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BIOSTRATIGRAPHY AND EVOLUTION OF LARGER ROTALIID FORAMINIFERA IN THE CRETACEOUS-PALEOGENE TRANSITION OF THE SOUTHERN OMAN MOUNTAINS

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Abstract: A site in the western flank of Jabal Ja'alan (Oman Mountains) reveals an exceptional succession across the Cretaceous-Paleogene boundary. The sampled interval comprises a series of carbonates deposited in shallow-water platform environments and belonging to the Murka Formation, which lies between the Simsima and Abat formations of latest Cretaceous and Thanetian age, respectively. The larger foraminifera recovered from this interval belong essentially to the group of larger rotaliids (Rotaliidae). Two new genera and two new species are here described, Praelockhartia neoakbari gen. nov., sp. nov. and Rotaliidium parvum gen. nov., sp. nov. The former shows a very characteristic architecture of an umbilicus with strong piles and two types of umbilical cavities, while the latter has characteristic dorsal supplementary chamberlets. Other species such as Rotalia cf. jacobi, Rotorbinella hensoni, Rotospirella conica and Lockhartia sp. complete the rotaliid assemblage. The entire assemblage can be considered to be of late Danian age and to belong to shallow benthic zone SBZ 2. The larger rotaliids appear to have recovered and diversified earlier than any other larger benthic foraminifera in the region after the K/Pg crisis. The rotaliids from the Murka Formation also appear to be linked to the Lockhartiinae and to play a special role in improving our understanding of subsequent diversification in the Lockhartia Sea. A new subfamily, Praelockhartiinae, is erected to accommodate all primitive forms that are architecturally close to lockhartiids.

Key words: Foraminifera, Rotaliidae, Maastrichtian, Danian, Paleocene.

AFTER the great evolutionary success of larger benthic foraminifera during the Late Cretaceous maturation cycle (*sensu* Hottinger 2001), which resulted in a wide distribution and diversification in shallow-marine settings at tropical and subtropical latitudes, the vast majority of species failed to survive the global biological crisis across the Cretaceous-Paleogene (K/Pg)

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boundary. Whilst these complex-celled, symbiont-bearing organisms suffered greatly from this crisis, the deep-sea benthic foraminifera show lower extinction rates globally (Alegret & Thomas 2005, 2013). The loss of larger foraminifera at the end of the Cretaceous might be linked to critical changes in environmental parameters along shallow-marine platforms such as temperature, light, depth and nutrient supply, i.e., parameters that impacted the mode of life and distribution of larger foraminifera (see, among others, Leutenegger 1984; Hallock 1988; Hohenegger 1995; Goldbeck & Langer 2009).

The K/Pg boundary is one of the best-studied geological crises worldwide, but the paucity of continuous successions across this interval in shallow-water carbonate-platform facies hinders any characterisation of the evolution of benthic communities. In spite of the existence of such carbonate, larger foraminifera-bearing successions (Roger *et al.* 1998; Schlüter *et al.* 2008) in the Oman Mountains, detailed studies of the architecture and phylogenetic relationships of these organisms are still lacking.

The present paper focuses on the micropalaeontological content of an important site on the western flank of Jabal Ja'alan (Oman Mountains; Fig. 1) that exposes an exceptional succession across the Cretaceous—Paleogene boundary. To date, this has remained largely unstudied, at least as far as larger foraminifera are concerned. Among the foraminiferal assemblages recovered from the stratigraphical succession sampled, we have focused on an analysis and characterisation of the larger rotaliids from the Murka Formation, which encompasses the K/Pg transition (Roger *et al.* 1998; Schlüter *et al.* 2008). The aims of the present paper are to describe the species found in this stratigraphical unit and discuss their phylogenetic relationships. These objectives have allowed a better evaluation of the environmental impact of this global crisis on the history of earliest Paleogene larger foraminifera from a local and a regional perspective.

GEOLOGICAL SETTING AND STRATIGRAPHY

The larger rotaliid foraminifera studied in the present paper were collected from shallow-water platform deposits assigned to the Murka Formation, which comprises uppermost Cretaceous and lowermost Paleogene strata that crop out along the western flank of Jabal Ja'alan in the Oman Mountains. These mountains constitute a geographical unit along the northeastern margin of the Arabian Plate. Due to this location, its geological history has been strongly influenced by major tectonic events related to the collision and suturing of the Tethyan Ocean (Filbrandt *et al.* 1990; Fournier *et al.* 2006). The palaeoenvironmental changes resulting from these tectonic events can be clearly observed, especially in the mid-Cretaceous to lower Paleocene successions, reflecting the change from a stable tectonic period that controlled the sedimentation during the Albian and Cenomanian to the various phases of deformation that occurred during post-Turonian times (Hughes-Clarke 1988; Scott 1990; Van Buchem *et al.* 1996; Grélaud *et al.* 2010, among others).

During the late Maastrichtian, regional tectonic activity came to a halt and the margins subsided and permitted the persistence of carbonate sedimentation up to the end of the Cretaceous and into the early Paleogene (Roger *et al.* 1998; Serra-Kiel *et al.* 2016). This

resulted in deposition of shallow-marine limestones that are now assigned to the Simsima and Murka formations, the latter under a more restricted platform conditions. The Murka Formation, from which the larger rotaliidsof the present paper were collected, is a late Maastrichtian to Danian unit that is restricted to the Sur area (Roger *et al.* 1998), overlying the Maastrichtian rudist-bearing Simsima Formation (Glennie *et al.* 1974; Fournier *et al.* 2006 and references therein) and overlain itself by Paleocene and Eocene carbonates and marls of the Abat Formation. In the northern Sur area, on top of the Murka Formation rest upper Danian to lower Selandian carbonates and marls of the Sayq Formation (Serra-Kiel *et al.* 2016). The Murka Formation at Jabal Ja'alan consists of a succession of around 70 metres of carbonates, essentially wackestones, packstones and grainstones that formed in shallow-water platform settings. The first 10 metres are characterised by the absence of larger foraminifera. The overlying limestones yield assemblages that are relatively rich in rotaliids and calcareous algae (Fig. 2).

