrated with views from the dorsal side. No scale is implied.

A test outline can appear nearly circular in cases where none of the three above-mentioned features is well-developed. An outline in which the sutures are deeply incised is referred to as lobate. This is the most frequent type of outline in globotruncanids and is often associated with the development of chambers with a petaloid shape as seen in the dorsal view. Development of straight portions of the periphery results in a subpolygonal outline, which can be found in different terminologies developed in the past as polygonal, polygonal rounded and rounded subpolygonal. Subpolygonal outline is mostly associated with the evolution of tests with a high trochospire and chambers that are strongly elongated in the direction of growth. Evolution of chamber backward extensions results in the development of a stellate outline; such an outline is associated with the development of short tubulospine-like backward oriented projections.

1.3 Test shape

Test shape is a general morphological feature that is best evaluated in edge view. In fact, it is a complex feature that consists of two distinct components: trochospire height and test relative convexity/concavity (Fig. 3). Each of these features requires a distinct evaluation and terminology.

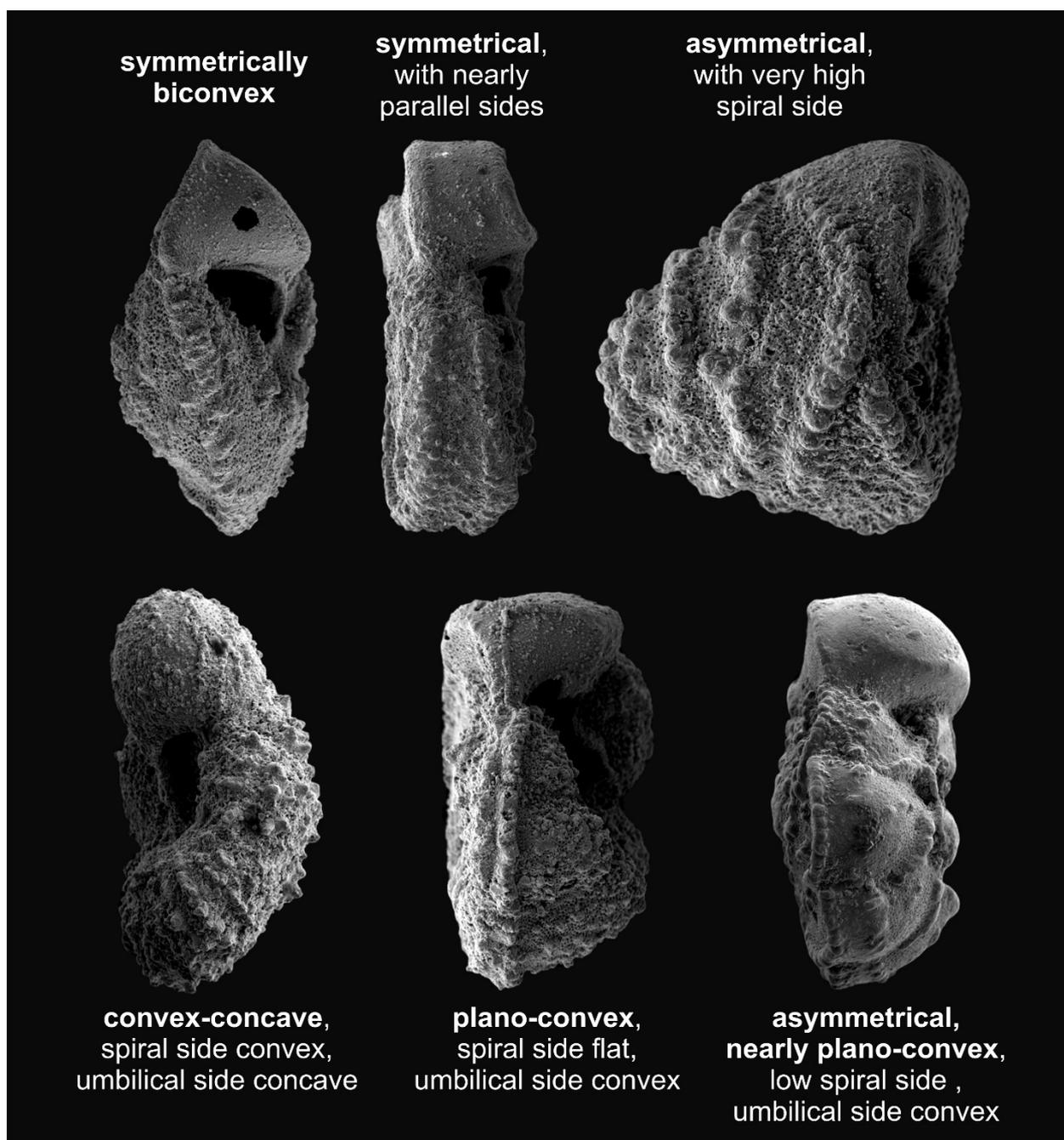


Fig. 3. Types of test shape defined in edge view. No scale is implied.

Trochospire height represents the relative distance along the coiling axis from the proloculus to the coiling plane of the last whorl. Globotruncanid taxa frequently exhibit a constant rate of addition of new chambers along the coiling axis during the ontogeny. This rate can vary resulting in distinct growth stages in a relatively small number of taxa. Trochospire height is described by using qualitative terms: very low, nearly flat, low, medium high, high or very high. Such terms are self-explanatory and in general are used in a similar way by different authors.

Test relative convexity/concavity refers to the general aspect of the spiral and umbilical sides as seen in edge view. Each of the two faces can be convex, flat or concave. Test shape is described by putting together the terms that describe in order the spiral and umbilical sides (e.g., convex–flat, convex–concave and plano–convex). A test in which the two sides are convex is referred to as biconvex and can be symmetrical or asymmetrical according to the relative convexity of the spiral and umbilical sides. Tests in which the two sides of the test are nearly flat and parallel to each other are also known. The description of the convexity/concavity of the spiral and umbilical sides can be combined with the description of the chamber shape on each of the two sides of the test (e.g., flat or slightly inflated on the spiral side and strongly inflated, nearly hemispherical on the umbilical side, etc.). Such usage often results in a more complex but also a more accurate description. In some taxa, the convexity and concavity can vary on the same side of the test and in the same individual; this situation is mostly encountered in plano–convex tests. In such specimens, the spiral side, which is generally described as flat (plano–), can be slightly convex in the region of the inner whorls, which frequently results in the occurrence of a small apical cone, and slightly concave in the portion of the last-formed few chambers.

1.4 Peripheral structures

The simplest peripheral structure that occurs in globotruncanid foraminifera is the imperforated peripheral band that in general is developed over the earlier chambers of the final whorl. Evolution of more complex peripheral structures is apparent in the earlier stages of the test by the development of irregularly arranged pustules and aligned pustules forming rows situated at the margins of the imperforated band. Pustules in the peripheral region can fuse frequently and form rugosities (Fig. 4).

