
Abstract

Large Paleogene Rotaliidae all represent moderate K-strategists similar to the nummulitids to which they are associated. They arise as Tethys-wide groups during the Paleocene and reach their highest diversity during the earliest Lower Eocene (SBZ 5). They document a Global Community Maturation cycle that ends for the rotaliids by their disappearance after the Middle Eocene while other groups like the nummulitids and the orthophragminiforams continue up to the Eocene-Oligocene boundary. Under the generic definitions the species are grouped in order to reflect what is supposed to represent a phylogenetic lineage in the order of their appearance in geological time. This meets the demands of an easier taxonomic identification and to reflect in the same time a phylogenetic hypothesis.

2.1 Overview

Large Paleogene Rotaliidae belongs to the new subfamilies Daviesininae, Kathininae, Laffitteininae, Cincoriolinae and Lockhartiinae. By their large size, their strong dimorphism and their distribution of canal orifices on the surface of their shells they all represent moderate K-strategists similar to the nummulitids to which they are associated. Their strategy of life obliges them to adapt rapidly to the changing conditions in shallow water. They arise as Tethys-wide groups during the Paleocene and reach their highest diversity during the earliest Lower Eocene (SBZ 5). Later, the representatives of the lockartiines, *Lockhartia*, *Dictyoconoides* and *Sakesaria*, dominate the rotaliid associations

and sometimes the complete shallow benthic communities.

The rotaliid distribution pattern on the time scale reflects the basic rules of global community maturation (GCM) cycles, that is: (a) preparing the metabolism for K-strategy, (b) experimenting with ways of life, (c) revelling in success, (d) gaining size and endemism. Thus, they document a GCM cycle that ends for the rotaliids by their disappearance after the Middle Eocene while other groups like the nummulitids and the orthophragminiforams continue up to the Eocene-Oligocene boundary. In the Middle Eocene already the first K-strategists of the conservative neorotalias appear with a new species that has microspheric specimens with incomplete chamberlet cycles like a

miogypsinid. These neorotalias will partially substitute the extinct Lockhartiinae.

The biogeographical distribution of the Rotaliidae starts with species that are ranging throughout the western and central Neotethys during the Paleocene. In the earliest Early Eocene, most rotaliids disappear from the eastern shores of the Atlantic, in particular from the Pyrenean Gulf, may be by the numerous nummulitid competitors. During the following periods, the biogeographic range of the larger rotaliids is restricted to the central part of the Neotethys, from Turkey to Tibet in Asia, and from Egypt to Somalia in Africa. Another index fossil with an identical range is the porcelaneous *Somalina*, whereas the archaiasines are newcomers in the Bartonian. This is what we call the Lockhartia Sea. The large carbonate platforms in the South of the Arabic Peninsula (Dhofar in Oman in particular) exhibits in addition numerous porcelaneous genera of which several are new. The relations of the Tethyan Rotaliids with the Caribbean forms on the other side of the Atlantic remain obscure as long as these taxa have not been revised.

The arrangement of the taxa in the text below tries to meet the demands of an easier identification of the taxa and to reflect in the same time a phylogenetic hypothesis. Thus, under the generic definitions the species are grouped in order to reflect what is supposed to represent a phylogenetic lineage in the order of their appearance in geological time.

The taxa selected for this paper characterize a community indicating a hot spot of diversity in the Middle and Near East during the Late Paleocene. This community is geographically restricted to the shallow shelves around the Western Indian Ocean and the Himalayan shores of the Neotethys. The corresponding marine area is called the Lockhartia Sea. The present paper may also serve to enhance the census of this particular community.

2.2 Superfamily Rotaliacea Ehrenberg: Family Rotaliidae Ehrenberg, 1839

The superfamily Rotaliacea needs an entirely new systematic concept, in order to integrate the advances in structural analysis of the architecture of the shells during the last century. Loeblich and Tappan's (1987) definition of the family Rotaliidae obviously is insufficient: "test trochospiral throughout, with radial canals or fissures and intraseptal and subsutural canals". This definition obliges to unite too many benthic genera with different architectural patterns and stratigraphic ranges in a family that loses any significance. Already in 1963, Reiss laid the foundation for a new classification of the perforate foraminifera that integrated Smout's (1954) lamellar theory of foraminiferal shell construction with ideas of J. Hofker sen. (1927, 1951) about the tooth-plates and their relation to teeth in imperforate forms. Taking into account these structural elements in the umbilical region of the shell leads to the recognition of three main groups of rotaliaceans with family rank: (1) the rotaliids, a Late Cretaceous to Paleogene group of bilamellar, trochospiral shells with an umbilical plate, (2) the ammoniids, a Neogene group with an umbilical cover plate, and (3) the pararotaliids, a conservative group reaching from Late Cretaceous to Recent, with a kind of tooth-plate. There are supplemental groups of similar rank, *Laffitteina* for instance. The systematic ambient environment of the Rotaliidae is too poorly known to decide where and how to place the laffitteinas in the system. The present paper is limited to the revision of the rotaliid genera and species from the Paleogene, in particular from the Lockhartia Sea. The Late Cretaceous ancestors are discussed and illustrated by Boix et al. (2009). Moreover, some taxa resembling rotaliids but belonging to other families are