MATERIAL AND METHODS

The section studied is located along the western flank of Jabal Ja'alan (UTM 40 Q 737792 2452885; co-ordinates 22°9'53.40"N, 59°18'21.39"E; see Fig. 1) and comprises deposits of a shallow-water platform domain that persisted from the Maastrichtian to the early Paleocene. The palaeontological content of the samples collected was studied by taking thin sections of the hard carbonate rocks. The material illustrated in the present paper (Table 1; Supplementary material) is housed in the palaeontological collections of the Museu de Ciències Naturals de Barcelona (abbreviation MGB).

SYSTEMATIC DESCRIPTIONS (by Vicent Vicedo and Raquel Robles-Salcedo)

This published work and the nomenclatural acts it contains have been registered with Zoobank: http://zoobank.org/References/2C593081-4021-4396-9FE1-3CA5E22596E5

Class GLOBOTHALAMEA Pawlowski, Holzmann & Tyszka, 2013

Order ROTALIIDA Delage & Hérouard, 1896

Superfamily ROTALIOIDEA Ehrenberg, 1839

Family ROTALIIDAE Ehrenberg, 1839

Subfamily ROTALIINAE Ehrenberg, 1839

Genus ROTORBINELLA Bandy, 1944

Type species. Rotorbinella colliculus Bandy, 1944.

Rotorbinella hensoni (Smout, 1954)

Figure 3

1954 Rotalia hensoni Smout, p. 45, pl. 15, fig. 8.

1972 Rotalia perovalis (Terquem); Samuel et al., pl. 37, figs. 1–4.

1972 Rotalia sp. 1; Samuel et al., pl. 37, fig. 5.

1972 Rotalia? sp. 2; Samuel et al., pl. 37, fig. 6.

2006 Rotorbinella sp.; Hottinger, p. 86, pl. 2, figs. 11–16.

2014 Rotorbinella detrecta Hottinger, p. 26, pl. 3/4A-H.

Description. Shell lamellar, with low conical morphology. Periphery acute with imperforate keel. Dorsal side evolute and convex with smooth surface; ventral side flat to slightly convex. Aperture simple and in interomarginal position. No dimorphism recognised. Proloculus around 40–45 μm in diameter, followed by trochospirally arranged chambers. Adult shells with diameters of 0.7–0.9 mm and height of 0.3–0.5 mm, with 3–4 trochospiral whorls and 7–8 chambers in ultimate whorl. Height/diameter (H/D) ratio varying between 0.7 and 0.9. Umbilical zone filled with massive structure consisting of single umbilical pile, or umbilical plug, standing free and separated from foliar tips bydeep spiral fissure. Umbilical plate separating main chamber lumen from umbilical spiral canal. Folia small and imperforate, with foliar sutures.

Remarks. As pointed out by Hottinger (2014, p. 24), R. hensoni has traditionally been used to encompass "Rotorbinellas lacking features of specific character" and appearing over an extensive wide stratigraphical range, from the Paleocene to lower Ypresian. The controversy surrounding R. hensoni is rooted in the original paper by of Smout (1954), who described the species solely on the basis of external characters, without mention of the nature of its internal features such as the size of the embryo or the number of chambers per whorl. According to current consensus, however, morphometric data are essential in the study of populations and, in particular, in specific classification. The fact that Smout illustrated only a single specimen (Smout, 1954, pl. 15, fig. 8) did not help in the clarification of the specific characters of R. hensoni, hampering later revisions of this species. Aware of all the controversy around R. hensoni, Hottinger restudied the type material in the collections of the Natural History Museum (London). It would appear that Hottinger was not able to complete this architectural revision in particular before his death, as is suggested by the unfinished sketch of the holotype published in his monograph (Hottinger, 2014, p. 28, fig. 3.2). In line with this, Hottinger's remarks on R. hensoni (op. cit., p. 24) did not clarify the controversy because he did not present any detailed description of the type material in terms of morphometry. To make matter worse, some important features that can be observed in his illustrations do not match those mentioned by Smout. The scale bar of Hottinger's sketch of the holotype indicates a diameter of 1.3 mm, i.e., larger than the 0.9 mm given in the original description by Smout as maximum diameter. Further, Hottinger's illustrated specimens of R. hensoni were collected from upper Paleocene and lower Eocene strata in southern France, which means a different stratigraphical and palaeogeographical context to that of Smout's material, which was from "the lower part of the Paleocene of Qatar". Considering all these facts, we can affirm that R.

hensoni remains a taxon of uncertain architectural characteristics that needs a careful revision and redefinition by means of a restudy of the type material. This is beyond the scope of the present paper. Any future study should include a comprehensive overview of all populations that have been attributed to date to *R. hensoni* in order to evaluate its intraspecific variability based on a solid stratigraphical background. In the meantime, the external description and dimensions given by Smout for *R. hensoni* should be used to constrain the specific identification, grouping all the "small-sized" and stratigraphically older populations. The specimens illustrated by Hottinger as *R. hensoni* could represent a different species, due to the larger size and different (i.e., younger) stratigraphical context. In contrast, both the external features of our specimens and their stratigraphy match the description supplied by Smout for *R. hensoni*. Further, the species *R. detrecta*, described by Hottinger (2014), from the shallow benthic zone (SBZ) 2 of the Pyrenees shows similar morphometrics to *R. hensoni* (i.e., maximum diameters of 0.8 mm and 0.9 mm, respectively; height of 0.3 mm and H/D ratios of 0.4 for both species). *Rotorbinella detrecta* should be considered a junior synonym of *R. hensoni*.

Genus ROTALIA Lamarck, 1804

Type species. Rotalites trochidiformis Lamarck, 1804.

Rotalia cf. jacobi Sander, 1962

Figure 4

1962 Rotalia jacobi Sander, pp. 15, 16, pl. 3, figs. 13–20.

1991 Rotalia saxorum d'Orbigny; Wan, p. 10, pl. 1, figs. 11–12.

Description. Test conical with thin lamellar wall. Dorsal side smooth and evolute, lacking ornamentation, showing merely weak spiral suture. Ventral side flat to slightly convex. No dimorphism observed. Embryo composed of protoconch and deuteroconch with diameters of 66–78 μ m and 53–65 μ m, respectively, followed by chambers arranged trochospirally in at least 2 to 3 whorls, with 7–9 chambers in ultimate whorl. Maximum diameter observed about 0.9 mm and height about 0.5 mm. H/D ratio around 0.6. Umbilical zone filled with characteristic columella produced by fusion of foliar adaxial tips. Ventral face covered by thin cylindrical papillae. Foliar suture strongly marked, easily identified as very typical infold in both axial and transverse sections.