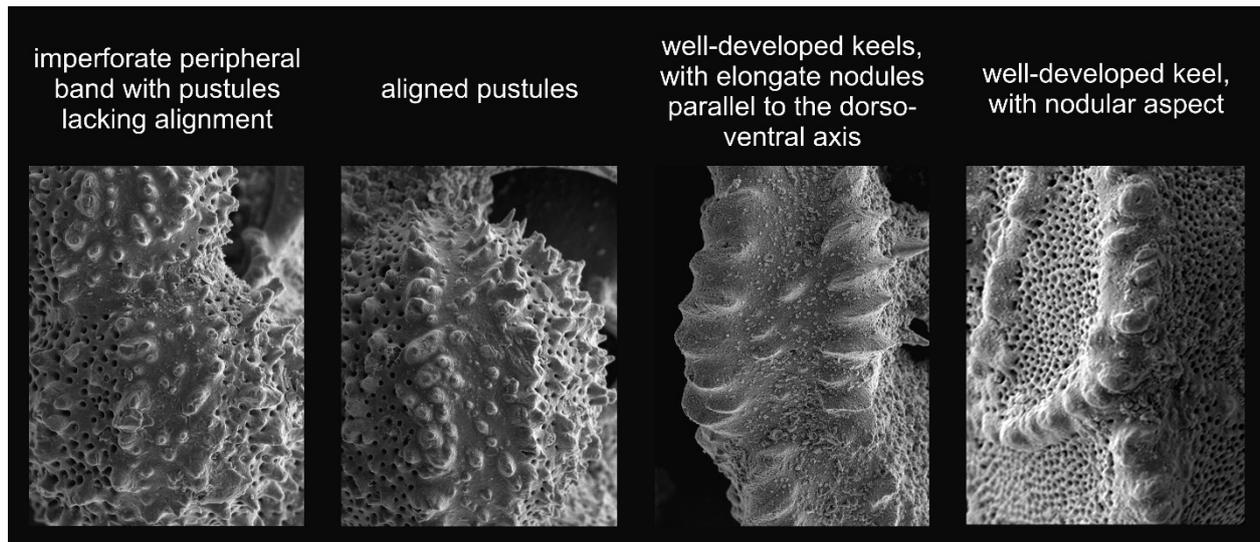


Fig. 4. Types of peripheral structures illustrated on the earlier chambers of the final whorl. No scale is implied.

Keels are the most frequent peripheral structures in the globotruncanid foraminifera and they evolved iteratively several times in the group's evolutionary history. There is a significant variability in the keel ultrastructure across the globotruncanid taxa. In some species and genera, the keels consist of aligned pustules and especially over the periphery of the earlier chambers pustules can fuse to form rugosities that occasionally show a preferential alignment. In some taxa, the aligned pustules are extremely large conferring a nodular aspect to the keel. In others, the keels can have a solid aspect, which is given by the well-fused ornamentation elements. One of the most spectacular cases of development of the peripheral keels is that in which the keel consists of elongated narrow nodules or ridges, which are transversally oriented to the keel long axis (Fig. 4).

1.5 Peripheral and non-peripheral keels

Globotruncanids are considered keeled taxa that have one or two such peripheral structures. Globotruncanid keels are ornamentation structures that are apparent both in detached specimens and thin sections. They are imperforated and in most of the taxa are more prominent over the earlier chambers of the test due to the addition of successive layers of calcite during the ontogenetic development. Occasionally, the two peripheral keels were referred

to as dorsal and umbilical keel respectively, but these terms were used without being part of a consistently developed terminology.

The re-evaluation of the keel position over the test surface, which is based on high-resolution SEM observations, indicates that four types of keels can be recognized. Most of the globotruncanid taxa present two keels, which occur around the periphery. According to their position towards the dorsal and ventral side, they are termed dorsal keel and ventral keel respectively (Fig. 5). The occurrence of the two peripheral keels is a morphological feature of paramount importance in defining the globotruncanid group.

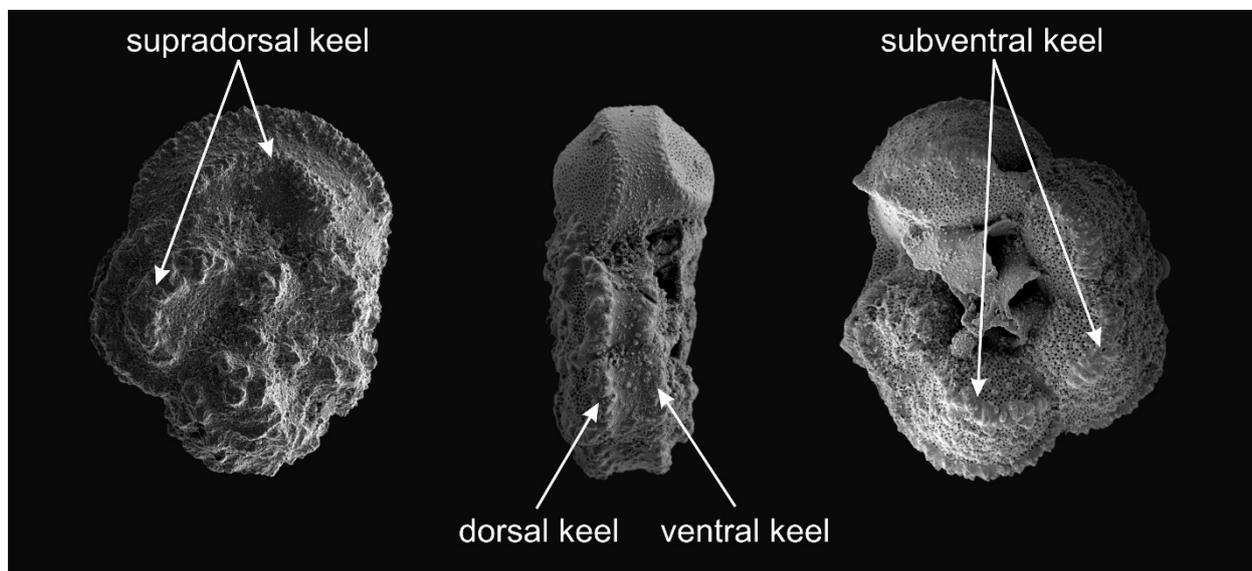


Fig. 5. Peripheral and non-peripheral keels. No scale is implied.

Two other types of keels can occur on the dorsal and ventral side respectively and are recognized herein for the first time (Fig. 5). Supradorsal keels occur on the spiral side of a small number of taxa from the upper Campanian–Maastrichtian stratigraphical interval and are formed through the concentration of the ornamentation structures; this keel is discontinuous and occurs only on the last-formed few chambers of a specimen. Subventral keels are known from only one taxon of the Santonian age and results from the development of the periumbilical ridges, which eventually form a continuous or discontinuous keel around the umbilicus. Therefore, one species with all the four types of keels is not known. The maximum number of keels that can occur is three in one of the two combinations: supradorsal–dorsal–ventral and dorsal–ventral–subventral.

1.6 Aperture and periapertural structures

Globotruncanid test aperture that is invariably situated on the umbilical side has the shape of an arch, which according to its height can be qualitatively described as low, medium or high. The new observations led to a complete reconsideration of the aperture position across the globotruncanid group. The aperture position was conferred a paramount importance in most of the previous taxonomical studies and classifications and several genera were described simply according to slight changes in the aperture position.

Aperture intersects the umbilical margin in most specimens and, therefore, is often described as umbilical–extraumbilical or extraumbilical–umbilical (Fig. 6A). In a rigid terminology the two can be regarded in a different sense as follows: if most of the aperture length is situated outside the umbilicus then the aperture is extraumbilical–umbilical and if most of it is inside the umbilicus then is referred to as umbilical–extraumbilical. In the course of this study it was noted that specimens with extraumbilical–umbilical and umbilical–extraumbilical apertures occur in the same species and for this reason the two terms are herein considered as interchangeable. The aperture is situated completely within the umbilicus in a relatively small number of taxa. In such cases the aperture is referred to as umbilical (Fig. 6C). Taxa in which the aperture is consistently situated outside the umbilical region are not known. Notably, certain difficulties in evaluating the position of the aperture can occur in the case of well-preserved specimens where the periapertural structures were not destroyed through fossilization (Fig. 6B, 6D).