also discussed and illustrated here in order to elaborate the definition of the Rotaliidae by showing what is not a rotaliid.

A revised diagnosis of the Rotaliidae is proposed as follows: Bilamellar-perforate shell composed of trochospirally arranged chambers that are connected by a single intercameral foramen in interiomarginal position. The chamber lumen is separated from the umbilical interocular space by an umbilical plate that is an extension of the septal flap. The umbilical plate delimits with a suture the folium, a triangular umbilical extension of the ventral chamber wall that has an anterior or median-ventral foliar aperture. There is a spiral and an intraseptal interocular space transformed in various ways into a canal system. The umbilicus is filled with shell material forming free umbilical plugs, numerous umbilical piles or a solid mass perforated by funnels.

Excluded from the rotaliids are trochospiral, bilamellar benthic foraminifera that lack any kind of columella, or with multiple foramina or with a tight system of enveloping canals on both, ventral and dorsal sides of the shell.

The Rotaliidae are subdivided here into subfamilies that have each a separate phylogenetic root in the Late Cretaceous or the Early Paleocene: the Rotaliinae with *Rotorbinella* since the Cenomanian, the Redmondinae with the Paleocene *Redmondina*, the Lockhartiinae with *Rotospirella* (Senonian), the Kathiniinae with *Kathina aquitanica* (Paleocene) and the Daviesiniinae with *Daviesina fleuriauxi* (Maestrichtian).

A key to the subfamilies and their generic subunits is given below. It is designed to help finding particular taxa discussed in this paper. Note that the key has been formulated for only those taxa discussed in this paper, not for all rotaliid genera mentioned by Loeblich and Tappan (1987). Thus, the key helps to find one's way in the systematic part of this paper but is not an instrument for classifying all described rotaliids.

2.3 Identification Key to the Paleogene Genera of the Superfamily Rotaliacea

Shell walls lamellar-perforate; chamber arrangement trochospiral; foramen single, in interiomarginal position; folium and umbilical plate present; face ventral	ROTALIACEA
Dorsal side smooth; periphery angular to sharp; dorsal side of shell evolute, ventral side involute; umbilicus filled with a single, undivided axial pile or a columellar filling	ROTALIIDAE
Columellar filling of the umbilicus by superposed folia fused at their adaxial tips or by a single, undivided pile. Few funnels may appear in the columellar umbilical fill revealing their composite nature	ROTALIINAE
Umbilicus filled with a single pile in axial position. Folia short, mostly free, unfused. Ventral septal furrows without feathering	<i>Rotorbinella</i>
Low trochospiral shells with a sharply angular periphery. Umbilicus covered by heavy, oblique foliar walls that do not fuse in the axis of the shell. No feathering nor an umbilical plug but an incipient columella formed by the foliar "propeller blades"	<i>Pyrenerotalia</i>
Hemispherical to conical shells with a coarse, dense perforation. Periphery rounded to angular but lacking any keel or imperforate bands. Sutures flush. The narrow umbilicus is filled with slender parallel piles, a single one per folium and separated by narrow funnels. The thin but extended folia cover more than half of the umbilical cavity	<i>Rotospirella</i>
Evolute dorsal surface of the shell smooth. Umbilicus filled with a columellar structure	<i>Rotalia</i>

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produced by the fusion of the adaxial tips of the folia with their secondary lamellation; shoulders of septal furrows feathered or smooth. Few, irregularly directed funnels

Umbilical silling fused to a compact mass perforated by few, large funnels that are not always parallel to the axis

Medocia

Umbilical walls very coarsely perforate. Spiral and cameral sutures flush, unmarked by imperforate shell material. Periphery rounded. Canal system with low numbers of dorsal orifices. Umbilicus empty or filled with parallel radial piles resulting from a thickening of the mostly imperforate foliar walls in successive whorls

REDMONDININAE

Spiral chambers dorsally evolute and inflated. Folia short, in the axis of the spiral chamber, free or touching each other to form a ring of imperforate material or small umbilical piles. Intraseptal interocular space undivided, an open radial slit on the ventral side, a single orifice at the dorsal intersection of the cameral with the spiral suture. There is a dorsal umbo producing a scarcely perforated, often brilliantly white cap on the apex of the shell