Remarks. The specimens of *Rt.* cf. *jacobi* illustrated by Sander (1962) in the original description appear to show dissimilar external features. The author himself admitted that "ornamentation is variable" (see Sander 1962, p. 15) among specimens. Whether these external differences observed are a consequence of differential preservation or the result of grouping different morphotypes is a question that cannot be resolved here, but for now we favour the latter hypothesis. A detailed analysis of external features of the type population shows that two

morphotypes can be distinguished. One of these seems to have a more delicate chamber wall with dorsal ornamentation and fine sculpture on pronounced spiral and chamber sutures (see Sander 1962, pl. 3, figs. 13–15). This morphotype also reveals a flat ventral side with an umbilical structure composed of folia fused at their adaxial tips, which suggests a columellar structure. The other form shows a smooth dorsal side, lacking any ornamentation, and an umbilical structure based on free-standing piles (see Sander 1962, pl. 3, figs. 16–18). This umbilical structure extends towards the direction of growth giving it a marked degree of convexity. We agree with Sander (1962) in identifying the first morphotype as a species of *Rotalia*, but we have serious doubts about the generic placement of the second, which is externally closer to *Rotospirella conica* or *Praelockhartia neoakbari* gen. nov., sp. nov. than to a true member of *Rotalia*. This issue is even more difficult to resolve because Sander did not designate a holotype. More material, a designation of a lectotype and a proper description of the internal characteristics are needed in order to confirm or reject identifications. We tentatively ascribe our specimens of *Rotalia* to *Rt.* cf. *jacobi* on account of their similar features such as external ornamentation and size.

Praelockhartiinae subfam. nov.

LSID. urn:lsid:zoobank.org:act:B8AB164F-7268-4C60-AA3A-69A71BBCA488

Type genus. Praelockhartia gen. nov.

Diagnosis. Rotaliid with coarse perforated test. Dorsal side smooth or showing slight to thickened spiral suture due to inflational ornamentation of chamber margin. Ventral side flat to slightly concave with piles. Umbilical structure based on folia differentiated from chamber wall by marked notch. Folia fused at adaxial tips forming piles. Secondary lamellation producing two types of umbilical cavities: one located irregularly among piles (i.e., interpile umbilical cavities) and other produced by folium foldings at peripheral part of umbilical zone, betweenchamber wall and piles (i.e., umbilical peripheral cavities). Second type forming complex structure of irregular cavities consisting of both well-developed foliar chamberlets and cavity produced by notch suture when covered by outer lamella of following chambers.

Differential diagnosis. The new subfamily differs from representatives of other rotaliid subfamilies by the combination of umbilical piles and the complex and irregular structure of peripheral umbilical cavities.

Remarks. In addition to the new genus Praelockhartia (see below), we assign the genus Rotospirella Hottinger, 2014 to the Praelockhartiinae subfam. nov. We also include Rotalispira Hottinger, 2014 because its type species, R. scarsellai (Torre, 1966), shows some poorly developed umbilical cavities (see Hottinger 2014, pl. 5.1, figs. 9, 16, 20 and 21) and R. pyrenaica Hottinger, 2014 has slender umbilical piles. In our opinion, the recently described Cretaceous species Rotalispira vitigliana Consorti, Frijia & Caus, 2017 and R. maxima Consorti, Frijia & Caus, 2017 should be restudied and their generic attribution re-evaluated as they appear to show an umbilical structure that is dissimilar to the one of the type species of the genus; both seem to lack any kind of umbilical cavity. The genus Rotalispirella Consorti,

Villalonga & Caus, 2017 could also be included in the new subfamily, because of the presence of thin umbilical piles and poorly developed interpile cavities (see Hottinger 2014, figs. 5.13 and 5.25). However, the architecture of this genus should be addressed because the main traits are not detailed in the original description. *Rotalispira acuta* Consorti, Villalonga & Caus, 2017 shows architectural features that are similar to those of *R. scarsellai*; for example, see the incipient double-keeled test in Hottinger 2014, fig. 5.1–22.

PRAELOCKHARTIA gen. nov.

LSID. urn:lsid:zoobank.org:act:F2752076-39D0-45CB-AE96-6D3B52ED78A3

Type species. Praelockhartia neoakbari sp. nov.

Etymology. Prae-, Latin for 'before', and Lockhartia; gender feminine.

Diagnosis. Test coarsely perforated, conical to hemispherical. Aperture simple, consisting of slit in interomarginal position. Embryo composed of three subspherical chambers (triconch) followed by chambers arranged trochospirally. Chambers with rounded periphery and thick wall. Dorsal side convex, evolute and smooth, lacking ornamentation. Spiral suture visible by absence of coarse perforation. Ventral side flat to slightly convex, ornamented with piles. Strongly marked notch extending into internal infold or furrow in lateral-ventral chamber wall (foliar suture), separating main chamber lumen from foliar chamberlet. Irregular peripheral umbilical cavities present. Long folia fused at adaxial part of umbilicus, forming piles separated by very narrow funnels. Poorly developed umbilical cavities present between piles. Main chamber lumen and umbilical spiral canal separated by umbilical plate (see architectural model in Fig. 5).

Differential diagnosis. Praelockhartia gen. nov. differs from other genera included in the Lockhartiinae by Hottinger (2014) by its more massive umbilical structure (based on strong piles and an absence of regular interpile umbilical cavities) and by its smooth dorsal surface. Rotospirella and Rotalispira differ from Praelockhartia gen. nov. by the absence of strong piles, by their thinner and more delicate folia and slightly smaller notches.

Praelockhartia neoakbari sp. nov.

Figures 6-8

LSID. urn:lsid:zoobank.org:act:E9D9E46D-13DA-4374-BA23-FE27A4ECDAE7

(?)1978 Lockhartia n. sp.; Rahaghi, pl. 12, figs. 5-6.

1983 Rotalia aff. trochidiformis; Rahaghi, p. 36, fig. 10.

Etymology. From the Greek *neo*, meaning new, and *akbari*, the species formerly considered a biomarker of SBZ 2 (see below).

Ttypes. The holotype is MGB 59865 LP2.95 (Fig. 6M); axial height 560 μ m, equatorial diameter 790 μ m. The other specimens illustrated in Figures 6–8 are paratypes.