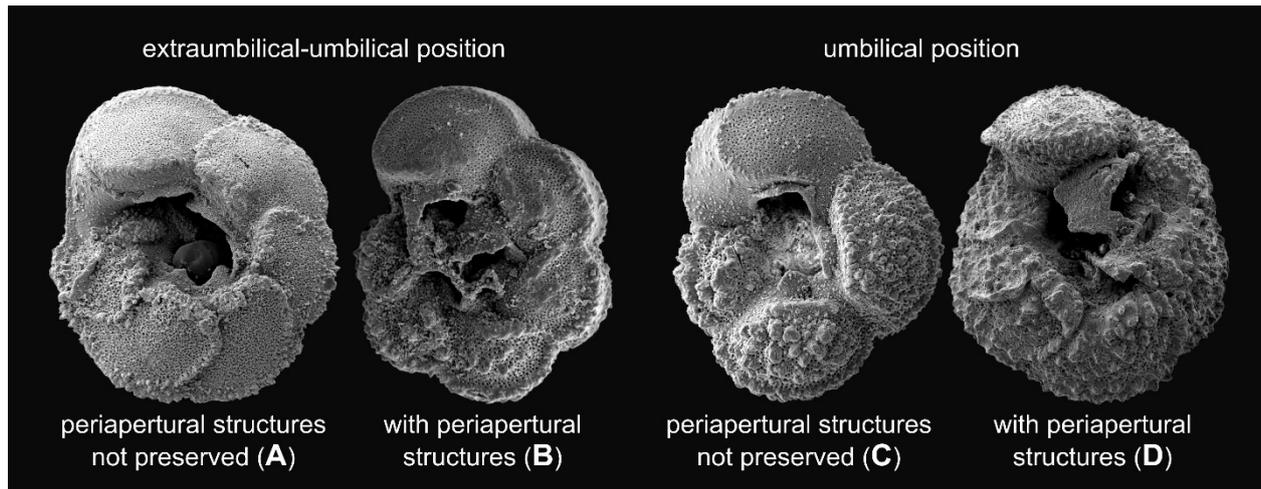


Fig. 6. Globotruncanid specimens showing the two main types of position of the test aperture: extraumbilical–umbilical and umbilical. No scale is implied.

Delicate calcitic structures, which are rarely preserved, occur in the umbilical region and border the aperture; they are known under the general term of periapertural structures. Periapertural structures have often a complex morphology, so it is important to define a system of directions that will help in describing them accurately. The anterior and posterior directions are the homonym directions defined according to the test growth; proximal and distal directions are towards the umbilicus margin and center respectively (Fig. 7A).

The newly reassessed variability of this structure determined the abandonment of the classical terminology based on qualitative categories such as porticus, tegillum, etc., which had been in use for many decades (Robaszynski et al., 1979, 1984; Caron 1985). Notably, a much wider range morphological variability shown by the periapertural structures was subsequently demonstrated (Norris, 1992; Weidich, 1997).

In general, a periapertural structure consists of one elongated plate termed the main periapertural plate with the longitudinal axis perpendicular or oblique to the umbilicus margin (Fig. 7B). In some taxa, a narrower extension can occur in anterior position from the main periapertural plate; this structure is herein termed the anterior segment of the periapertural structure. Similarly, a short and narrow posterior segment of the periapertural structure can occur posteriorly from the main periapertural plate. There are only a few taxa in which all three components of the periapertural structure occur. The anterior and posterior segments are narrow and free, whereas the main periapertural plate can be attached to the previous similar structures from the umbilical region or to the periumbilical ridges of the opposing chambers across the umbilicus. Narrower segments can diverge from the main periapertural plate and independently attach to the previous similar structures or other chambers. The main periapertural plates and narrower structures that posteriorly branch from them can result in the formation of empty spaces with the aspect of supplementary apertures. Such supplementary apertures can occur between one periapertural structure and other similar structures in the umbilicus, or between them and the umbilical margin. More complex features that occur in the periapertural structures of some evolved taxa include undulated surfaces and rimmed margins.

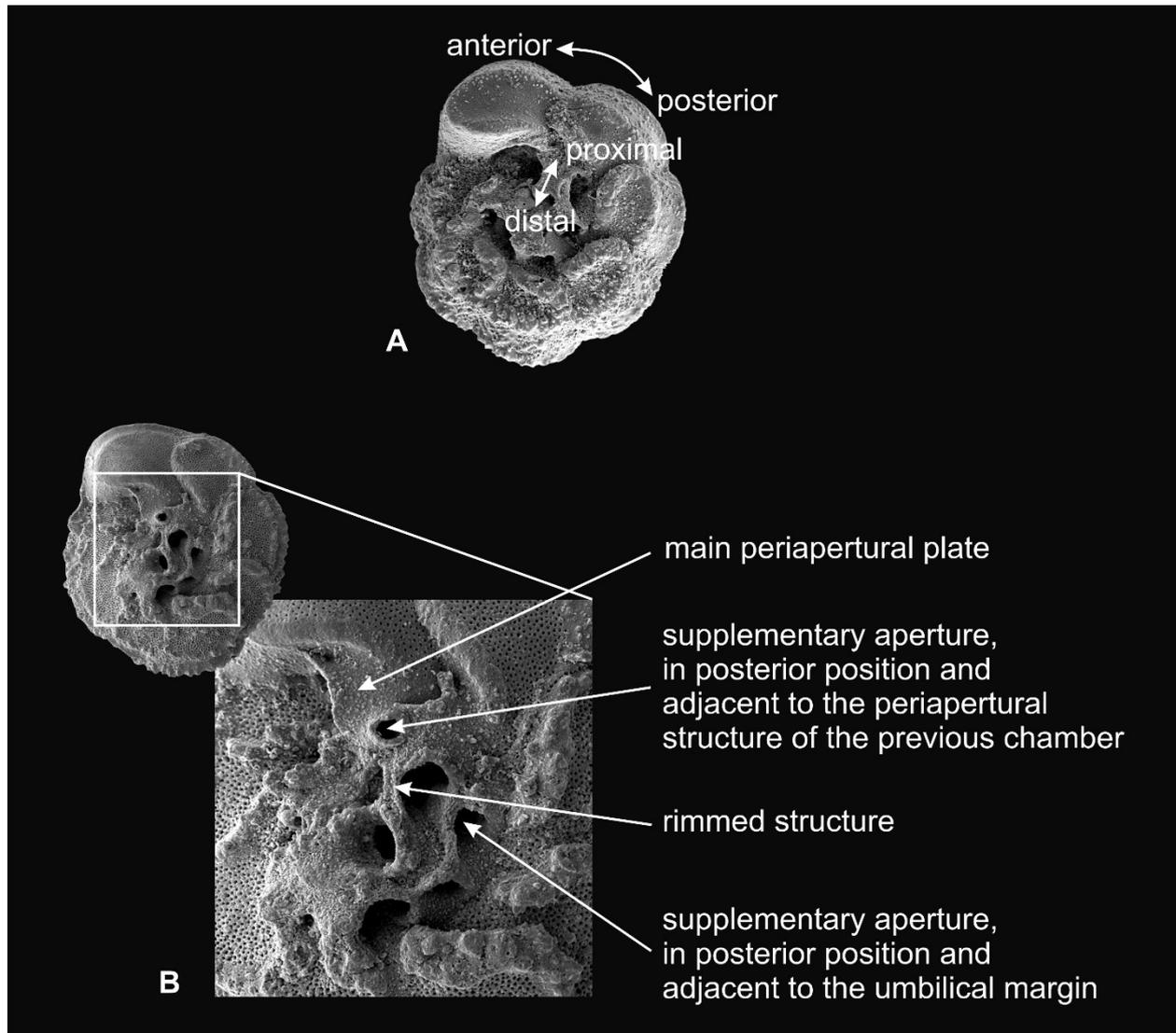


Fig. 7. Directions used in the terminology of aperture orientation (A) and morphological features of the periapertural structures (B). No scale is implied.