Redmondina

Broadly conical to lenticular shells with a wide umbilicus filled with umbilical piles that are generated by the thickening of the foliar walls and fused to a solid mass. In between the piles, numerous coarse funnels represent the umbilical interocular space. They spring from the triangular interocular space at the confluence of the interseptal space and two successive foliar chamberlets

Slovenites

Subspherical to hemispherical shells with coarsely perforated chamber walls covered by an enveloping canal system on the dorsal and the ventral sides of the shell. Some irregularly placed funnels maintain the communication in the umbilical cavity that is obscured by the ventral enveloping canal system

Rotaliconus

covering also large parts of the foliar walls

Subspherical shells with very thick, coarsely perforated walls. The dorsal side including the peripheral part of the shell exhibits an enveloping canal system. Umbilicus filled with radial, heavy piles fused to a solid umbilical mass pierced by funnels. No ventral enveloping canals

Pachyrotalia

Dorsal side evolute with various ornamental patterns or smooth, ventral side covered with a dense population of piles of similar, uniform size, without marking the axial realm. The folia cover each large parts of the shell face and support each the site of origin of the free umbilical piles. The folia exhibit an aperture in the foliar suture that is a slit approximately symmetric to the axis of the chamber. Foramen single, in interiomarginal position and of small size. Large shells may be constructed with multiple spirals of main chambers and a more or less distinct dimorphism of generations

LOCKHARTIINAE

Hemispherical shells with coarsely perforated chamber walls. Periphery angular to sharp and distinctly keeled. Spiral and cameral sutures imperforate and raised. Umbilicus often with few or without piles but filled with perforate, very long folia superposed like blades of a propeller. There is a large spiral canal

Rotalispira

Low-trochospiral shells with an evolute dorsal side and a wide umbilicus filled with numerous umbilical piles. Structural features corresponding to the definition of the subfamily. Dimorphism usually restricted to the nepiont. There are many species grouped according to their dorsal ornamental patterns in four parallel phyletic lines

Lockhartia

Low-trochospiral, large sized shells of low-conical to discoidal shape. Chamber arrangement in multiple spirals, at least in the microspheric

Dictyoconooides

(continued)

generation. The megalospheric generation has much smaller shells and may lack supplemental spirals. Foramen of small size, a compressed arch in interiomarginal position

High-trochospiral shells with a dorsal ornamentation of various kinds that characterizes the numerous species described in the literature. The surface of the shell face is restricted in size and much inclined in respect to the axis of the shell. The umbilical architecture is dominated by the large folia supporting umbilical piles. Due to the high-spined shell, the umbilical structures are distorted around the coiling axis

Sakesaria

Discoidal to roughly lenticular or conical shells. Chamber arrangement organized in single or multiple spirals. Chambers per whorl numerous and dense. Foramen single, a low arch or slit in interiomarginal position, immediately below the dorsal cover of the spiral chamber. The folia are small, inclined forward. Their tips are fused to each other and with the umbilical fill produced by the previous chambers to form a solid mass perforated by numerous parallel funnels. Some species may have a massive central umbo. No feathering

KATHININAE

Shells with simple spiral chamber arrangement. Umbilical architecture corresponding to the subfamily Kathinininae

Kathina

Shell discoidal, often distorted and irregular. Spiral multiple in both generations. Umbilical architecture conforms to the Kathinininae

Dictyokathina

Shell lenticular, with an unkeeled periphery. Chamber

Plumokathina

arrangement always single-spined. Umbilical plates heavy, admitting on their umbilical side a broad, spiral interocular space considered as a spiral canal. Dorsal and ventral umbos almost of equal size, smooth. Ventral intraseptal interocular space undivided, a radial slit with massive feathering visible also in axial sections as vertical striations

Heavily ornate, biumbilical shells with almost identical appearance on both sides of the shell. Dorsal surface ornate with pustules and pseudospines. Ventral surface with similar ornaments alined between radial furrows marking the septal sutures. Chambers dorsally and ventrally involute, almost symmetrical. Foramen asymmetrically V-shaped, bearing an asymmetrical “tooth” in axial section. The foramen is riding on the periphery of the previous whorl. Its asymmetry helps to identify the ventral and the dorsal side of the shell. The umbilical plate separates in both umbilici the chamber lumen from a kind of narrow umbilical canal on both sides of the shell

DAVIESININAE

Today the subfamily is not subdivided into several genera in spite of the recognition of four phyla evolving in parallel lineages. The reason for this is to stress the nevertheless close relationship of taxa that were attributed to many different families such as the *Miscellaneidae* or the *Nummulitidae*. Thus, coarsely or finely ornamented shells without or with trabecules, or forms with supplementary stolons resulting in folded septal flaps all bear the same generic name. More accurate definitions are revealed on species level

Daviesina

2.4 Identification Key to Some Genera Excluded from the Rotaliacea

Trochospiral shells with single, areal foramina and a “toothplate” as umbilical closure of the spiral chamber, with or without a dense enveloping canal system extending over the whole surface of the shell, or trochospiral shells with multiple areal foramina lacking any kind of plates.