Diagnosis. Lamellar-perforated wall with coarse pores. Test conical to hemispherical. Simple, slit-shaped aperture in interomarginal position. Rounded periphery with imperforate margin. Dorsal side evolute and smooth, lacking ornamentation; spiral suture slightly marked. Ventral side flat to slightly convex, ornamented with piles. No dimorphism observed. Protoconch diameter 85–115 μm.Embryo followed by chambers arranged trochospirally, composed of up to 2.5–3 whorls. Adult shells with diameter of around 1 mm (0.9–1.2 mm, minimum and maximum observed) and height of about 0.6 mm, with H/D ratio of conical shell around 0.6–0.7. Main chamber lumen separated from umbilical spiral canal and foliar chamberlet by umbilical plate. Chambers increasing in size during growth. Spiral suture visible by absence of coarse perforation. Notch strongly marked extending into internal infold or furrow in lateral-ventral chamber wall forming kind of foliar suture separating ventral part of chamber from folia at umbilical zone. Notch covered by secondary lamellation forming irregular peripheral umbilical cavities. Long folia fused at adaxial tips, forming piles separated by very narrow vertical spaces or funnels. Primitive, poorly developed umbilical cavities appearing in umbilical zone.

Genus ROTOSPIRELLA Hottinger, 2014

Type species. Lockhartia conica Smout, 1954.

Previous remarks. This genus was described by Hottinger (2014) to accommodate the rare original material of *Lockhartia conica*, a species described by Smout (1954) from the Paleocene of Qatar, and other specimens from the Zagros Mountains, Iran (no age given for thelatter). Hottinger (2014) presented only a brief description of *Rotospirella*, not a true diagnosis, failing to provide a full explanation of all basic architectural traits. In order to avoid any future controversy, we consider it of importance to complete the generic and specific diagnoses by describing other diagnostic key traits not considered by Hottinger. In order to do so, we have re-examined high resolution pictures of the type series of *R. conica* (paratypes are available online through the webpage of the Natural History Museum, London) and of the material from Iran figured by Hottinger (2014).

Diagnosis (emended). Lamellar-perforated, conical shell with trochospiral chamber arrangement and rounded periphery. Very thick, coarsely perforated wall. Dorsal side evolute with smooth surface. Ventral side slightly ornamented with rounded protuberances produced by umbilical piles. Single aperture in interomarginal position. Main chamber lumen and umbilical spiral canal separated by umbilical plate. Long and delicate folia extending and fusing at adaxial part forming piles and funnels. Two types of cavities appearing in umbilicus: umbilical interpile cavities and umbilical peripheral cavities. Dimorphism not observed.

Differential diagnosis. Rotospirella differs from all other genera included in the subfamilies Rotaliinae Ehrenberg, 1839 and Lockhartiinae Hottinger, 2014 by having an umbilical structure based on piles and two types of umbilical cavities.

Rotospirella conica (Smout, 1954)

Figure 9

1954 Lockhartia conica Smout, p. 53, pl. 4, figs. 1–3.

1991 Lockhartia conica Smout; Wan, p. 162, pl. 1, figs. 28, 29.

2011 Lockhartia conica Smout; Boukhary et al., p. 44, pl. 4, figs. 1–4.

2014 Rotospirella conica (Smout); Hottinger, p. 31, fig. 3.6.

Diagnosis (emended). Lamellar-perforated and high conical shells with rounded apex and periphery. Very thick, coarsely perforated wall. Dorsal side evolute with smooth surface. Ventral side flat, slightly concave and ornamented with rounded protuberances produced by umbilical piles. Single aperture in interomarginal position. Dimorphism not observed. Megalospheric generation starting with large proloculus of around 150 μ m, followed by chambers arranged trochospirally. Umbilical spiral canal connecting all chambers at umbilical zone. Long and delicate folia extending and fusing in their adaxial part forming piles and funnels. Umbilical cavities appearing in peripheral part of umbilicus and between piles. Axial diameter for adult specimens around 1–1.5 mm (mean1.3 mm) and 2–3 whorls. H/D ratio around 0.8.

Remarks. We refer some of our material to this species on account of their general architecture and delicate folia.

Subfamily LOCKHARTIINAE Hottinger, 2014

Genus LOCKHARTIA Davies, 1932

Lockhartia aff. conditi (Nuttall, 1926)

Figure 10

Description. The rare material collected shows a conical test with rounded periphery; axial section with an oval outline. Dorsal side evolute with slight ornamentation. Aperture as a slit, located in interomarginal position. Folia very long and fusing to form piles and funnels. Regular umbilical cavities appearing among piles; typical of genus. Maximum diameter observed around 1.1 mm and H/D ratio around 0.6, with proloculus of about 55 μ m.

Differences and similarities. Our specimens seem to be architecturally close to Lockhartia conditi, but are smaller. We have left them in open nomenclature in view of the paucity of the material.

ROTALIOIDEA indeterminate

Genus ROTALIIDIUM nov.

LSID. urn:lsid:zoobank.org:act:6A8B4458-C1AE-4810-A73B-8D24EFC7DC86

Type species. Rotaliidium parvum sp. nov.

Etymology. From the rotaliform shape and the Latin suffix -idium, a diminutive form in reference to its small size; gender neuter.

Diagnosis. Lamellar-perforated test with low to very low trochospiral chamber arrangement. Dimorphism not observed, but presumably restricted to early stages of growth. Aperture slit in interomarginal position. Advolute chambers with rounded periphery. Umbilicus filled with fused folia forming small and massive plug. Dorsal and ventral sides slightly convex. Supplementary spiral apertures along spiral suture connecting main chamber lumen with dorsal supplementary spaces or chamberlets. Umbilical spiral canal and main chamber lumen separated by umbilical plate.

Differential diagnosis. This new genus is closely related to *Rotorbinella*, the umbilical structure based on fused folia forming a massive plug being similar in both genera. However, the former differs from the latter in having dorsal sutural apertures that connect the main chamber lumen with the small dorsal supplementary spaces or chamberlets. The combination of these two features, i.e., the umbilical plug and dorsal supplementary chamberlets, in the same morphotype, differentiate the new genus from all other rotaliids described to date.

Rotaliidium parvum sp. nov.