1.7 Periumbilical structures

Some of the most frequent ornamentation structures of the globotruncanid tests are the periumbilical structures; they evolved independently several times in the group's evolutionary history. The formation of periumbilical structures can begin with the development of a wall flexure termed periumbilical shoulder (Fig. 8). Pustules and rugosities start accumulating over the periumbilical shoulder in the next stage of development. Taxa in which the agglomerations of pustules and rugosities are formed simultaneously with the periumbilical shoulder are also known.

Fused pustules and rugosities confer a solid aspect to the periumbilical ridges that can be oriented parallel or oblique to the umbilical margin. In many globotruncanids the periumbilical ridges are in connection with the sutural ridge and further with the ventral keel of the double-keeled taxa or the only keel in single-keeled ones, forming an anteriorly curved ornamentation structure. The periumbilical structures can be continuous or discontinuous around the umbilicus. One special case of development of the periumbilical structures is that in which they are connected forming a continuous structure around the umbilicus; such structure is also referred to as a subventral keel (Fig. 8).

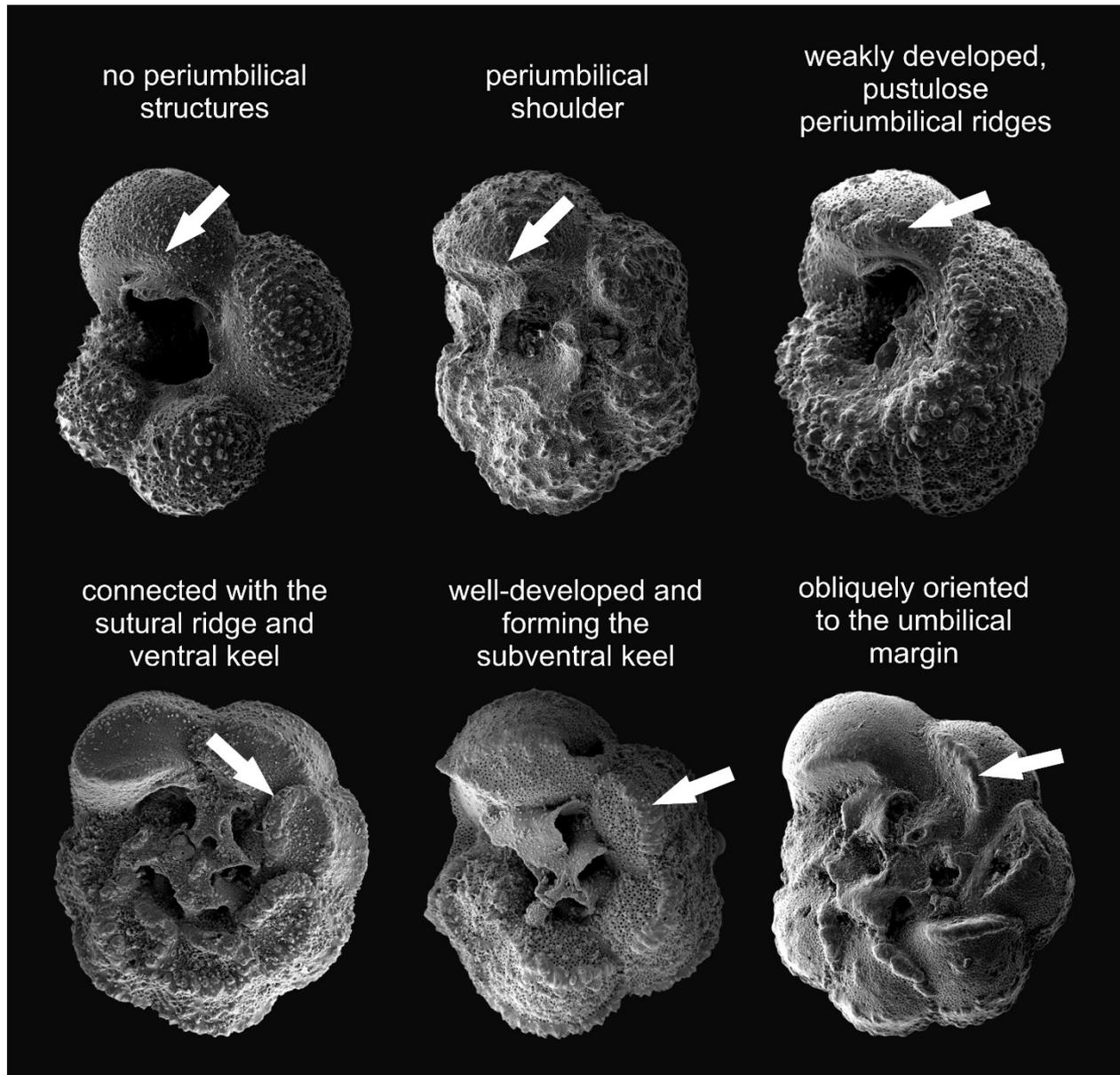


Fig. 8. Types of periumbilical structures. No scale is implied.

1.8 Pores and their types

Pores are small-sized, often cylindrical canals through the test wall, which make the connection between the chamber interior and test exterior. Two types of pores are encountered in the globotruncanid group: simple and vuggy (Fig. 9). The simple pores are smaller and can have a circular, elliptical or (more rarely) irregular outline. Vuggy pores occur only on the spiral side and are considerably larger than the simple ones; they occur only in those portions of the test surface where the layers of calcite successively added through ontogeny form a complex wall ultrastructure. Pore mounds and scalaropores are not recorded in the taxa of the globotruncanid group. Many of the globotruncanid tests present pores of equal dimensions on the spiral and umbilical side. New and accurate observations indicate that in some taxa the pores are larger on the spiral side than on the umbilical one.

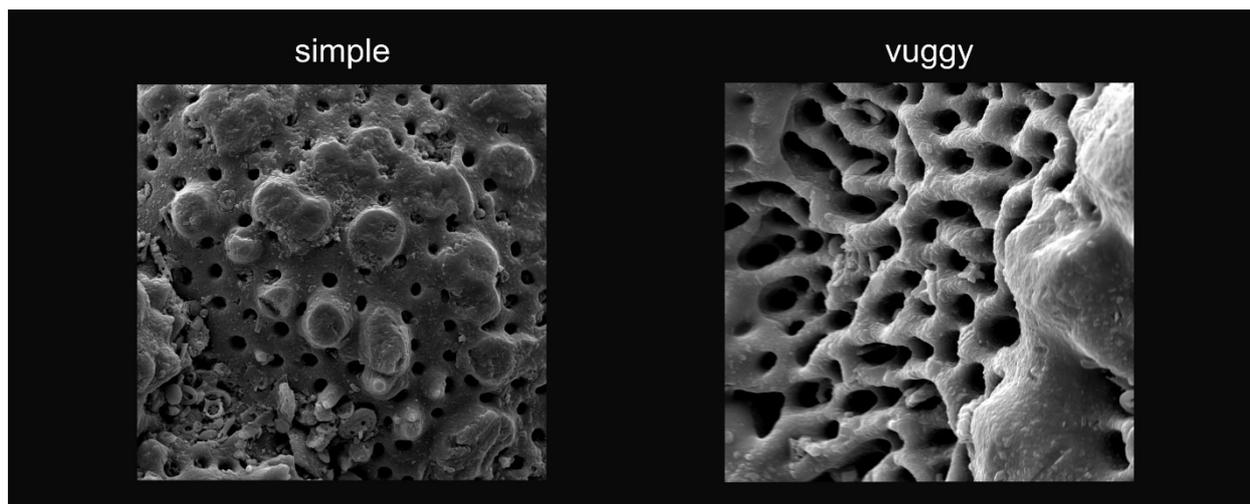


Fig. 9. Types of pores encountered in the globotruncanid group. No scale is implied.