Chambers arranged in a single, low trochospiral. Spiral chambers evolute on the dorsal side, involute on the ventral side, keeled and covered with spinose ornaments. Foramen a single, areal slit in the apertural face of the chamber. Presence of a “toothplate”	PARAROTALIINAE
Adaxial, umbilical piles separated from the more peripheral realm by a deep circular slit that represents the major part of the umbilical cavity	<i>Pararotalia</i>
Furrow between adaxial umbilical piles and more peripheral ventral ornaments covered by an extension in adaxial direction of the umbilical flap	<i>Neorotalia</i>
Ventral, bilamellar chamber walls extending as flying cover over a large part of the umbilical cavity. They are supported by radial piles like in <i>Lockhartia</i>	<i>Paralockhartia</i>
Chambers arranged in a single, almost plane spiral, involute on both sides, and covered on both sides by a narrow system of enveloping canals. Adaxial realms with umbos pierced by numerous funnels. Foramen a single, narrow slit extending obliquely over the adaxial apertural face. An umbilical plate separates the chamber lumen from the umbilical cavity	LAFFITTEININAE
Almost planispiral-involute shells with a rounded periphery. Enveloping canal system initiated by a double row of	<i>Laffitteina</i>

intraseptal canal orifices, similar on both sides of the test	
Lenticular shells with almost planispiral chambers that are involute on both sides. Periphery sharp but unkeeled. Foramen areal, comma-shaped slit. The enveloping canal system is derived from heavy feathering of the ventral septal sutures. Both umbos perforated by numerous radial funnels opening to the ambient environment as polygonal network	<i>Cuvillierina</i>

2.5 Identification Key for Some Rotalids with Single Foramina and Lacking Umbilical Plugs or Umbos

Small-sized, almost planispiral-evolute shells with a single foramen. Umbilical area flat or concave filled with long spikes. Ornamentation consisting of heavy parallel costae separately disposed over the lateral surface of each chamber in oblique direction in respect to the radius of the spiral	<i>Thalmannita</i>
Small-sized, trochospiral shell with a flat dorsal side and a concave umbilical side with an open umbilicus. Periphery truncate, with a double carina. Single areal foramen. Interocular space wide open in the septa and with a large, spiked orifice opening to the ambient environment in the septum between the two peripheral carinas	<i>Civrieuxia</i>

2.6 Identification Key for Some Rotaliid Shells with Multiple Areal Foramina

Small-sized shells near to planispiral, with an inflated rounded periphery. Foramina multiple, each with a circular peristome. Umbilicus covered by extensions of the ventral wall of the spiral chambers. These support	<i>Scarificatina</i>
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an abaxial ornamentation of radial rows of minute pustules. The axial area of the umbilicus is dominated by one or several parallel, straight ridges that are independent of the number or shape of the spiral chambers. Each ridge separates a double line of tubular openings	
Trochospiral, lamellar-perforate shells with sets of multiple areal foramina with peristomes. They cover large, interiomarginal areas of the septal face. No true umbilicus nor canal system	CINCORIOLINAE
Hemispherical, dorsally evolute and ventrally involute shells with smooth walls that present a uniform, dense perforation. Periphery rounded or sharply angular. Septa dorsally straight, bent backwards and ventrally extending over the axial area, covered by numerous, closely spaced foramina that extend over the whole face of the shell. There is no true umbilicus nor umbilical plates	<i>Cincoriola</i>
Lenticular to subspherical shells with involute spiral chambers. Septa extending over the axial area of the shell, with multiple foramina bearing heavy, circular peristomes. Septa with intraseptal canal systems opening into both, dorsal and ventral umbilicus	<i>Rahaghia</i>
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2.7 Identification Key for Some Rotaliid Shells of the Family Victoriellidae	
Dorsally evolute, ventrally involute, subspherical to conical shells with a false umbilicus filled with partially fused pustules growing on the shoulder of the umbilical depression. Interocular space opening dorsally in a single orifice. Foramen a single, interiomarginal arch	<i>Gyroidinella</i>
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