Figures 11-12

LSID. urn:lsid:zoobank.org:act:5630898A-6760-4C04-B322-7510F23F1D87

Etymology. From the Latin parvum, meaning small, in reference to its size.

Types. The holotype is MGB 59865 LP6.134 (Fig. 11D), axial height 175 μ m, equatorial diameter 300 μ m. The other specimens illustrated in Figures 11 and 12 are considered paratypes.

Diagnosis. Lamellar-perforated test with low to very low trochospiral chamber arrangement and rounded periphery. Single, slit-shaped aperture in interomarginal position. Advolute chambers. Umbilicus filled with small massive plug. Dorsal and ventral sides slightly convex, smooth surface, lacking ornamentation. Small proloculus of around 4 μ m in diameter. Maximum diameter of adult specimens around 300–340 μ m. H/D ratio of around 0.6. Spiral apertures connect main chamber lumen with dorsal supplementary chamberlets. Umbilical spiral canal separated from main chamber lumen by umbilical plate.

THE K/Pg INTERVAL IN THE OMAN MOUNTAINS: DROP AND INCREASE OF THE LARGER FORAMINIFERAL DIVERSITY

When considering 'a community' to be a group of species living together in a certain area and delimited by discontinuities (Hottinger 2001), the different populations of larger benthic foraminifera observed across the K/Pg interval in the Oman Mountains represent different states of equilibrium between species and environment. The K/Pg boundary represented a negative turning point for K-strategists among foraminifera, the vast majority of Late Cretaceous species going extinct. Based on our observations at Jabal Ja'alan, it seems that it took millions of years for the larger foraminiferal community to reach a peak of maturation again thatwas characterised by a rich and diverse assemblage of species (see distribution chart; Fig. 13).

The latest Cretaceous representatives

The mature larger foraminiferal community, documented by a great abundance and diversity of species, during the Late Cretaceous is represented in the Oman Mountains by populations in the Qhalah and Simsima formations (Roger et al. 1998; Abdelghany 2003, 2006). At Jabal Ja'alan, the uppermost strata of the Simsima Formation contain an assemblage of larger foraminifera that comprises *Broeckina* cf. dufrenoyi (d'Archiac & Haime, in d'Archiac, 1854), Fissoelphidium operculiferum Smout, 1954, Loftusia morgani Douvillé, 1904, Omphalocyclus macroporus (Lamarck, 1816), Pseudomphalocyclus blumenthali? Meriç, 1980, Siderolites calcitrapoides? Lamarck, 1801, Stomatorbina binkhorsti (Reuss, 1862) and the dasycladacean alga Trinocladus radoicicae Elliott, 1968 (Fig. 14). This assemblage, which can also be observed in several other sections exposed in the Abat region and the remainder of the Oman Mountains, is of Maastrichtian age and its members can be considered to be the latest representatives of the Cretaceous in the study area. These abundant and diverse Omani Cretaceous populations deserve detailed taxonomic studies in the future, as they show architectural differences with respect to their western Tethyan relatives. Such is the case with siderolitids, which have dissimilar structural traits in respect to the forms described to date.

The earliest Paleogene representatives

The palaeoecological conditions that allowed the development and spread of such a high diversity during the Late Cretaceous subsequently changed. The assemblage of the Murka Formation is composed mainly of the larger rotaliid species *Praelockhartia neoakbari* gen. nov., sp. nov., *Rotaliidium parvum* gen. nov., sp. nov., *Rotalia* cf. *jacobi*, *Rotospirella conica*, *Lockhartia* aff. *conditi* and *Rotorbinella hensoni*. In some samples, other taxa co-occur, including *Idalina* sp., *Valvulina triangularis* d'Orbigny, 1826, *Gyroidina* sp., *Quinqueloculina* sp. and *Stomatorbina binkhorsti* (Reuss, 1862) (Fig. 14). At Jabal Ja'alan the K/Pg boundary was difficult to identify as it is restricted to a minor sedimentary discontinuity, as pointed out by Roger *et al.* (1998, p. 267). The presence of the dasycladaceans *Halimeda* sp., *Jodotella* sp., *Cymopolia* sp., *Indopolia satyavanti* Pia, *in* Rao & Pia, 1936, *Clypeina* sp., *Neomeris* sp. and Bryopsidales indet. (Fig. 15) in association with the larger rotaliids suggest that the deposits are of Paleocene age (see Schlüter *et al.* 2008, for a similar Paleocene assemblage). The absence of biomarkers of SBZ 3, which appear higher in the succession (see below) and correlation of the Murka Formation with the planktonic biozones P1 to P3 in neighbouring areas (see Roger *et al.* 1998;Serra-Kiel *et al.* 2016), allows us to suggest that the rotaliid

assemblage belongs to SBZ 1 or 2, of Danian age. Concerning these two SBZs, it is fairly well known that there is no clear biomarker for SBZ 1, with the exception of *Bangiana hanseni* Drobne, Ogorelec & Riccamboni, 2007, because *Laffitteina bibensis* Marie, 1946, also recorded to be characteristic of this biozone, has a longer range (Inan *et al.* 2005). On the basis of our observations at Jabal Ja'alan, the SBZ 1 seems to be restricted to a thin interval with no significant foraminiferal benthic biomarkers, as observed in lowermost Paleocene deposits outcropping in other regions such as the western Pyrenees (Serra-Kiel, J., Vicedo, V., Baceta, J.I., Bernaola, G. and Robador, A., unpublished data) and other areas in the Neo-Tethys (Zhang *et al.* 2013). At Jabal Ja'alan, this lowermost short interval of the Murka Formation should be resampled and restudied in much more detail in future in order to discard definitively any hiatus due to erosion or non-deposition in the lowermost Danian.

The overlying Selandian to early Thanetian assemblage

The rotaliids of the Murka Formation are followed by another rich larger foraminiferal assemblage of the Abat Formation, comprising *Keramospherinopsis* sp., *Kathina* cf. *major* Smout, 1954, *Daviesina* sp., *Periloculina*? spp., *Lockhartia retiata* Sander, 1962, *L. diversa* Smout, 1954, *L.* cf. *altispira* Smout, 1954 and *L. praehaimei* Smout, 1954. This assemblage can be attributed to SBZ 3, indicating a Selandian to early Thanetian age (Fig. 16). The Abat Formation is equivalent, according to Roger *et al.* (1998), to the lower part of the Jafnayn Formation. This rich assemblage, which also calls for further research because of its extraordinary diversity, seems to mark the total recovery in this area of the palaeoecological conditions of shallow-water platforms.