1.9 Wall ultrastructure

The wall ultrastructure at the test exterior is one of the most reliable features in recognizing the evolution of different lineages of planktic foraminifera (Fig. 10). The simple wall presents a solid appearance, with simple pores separated by wide portions of test wall. The morphological changes through time from this feature follow two directions. One leads at first to the formation of a wall with simple aspect and more closely-spaced simple pores, which is termed incipiently simple-ridged. This can evolve further into a wall type in which the pores are closely-spaced and separated by ridge-like portions of the wall; the well-developed stage of this evolutionary path is termed simple-ridged wall. The other path in the evolution of wall ultrastructure is represented in the first stage by the incipiently reticulately-ridged wall, in which pores are closely-spaced and the wall between them has a low in-relief aspect. The well-developed ultrastructure in this path of evolution is termed reticulately-ridged. The two developmental successions are similar with those encountered in the rotaliporid planktics, thus demonstrating the general iterative evolution of wall ultrastructure in rotaliporids and globotruncanids. A more complex succession of ultrastructures was encountered in a relatively small number of taxa; this type occurs in the central portion of the spiral side. In this case, an incipiently reticulately-ridged ultrastructure can be superimposed over a simple-ridged one and further developed in a reticulately-ridged ultrastructure as a result of successively added layers of calcite during the ontogenetic development.

1.10 Ornamentation

Chamber surface ornamentation in globotruncanid taxa was rarely used in taxonomy and classification in the past. This methodology is no longer valid due to the developments in evolutionary classification, in which the high-resolution test features that include ornamentation were extensively studied and demonstrated their importance. Therefore, a terminology developed at the scale of the whole group is herein developed.

Chamber surface without ornamentation structures is referred to as smooth (Fig. 11). Smooth chambers occur in many globotruncanid taxa, especially over the last-added chambers in the final whorl. The simplest ornamentation structure is the pustule, which can have a dome-like or irregular aspect. Layers of calcite that are added over the chamber surface during ontogeny can result in a coarsening of the ornamentation over the earlier test chambers. As a result, the pustules can increase in size and fuse forming larger ornamentation structures, the most frequent of them being the rugosities. In general rugosities are formed by a small number of pustules, frequently two to four. Larger ornamentation structures, which have an irregular shape, occur mostly over the earlier chambers of the test. Pustules and rugosities can further develop in ridge-like ornamentation structures with elongated aspects termed costellae.

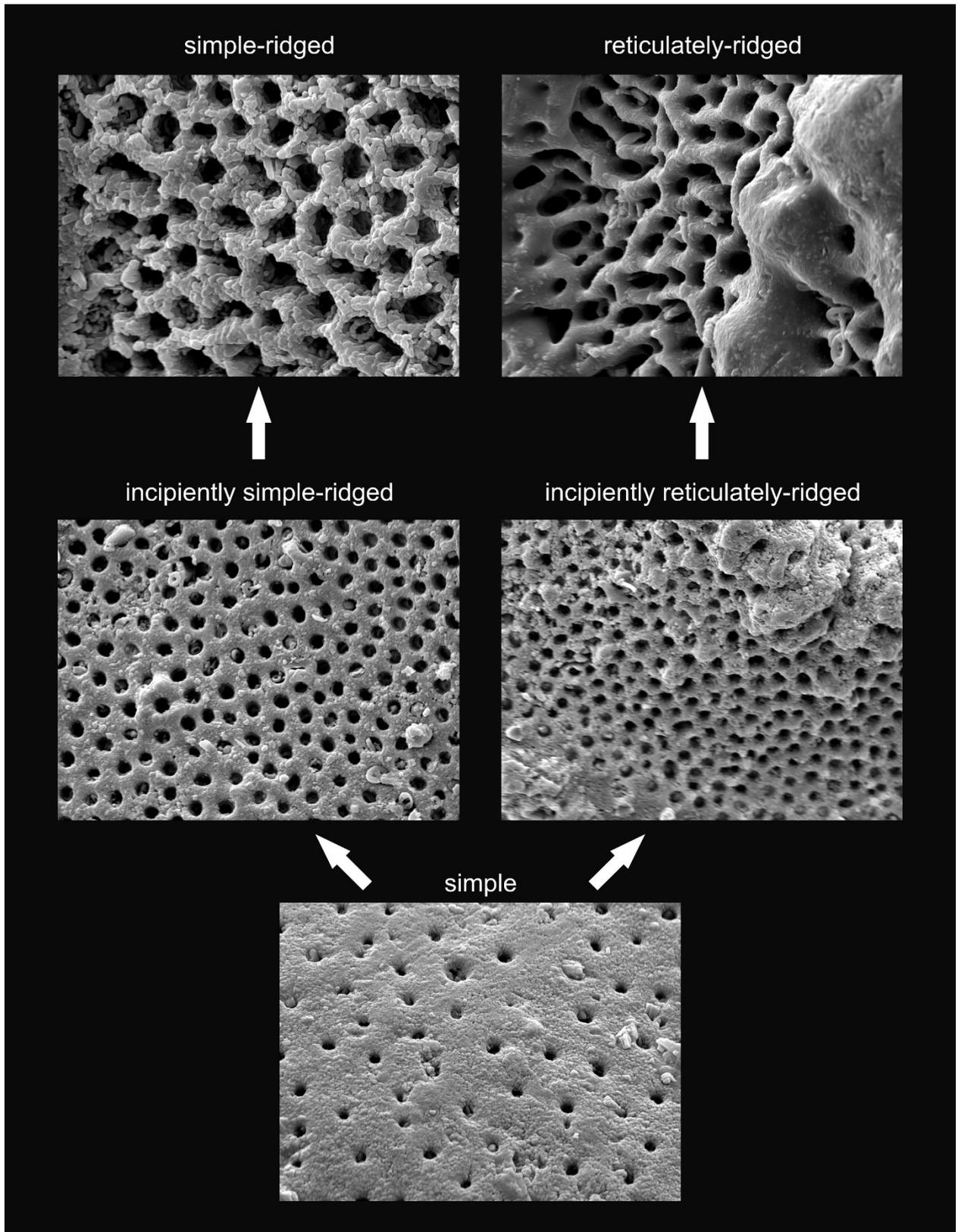


Fig. 10. Types of globotruncanid wall ultrastructures and the two paths recognized in their evolution. No scale is implied.