ROTALIIDS IN THE OMANI "CRETACEOUS-PALEOGENE TRANSITION"

The near-exclusive presence of rotaliids in the Murka Formation also appears to be in accordance with other findings in the K/Pg transition in Oman and surrounding areas. Micropalaeontological baseline studies for the Arabian Peninsula, such as the monographs by Sander (1952) and Smout (1954), dealt essentially with rotaliids as the most representative group of larger foraminifera of the early Paleocene. However, this pattern can also be found in other locations of the Neo-Tethys Ocean, such as the Indus Basin, where larger rotaliids are commonly reported from SBZs 1 and 2 (Afzal 2011; Afzal et al. 2011; Zhang et al. 2013; Kahsnitz et al. 2016, among others). The presence of rotaliids across the K/Pg transition at Jabal Ja'alan was also noted in a reference study by Roger et al. (1998). According to those authors, the upper part of the "basal sequence" of the Murka Formation contained "rotaliinés" such as Rotalia cf. trochidiformis and a "poorly evolved form" of Lockhartia diversa (Roger et al. 1998, p. 265). They considered this assemblage to be typical of the "Cretaceous-Paleogene transition" in restricted platform facies of the Arabian Peninsula. Despite the fact that they sampled the Murka Formation along the eastern flank of Jabal Ja'alan and in other neighbouring areas (see Roger et al. 1998, p. 264, figs. 8-9), it is very likely that their rotaliid morphotypes are the same as ours. Similar to Smout (1954), they distinguished two morphotypes, yet probably provided erroneous identifications. For instance, their Rotalia cf. trochidiformis could in fact be Rt. cf. jacobi and Lockhartia diversa might be a misidentification of some lockhartiform, such as Rotospirella conica or Praelockhartia neoakbari gen. nov., sp.

nov. If the latter, the confusion could be rooted in the resemblance of *RII. conica* to lockhartiines (see below). Further, other findings support the idea of such a misidentification, especially in the latter case, as recent studies have confirmed that *Lockhartia diversa* is younger, more complex and more evolved than *RII. conica* (see Hottinger 2014, p. 10, range chart) and *P. neoakbari* gen. nov., sp. nov. Therefore, it is highly improbable to find *L. diversa* in the middle part of the Murka Formation, considering that the age is constrained by the upper and lower larger foraminiferal assemblages. In any case, it seems clear that larger rotaliids played a dominant role in the shallow-water carbonate platform environments after the Cretaceous-Paleogene biotic crisis on a regional or even global scale.

THE SPECIES LOCKHARTIA AKBARI AS A BIOMARKER FOR SBZ2

Among all taxa considered in the literature as markers for SBZ 2, the current status of *Lockhartia akbari* and *Paralockhartia eos* is in need of some brief comments. These species were first mentioned in a reference paper by Serra-Kiel et al. (1998) as biomarkers of SBZ 2, together with *Miscellanites globularis* (Rahaghi, 1978) and *Ornatononion minutus* (Rahaghi, 1983). The former were cited as follows: "akbari Hottinger & Tambareau in press, *Lockhartia* [pl. 12, fig. 1-7: Rahaghi, 1978]

eos Hottinger & Tambareau in press, *Paralockhartia* [pl. 1, fig. 1-8: Hottinger & Tambareau, in press]"

Since then, these species have been mentioned as characteristic of SBZ 2 (Tambareau et al. 1997; Inan & Inan 2008; Khasnitz, 2017, among others), although they were not formally described. They were even included as biomarkers in the descriptive tables of SBZs included in successive editions of the Geological Time Scale (Gradstein et al. 2004, 2012). Eventually, the species Paralockhartia eos was validly published by Hottinger (2014). In contrast, Lockhartia akbari currently is a nomen nudum (Pignatti 1998; Kahstniz 2017). As a matter of a fact, Hottinger (2014) did not even mention this latter species in his monograph of the Paleogene rotaliids, and synonymised Rahaghi's specimens (cited in Serra-Kiel et al. 1998 as L. akbari) with Lockhartia retiata Sander, 1962. Judging from the architecture of Rahaghi's specimens and that of L. retiata, we disagree with the synonymy proposed by Hottinger. Some of Rahaghi's specimens, described in 1978 as Lockhartia n. sp., are, in our opinion, architecturally closer to our specimens of Praelockhartia neoakbari gen. nov., sp. nov. than to L. retiata (in particular, the specimen of Hottinger's 2014, pl. 12, figs. 5–6). Rahaghi's specimens seem to show a smooth dorsal side and an umbilicus with central pillars and peripheral umbilical cavities, which differs from the well-developed umbilical cavities of lockhartiines.

THE MURKA ROTALIIDS: A KEY TO UNDERSTANDING THE ORIGIN OF THE LOCKHARTIA SEA

The so-called *Lockhartia* Sea is a palaeogeographical area in which the group of *Lockhartia* communities spread and diversified during the Paleogene, becoming an important group of index fossils. According to Hottinger (2014, p. 3), the *Lockhartia* Sea was "a part of the Paleogene Neotethys, reaching in Asia from Tibet to Pakistan, Afghanistan, Iran and southern Turkey, in Africa from Somalia to Egypt and all over the Arabian Peninsula".

The larger foraminifera found in the Murka Formation, especially the Praelockhartiinae subfam. nov., can be considered to be crucial elements in the analysis and understanding of the evolution of Paleogene rotaliids. The architectural traits of some species identified in the present paper suggest the existence of some kind of phylogenetic relationship between these older forms and the younger and successful *Lockhartia* morphotypes. Following the extinction at the K/Pg boundary, *Praelockhartia neoakbari* gen. nov., sp. nov. was the first larger rotaliid that was architecturally close to species of *Lockhartia* appearing in our samples from Jabal Ja'alan. These specimens show a more primitive architecture, as based on thick folia and strong pillars and peripheral umbilical cavities. The dorsal ornamentation is also simpler, comprising merely a slightly marked spiral suture, contrasting with the highly ornamented dorsal side of lockhartiids.