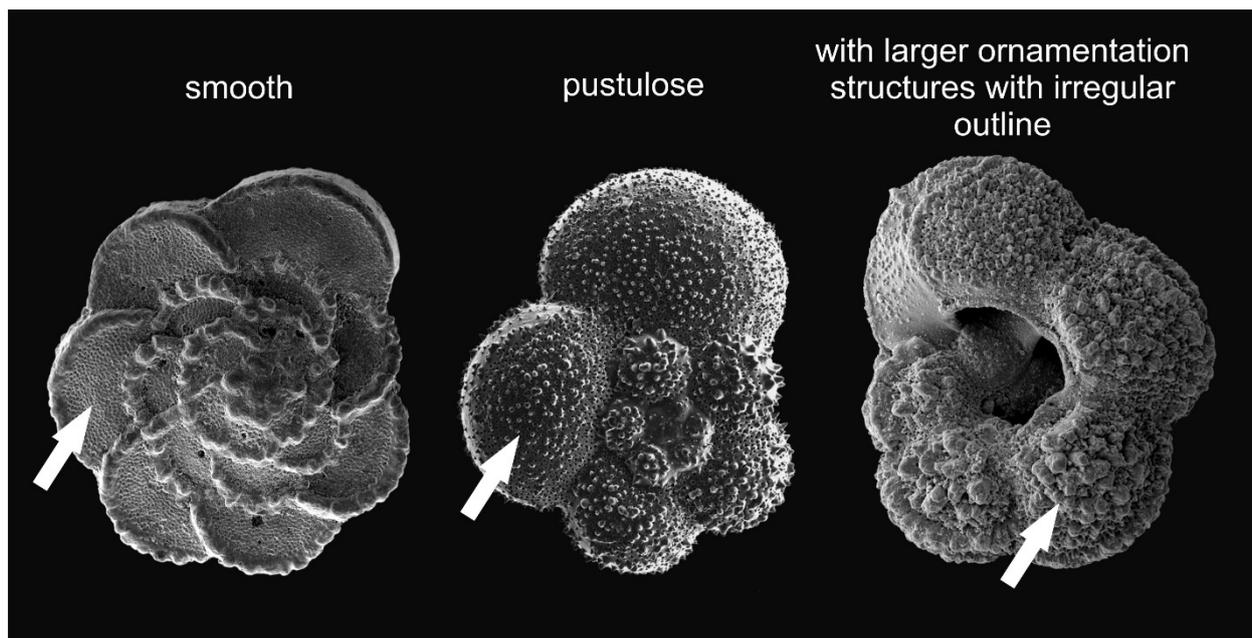


Fig. 11. Types of chamber ornamentation. No scale is implied.

In general, the ornamentation structures (pustules, rugosities and costellae) do not present a preferential arrangement at the chamber surface. Two preferential arrangement patterns can occur in some of the most advanced taxa of the globotruncanid group: parallel to the periphery on the spiral side and meridional on the umbilical one.

CHAPTER 2

A BRIEF HISTORICAL PERSPECTIVE ON GLOBOTRUNCANID STUDIES

Rosalina linneiana or *Rosaline de Linné* is the first reported, described and illustrated globotruncanid species (d'Orbigny 1839); the material was collected from the beach sands of Cuba and deposited in the collection of the Museum of Natural History in Paris. The specimen that was originally illustrated was subsequently reported lost in a thorough revision of the d'Orbigny Collection (Le Calvez 1977). Two other globotruncanid taxa were described shortly afterwards: *Rosalina marginata* from Bohemia (Czech Republic) and *R. canaliculata* from the surroundings of Salzburg (Austria) (Reuss 1845 and 1854 respectively). The other species described in this period of pioneering studies is *Planulina mississippiica*, which was illustrated but not described from a spot sample from Missouri (Ehrenberg 1854). The specimen used in the description of this species is preserved in one of the mica slides of the Ehrenberg Collection from the Museum of Natural Sciences in Berlin. Additional material from the sample of the original material was prepared and yielded the compelling evidence to demonstrate that this species is indeed a globotruncanid (Georgescu 2013). Following the description of these four species, relatively frequent reports of globotruncanids showed how frequently the representatives of this group occurred in rocks of Late Cretaceous age (Brown 1853; Eley 1859; Burrows et al. 1890; Jones 1896; Upton 1898; Egger 1902, 1908, 1909; Chapman 1908, 1917). The next step was the description of species based on specimens from thin sections, namely *Pulvinulina tricarinata* from the Upper Cretaceous (Maastrichtian) of Switzerland (Quereau 1893); this practice of describing new species based only on specimens studied in thin sections proved detrimental in the long term because some features that are crucial in taxonomy and classification cannot be evaluated (e.g., aperture position, periapertural structure morphology, wall ultrastructure and porosity, etc.). The description of a new species *Rosalina stuarti* from the Pyrénées of France led to the development of a new methodology of study (de Lapparent 1918). The novelty is represented by the wide variety of data used in description and these range from completely detached specimens to thin sections and exquisite partially detached individuals from indurated limestones.

A new series of studies that led to a considerable increase of the number of formalized globotruncanid species were carried out in the United States (Carsey 1926; Cushman 1926, 1927a, 1938, 1939, 1946; White 1928; Plummer 1931; Sandidge 1932a, 1932b). Notably, the first genus of Cretaceous coiled planktic foraminifera was described during this period: *Globotruncana* (Cushman 1927a). Meanwhile, in Europe the development continued and new species were described based on detached material (Brotzen 1934, 1936; Marie 1941; Gandolfi 1942); in addition, some European authors continued to describe new species based on material examined in thin sections (Vogler 1941; Bolli 1945). Overall, during 1926–1949 the number of valid species was higher than those that subsequently proved invalid. One major achievement during this period is the initiation of the evolutionary studies that can be considered with the first interpretation of the globotruncanid evolution (Glaessner 1937) (Fig. 12).

The most prolific period in globotruncanid study started in 1950 and is best illustrated by the high number of new species that were subsequently proved valid. Such proliferation should be considered the result of the taxonomic experimentation and the newly-discovered species were frequently described based on discrete morphological features (Nakkady 1950; Reichel 1950; Bolli 1951; Tilev 1951; Sigal 1952; Hagn 1953; Papp & Küpper 1953; Hagn & Zeil 1954; Dalbiez 1955; Gandolfi 1955; Brönnimann & Brown 1956; Bolli 1957; Reiss 1957, etc.). This is the time when the range of morphological variability at group level started to be revealed and this also led to the description of four new genera: *Rugotruncana* Brönnimann & Brown 1956, *Marginotruncana* Hofker 1956, *Abathomphalus* Bolli et al. 1957 and *Globotruncanita* Reiss 1957. One major achievement during these times was the recognition of the iterative pattern in globotruncanid evolution (Sigal 1952; Gandolfi 1955). In addition, the predictability of the new evolutionary studies was emphasized: “Some transitional forms could be postulated before they were actually found” (Gandolfi 1955, p. 78). Therefore, it appears evident that the germs of the evolutionary classification started to be developed at the beginning of the second half of the twentieth century. Furthermore, careful and detailed observations on the test morphological features provided new insights on the test ornamentation and its potential in deciphering globotruncanid evolution (Brönnimann & Brown 1956).

The time of massive accumulation of new data continued in the next two decades and this resulted in more refined classification and biostratigraphical frameworks. Three new genera were added to the pre-existing ones, namely *Archaeoglobigerina* Pessagno 1967, *Dicarinella* Porthault in Donze et al. 1970 and *Radotruncana* El-Naggar 1971. The number of new species and subspecies continued to increase in this period when larger and more comprehensive works dedicated to this group were published (Herm 1962, 1963; van Hinte 1963; Takayanagi 1965; Salaj and Samuel 1966; Pessagno 1967; Scheibnerová 1968; Hanzliková 1972). Some of the achievements of this period of massive experimentation need to be mentioned: evolution from *Hedbergella* to *Globotruncanella* and then *Abathomphalus* (Berggren 1962; Maslakova 1964), evolution from *Praeglobotruncana* to double-keeled *Globotruncana*

and then to single-keeled globotruncanids of the genus *Globotruncanita* (Reiss 1957) and iterative evolution of *Praeglobotruncana* and *Globotruncanella* from the taxa of the hedbergellid stock (Van Hinte 1963), etc.

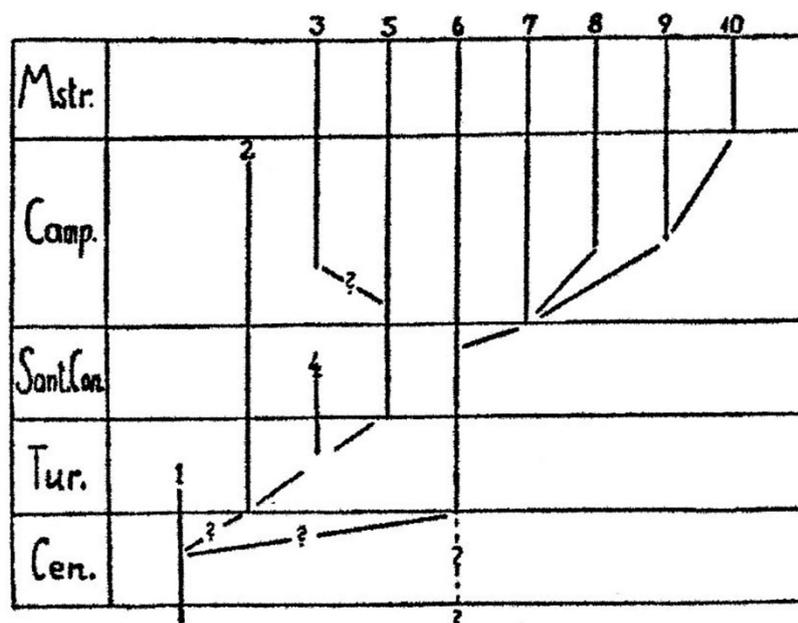


Fig. 5. Die hypothetischen Verwandtschaftsbeziehungen der Globotruncanen. 1—Gruppe der *G. appenninica*, 2—*G. marginata*, 3—*G. contusa*, 4—*G. cf. contusa*, 5—*G. fornicata*, 6—*G. linnei*, 7—*G. arca*, 8—*G. rosetta*, 9—*G. stuarti*, 10—*G. conica*.

Fig. 12. The oldest diagram showing inferred evolutionary relationships between globotruncanid taxa (from Glaessner 1937, fig. 5).

One road-opening event was the publication of the first study that used the scanning electron microscopy to illustrate globotruncanid tests (Funnell et al. 1969). In the next years the SEM micrographs would be extensively used to illustrate globotruncanids as well as other planktic or benthic foraminiferal groups. Another milestone in the late 1960s is represented by the beginnings of the DSDP that for more than half a century has brought a wealth of data on the globotruncanid group from the cores drilled in the deep portions of the Planetary Ocean. The results focused on biostratigraphy and the vast number of articles dedicated to the planktic foraminiferal assemblages recovered from Upper Cretaceous sediments consecrated the leading role of globotruncanids as index fossils. The first atlas dedicated to the Cretaceous planktic foraminifera also dates from this stage of development (Postuma 1971).

In the late 1970s comprehensive works with a monographic character started to be developed (Linares Rodríguez 1977; Masters 1977; Maslakova 1978). The oldest globotruncanid stem lineage was recognized as *Praeglobotruncana* – group of *Dicarinella canaliculata* – group of *Marginotruncana pseudolinneiana* – group of *Globotruncana linneiana* in one of these works (Linares Rodríguez 1977). Shortly afterwards, two atlases on the coiled planktics of Cretaceous age presented the results of The European Working Group on Planktonic Foraminifera under the editorship of F. Robaszynski and M. Caron in 1979, and F. Robaszynski, M. Caron, J.M. González Donoso and A.A.H. Wonders in 1984. One interesting feature of the two atlases is that they were the result of the work of numerous top specialists in the field, which added a considerable weight towards their wide acceptance in the scientific society worldwide. One review of the planktic foraminiferal Cretaceous biostratigraphy further advanced the ideas provided in the two atlases (Caron 1985); the biostratigraphical framework provided in this work was frequently referred to as the “standard biozonation” in the Cretaceous planktic foraminiferal biostratigraphy in which the globotruncanids play a dominant role for the Upper Cretaceous Series. In the following decades most of the studies focused on globotruncanids were reduced practically to applications of the standard zonation with little experimentation. This trend towards taxonomical simplification continued towards the end of the millennium and shortly afterwards to a point where the taxonomical features used in classification of the detached specimens and those studied in thin sections were almost unified.

A next stage in the development was initiated by the massive use of high-resolution morphological data acquired with the aid of the SEM in classification. This stage was referred to as the “ultrastructure revolution” (Georgescu 2014). This new methodology started to be developed and applied in other Cretaceous planktic foraminiferal groups (e.g., heterohelicids, globular-chambered trochospirals, praeglobotruncanids, etc.) and led to significant advances in evolutionary classification, in which taxa are grouped according to the ancestor–descendant relationships as demonstrated in the fossil record. The higher level of accuracy in observations and interpretations derived from them is apparent in several studies focused on different representatives of the globotruncanid group

published in the last decade (Georgescu 2012a, 2013, 2015, Georgescu et al. 2013, Georgescu & Sawyer 2013). Such studies paved the way towards the development of a new and improved classification of the globotruncanids.

CHAPTER 3

STUDIED MATERIAL AND ITS PROVENANCE

Most of the material used in this study was yielded by samples collected from inland sections and wells drilled offshore and onshore. Additional material that includes type and non-type specimens was studied in the collections of different institutions. Given the vast number of globotruncanid tests studied – as well as the multitude of locations from which they were collected – only the most relevant are presented herein. Notably, the most relevant sections are represented by eleven sites and holes drilled as part of the DSDP and ODP respectively (Fig. 13). Biostratigraphy at the eleven boreholes was completely restudied. This approach was necessary in order to provide an updated version of the biostratigraphical frameworks at each of these locations, which is paramount in an accurate assessment of the stratigraphical ranges of the species included in this work. There are some low-magnitude modifications when compared with the previous frameworks I provided in the past in different articles as part of the development of the evolutionary classification. Earlier studies were focused on species identification, assessment of high-resolution morphological features and ultrastructures, assessment of species variability and recognition of ancestor–descendant relationships, whilst the biostratigraphical frameworks used at that time were rather in an early stage of development. Such differences are inherent when developing as a vast project as an evolutionary classification that involves the study of more than 300 species and where differences between the results of the various stages of preparation of the study are expected. Other differences occur as the result of scientific advances at global scale and in this category is included the reassessment of the stratigraphical range of *Concavato truncana asymetrica* as middle Coniacian–Santonian rather than upper Santonian as considered in the past (Lamolda et al. 2014). Therefore, the biostratigraphy of the Coniacian–Santonian stratigraphical interval required revision at all locations where the sediments of this age occurred.

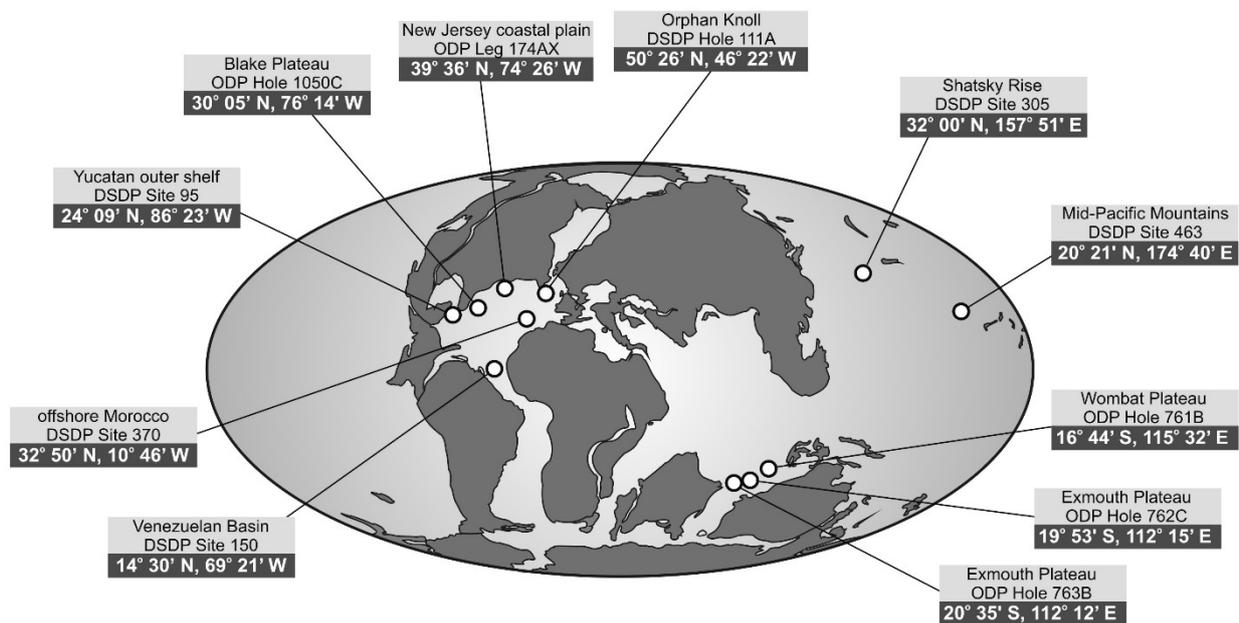


Fig. 13. Geographical position of the eleven DSDP and ODP sections that provided most of the material included in this study. Base map is a reconstruction at 100 m. y. (Hay et al. 1999).

Sample preparation followed the standard techniques. The soft sediments from the DSDP and ODP boreholes were disintegrated by soaking them in water. Ultrasonic tank, a procedure which was applied in the case of harder rocks, further helped in obtaining cleaner specimens; it was used in the case of the samples from DSDP Site 95 (Yucatan outer shelf), DSDP Site 150 (Venezuelan Basin) and DSDP Hole 111A (Orphan Knoll). Hydrogen peroxide was used to remove the clayey sediments, such as those from DSDP Site 370 (Deep basin off Morocco); calgon was also used for the disintegration of the clayey sediments, one method applied in the case of the samples from the ODP Leg 174AX (New Jersey coastal plain). Glauber's salt technique was used to disintegrate harder rocks that were collected from inland sections. The resultant residuum was sieved and then dried before proceeding to picking the specimens.

Stratigraphical range coverage was a crucial aspect throughout the preparation of this study and ultimately played a major role in the final decision to submit the manuscript for publication. A complete coverage of the stratigraphical ranges of all 61 species with material from studied samples was sought. Although this was realized close to 95% of the time, it was necessary to resort to data from the literature in order to define accurately the stratigraphical ranges of each species. Practically, the decision to submit the manuscript came with the realization that new material could have brought only small additions to the work as developed up to that time.

Species and genera coverage represents another paramount component of this work. The material collected and studied over more than 25 years of practice includes 61 globotruncanid species, which allows the development of a comprehensive and accurate study of the globotruncanid planktic foraminifera. There is one exception, namely the genus *Kassabiana* Salaj & Solakius 1984, which has *Globotruncana falsocalcarata* Kerdany & Abdelsalam 1969 as designated type species. This is a rare taxon reported from the upper Maastrichtian of the Middle East (Egypt, Iraq and Tunisia) and Asia (Pakistan). I have only two specimens from a borehole in the Western Atlantic Ocean at my disposal, both in poor state of preservation. It is evident that based on this material it is impossible to document the morphology, ultrastructures and evolutionary relationships of *Kassabiana falsocalcarata* at the same level as for the rest of the taxa included in the present work. Therefore, I decided to leave this taxon for a time when I can document it properly. As a personal note, I would mention that the absence of this taxon from the present work prevented the use of the word “monograph” in the title. Therefore, it should be considered a work with monographic character.

Biostratigraphical zonation used in this study is that based on planktic foraminifera and encompasses the uppermost Albian–Maastrichtian stratigraphical interval (Georgescu 2017). This framework consists of a succession of 24 biozones of taxon range, interval and partial taxon range types in which many of the index species belong to the globotruncanid group (Fig 14).

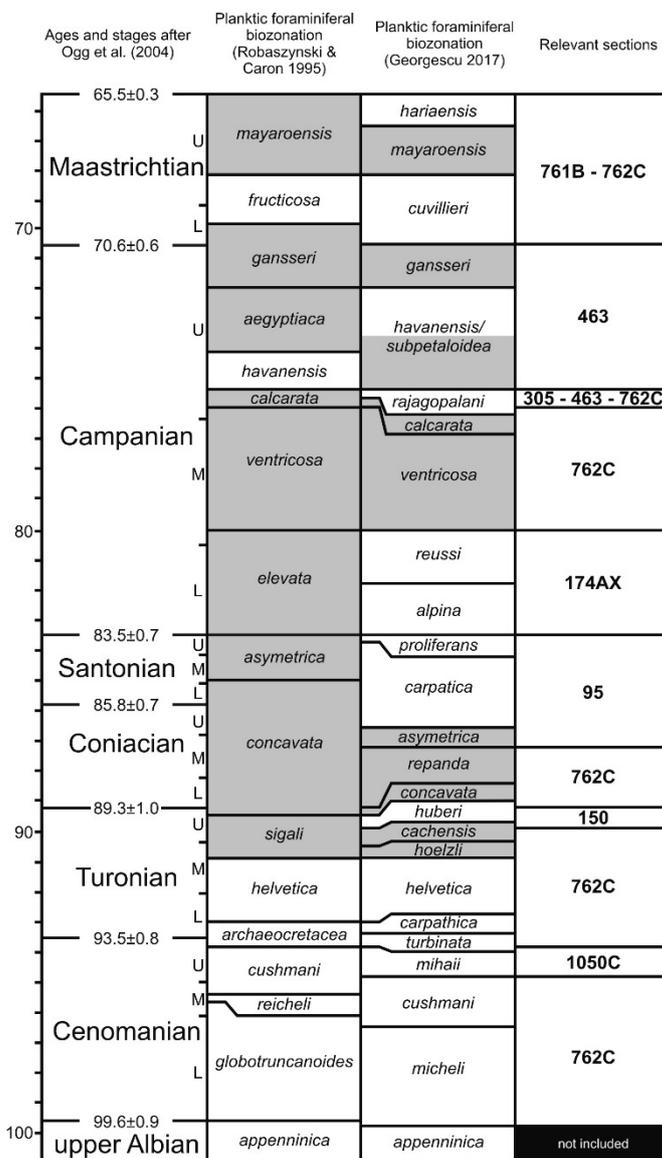


Fig. 14. Biostratigraphical frameworks used in this study; the reference biostratigraphical framework is in the middle column. Biozones with globotruncanid index species as considered in this study are given on gray background.