Rotospirella conica appears to have been the next step in the increasing complexity between praelockhartiines and lockhartiines, showing affinities to the latter group with regard to the umbilical structure and the distribution of piles. The folia of RII. conica are thinner and longer than those of P. neoakbari gen. nov., sp. nov. The morphostructural similarities of Rll. Conica with lockhartiines are likely to be the main reason why Smout originally ascribed it to the genus Lockhartia. Although Hottinger (2014) suggested that the origin of the group of lockhartiines could be found in the older forms ascribed to the genus Rotalispira, ruling out any type of relationship with Rll. conica, we believe, as Smout did, that this latter species is indeed phylogenetically related as based on architectural similarities of the test. The presence of umbilical cavities and their coarsely perforated tests are the main factors that support this hypothesis. In our opinion, the absence of heavy ornamentation is not a sufficient difference to warrant ruling out any kind of phylogenetic relationship between Rll. conica and lockhartiines. Generally speaking, the ornamentation is a structural pattern that is difficult to categorise in terms of phylogeny. Relatively high variability in ornamentation may be observed when looking closely at representatives of a population. For instance, we may refer to the thin sections of L. roeae (Davies, 1930) and L. conditi (Nuttall, 1926) as illustrated by Hottinger (2014, pl. 5.13 and pl. 5.14-15, respectively): all of these specimens seem to show relatively smooth dorsal sides in thin section.

Therefore, in general terms, we consider the Praelockhartiinae subfam. nov. to be a group of larger rotaliid foraminifera with a primitive architecture with respect to the younger and more evolved Lockhartiinae. *Rotospirella conica* could be considered as the link between the primitive *Praelockhartia neoakbari* gen. nov., sp. nov. and the more evolved forms of *Lockhartia* (*sensu lato*). This would mean that *Praelockhartia neoakbari* gen. nov., sp. nov. is a strong candidate for the true root in the Paleocene of lockhartiines and, therefore, potentially the origin of the later diversity in the *Lockhartia* Sea.

DISCUSSION

The most significant biotic communities, in terms of diversity and abundance, found in strata of the Murka Formation are rotaliids and green algae. This assemblage has been dated as early Paleocene (late Danian) and ascribed to SBZ 2. The rotaliids can be considered key to understanding the origin and evolution of the later Paleogene rotaliid populations, playing a

crucial role in the shallow-water carbonate platforms of the region during the K/Pg interval. It seems that rotaliids recovered more rapidly than other larger foraminifera after the massive extinction across the K/Pg boundary, or that they were more resistant to certain palaeoecological conditions that likely had yet to become favourable for other larger benthic foraminifera. The origin of one of the main groups of Paleogene larger rotaliids, the lockhartiines, seems to be rooted early in the Paleocene with representatives of the Praelockhartiinae subfam. nov., on the basis of their closely related architectures. The simple structure of 'rotorbinellas', which originated in the Cenomanian, seems to be the most successful or biologically advantageous in terms of functionality as it was replicated after two global biotic crises, i.e., the Cenomanian—Turonian and K/Pg boundaries.

CONCLUSIONS

A detailed revision of the larger rotaliids found in the K/Pg interval outcropping along the western flank of Jabal Ja'alan has allowed us to:

- Describe two new genera and two new species, i.e., *Praelockhartia neoakbari* and *Rotaliidium parvum*.
- Emend the diagnosis of both the genus Rotospirella and its type species, R. conica.
- Create a new subfamily, Praelockhartiinae, to accommodate primitive forms closely related to *Lockhartia*.
- Formulate a new hypothesis concerning the origin of the lockhartiines, one of the most diverse groups among Paleogene shallow-water benthics. This hypothesis revolves around considering the Murka Formation rotaliids the root of this group, being key to understanding the origin of the diversity found later in the *Lockhartia* Sea.
- Define the new rotaliid assemblage of SBZ 2 for this area, namely, *Praelockhartia* neoakbari gen. nov., sp. nov., *Rotaliidium parvum* gen. nov., sp. nov., *Rotalia* cf. jacobi, *Rotospirella conica*, *Lockhartia* sp. and *Rotorbinella hensoni*. Other benthic foraminifera found in the assemblage are: *Idalina* sp., *Valvulina triangularis*, *Gyroidina* sp., *Quinqueloculina* sp. and *Stomatorbina*.
- Present a detailed discussion of the state of the unavailable name *Lockhartia akbari*, considered a biomarker of SBZ 2.

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Captions

- **FIG. 1.** Geographical location of the stratigraphical section studied at Jabal Ja'alan (Oman Mountains). 17, 23, 35: roads. Scale bar represents 10 km.
- **FIG. 2.** Lithostratigraphy of the Murka Formation at Jabal Ja'alan (Oman Mountains) and position of the samples studied.

- **FIG. 3.** *Rotorbinella hensoni* (Smout, 1954) from the lower Paleocene (upper Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens **A–C**, **E–F**, **H–S**, **U–AI**, MGB 59865, from sample 6: A, LP16.24; B, LP17.11; C, LP19.8; E, LP2.56; F, LP6.93; H, LP18.13; I, LP2.3; J, LP11.114; K, LP9.10; L, LP5.8; M, LP1.88; N, LP12.22; O, LP6.76; P, LP11.96; Q, LP11.130; R, LP2.39; S, LP19.13; U, LP4.4; V, LP6.109; W, LP8.1; X, LP7.7; Y, LP12.89; Z, LP12.140; AA, LP21.3; AB, 21.4; AC, LP15.18; AD, LP6.28; AE, LP2.65; AF, LP1.33; AG, LP11.101; AH, LP18.26; AI, LP12.72; **D**, MGB 59867 LP1.20, from sample J2; **G**, MGB 84538 LP1.51, from sample J3 and **T**, MGB 84538 LP14.1, from sample J7. A–AA, axial sections. AB–AG, oblique sections. AH–Al35, transverse sections. Scale bar represents 500 μm. Abbreviations: E: embryo; f: foramen; foc: foliar cavity or chamberlet; fpil: foliar pile; ilsp: intraseptal interlocular space; k: keel; n: notch; p: pore; s: septum; spc: spiral canal; up: umbilical plate; upil: umbilical pile or plug.
- **FIG. 4.** *Rotalia* cf. *jacobi* Sander, 1962 from the lower Paleocene (upper Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens **A**, **C**–**D**, **V**, MGB 84538, from sample J7: A, LP14.9; C, LP14.5; D, LP10.4; V, LP4.2; Specimens **B**, **E**–**F**, **H**–**K**, **M**–**U**, **W**–**X**, MGB 59865, from sample 6: B, LP1.93; E, LP15.19; F, LP13.7; H, LP21.12; I, LP17.29; J, LP16.28; K, LP1.87; M, 59865 LP17.6; N, LP17.32; O, LP6.105; P, LP18.27; Q, LP18.19; R, LP18.28; S, LP11.67; T, LP18.8; U, LP6.68; Specimen L, MGB 59867 LP1.15, from sample J2. A–O, axial sections. P–U oblique sections. V–X transverse sections. Scale bar represents 500 μm. Abbreviations: col: columella; E: embryo; fol: folium; foc: foliar cavity or chamberlet; fpil: foliar pile; n: nocht; s: septum; spc: spiral canal; spsut: spiral suture; up: umbilical plate; upil: umbilical pile or plug.
- **FIG. 5.** Basic structural model of *Praelockhartia* gen. nov. Transverse section of the last whorl (not to scale).
- **FIG. 6**. *Praelockhartia neoakbari* gen. nov., sp. nov. from the lower Paleocene (upper Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation.

 Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens **A**, **P** and **R**, MGB 59867, from sample J2: A, LP1.3; P, LP1.22; R, LP1.29; Specimens **T**, MGB 84538 LP10.1, from sample J7 and **B–O**, **Q** and **S**, **U–V**, MGB 59865, from sample 6: B, LP17.7; C, LP12.68; D, LP2.98; E, LP13.11; F, LP6.92; G, LP15.21; H, LP11.17; I, LP13.9; J, MGB 59865 LP17.16; K, LP17.26; L, LP17.24; M, LP2.95 (holotype); N, LP17.28; O, LP18.5; Q, LP12.28; S, LP16.31; U, LP18.23; V, LP18.22. Axial sections. Scale bar represents 500 μm. Abbreviations: E: embryo; fol: folium; fpil: foliar pile; fu: funnel; lh: loop-hole; n: notch; p: pore; spc: spiral canal; spsut: spiral suture; uc: umbilical cavity; up: umbilical plate; upc: umbilical cavity; upil: umbilical pile.
- **FIG. 7.** *Praelockhartia neoakbari* gen. nov., sp. nov. from the lower Paleocene (upper Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens from sample 6, MGB 59865: A, LP18.16; B, LP1.8; C, LP1.50; D, LP15.13; E, LP18.10; F, LP11.71; G, LP1.92; H, LP18.2; I, LP17.31; J, LP15.2; K, LP17.23; L, LP11.124; M, LP12.76; N, LP12.135. Oblique sections. Scale bar represents 500 μm. Abbreviations: f: foramen; foa: foliar aperture;

foc: foliar cavity or chamberlet; ilsp: intraseptal interlocular space; p: pore; uc: umbilical cavity; up: umbilical plate; upc: umbilical peripheral cavity; upil: umbilical pile; s: septum; spc: spiral canal.

- **FIG. 8**. *Praelockhartia neoakbari* gen. nov., sp. nov. from the lower Paleocene (upper Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation.

 Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens **A–F**, **H–Q**, MGB 59865, from sample 6: A, LP16.36; B, LP12.127; C, LP11.72; D, LP6.90; E, LP19.13; F, LP6.99; H, LP16.22; I, LP11.7; J, LP18.1; K, LP18.6; L, LP17.17; M, LP17.22; N, LP18.21; O, LP18.3; P, LP17.25; Q, LP17.3; and specimen **G**, MGB 59867 LP1.11, from sample J2 . Oblique sections. Scale bar represents 500 μm. Abbreviations: E: embryo; f: foramen; fo: folia; ilsp: intraseptal interlocular space; n: notch; p: pore; s: septum; spc: spiral canal; uc: umbilical cavity; up: umbilical plate; upc: umbilical peripheral cavity; upil: umbilical pile.
- **FIG. 9.** *Rotospirella conica* (Smout, 1954) from the lower Paleocene (upper Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens **A–F**, MGB 84538, from sample J7: A, LP11.3; B, LP11.7; C, LP8.1; D, LP10.3; E, LP9.6; F, LP8.6. Scale bar represents 500 μm. Abbreviations: E: embryo; f: foramen; fol: folium; spc: spiral canal; spsut: spiral suture; uc: umbilical cavity; up: umbilical plate.
- **FIG. 10.** *Lockhartia* aff. *conditi* (Nuttall, 1926) from the lower Paleocene (upper Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens **A–E**, MGB 84538, from sample J7: A, LP11.2; B, LP12.5; C, LP9.19; D, LP14.10; E, LP9.15. Scale bar represents 500 μm. Abbreviations: f: foramen; fol: folium; fu: funnel; ilsp: intraseptal interlocular space; s: septum; spc: umbilical spiral canal; uc: umbilical cavities.
- **FIG. 11.** *Rotaliidium parvum* gen. nov., sp. nov. from the lower Paleocene (upper Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens, MGB 59865, from sample 6: A, LP2.17; B, LP1.34; C, LP1.17; D, LP6.134 (holotype); E, LP12.99; F, LP16.14; G, LP18.4; H, LP6.54; I, LP16.25; J, LP16.19; K, LP18.7. Axial, subaxial and oblique sections. Scale bar represents 200 μm. Abbreviations: sch: supplementary chamberlets; sap: f: foramen; fol: folia; s: septum; up: umbilical plate; upil: umbilical pile or plug.
- **FIG. 12.** *Rotaliidium parvum* gen. nov., sp. nov. from the lower Paleocene (upper Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens **A-F** and **H**, MGB 59865, from sample 6: A, LP21.6; B, LP20.5; C, LP21.2; D, LP19.6; E, LP19.4; F, LP19.1; Specimen **G**, MGB 59867 LP1.14, from sample J2. Scale bar represents 200 μm. Axial, oblique and transverse sections. Abbreviations: sch: supplementary chamberlets; E: embryo; n: notch; spc: spiral canal; up: umbilical plate; upil: umbilical pile or plug.
- **FIG. 13.** Larger foraminiferal and green algae biostratigraphy along the western flank of Jabal Ja'alan (Oman Mountains) (data on planktic foraminifera are from Roger *et al.* 1998 and Serra-Kiel *et al.* 2016).

- FIG. 14. Larger benthic foraminifera and dasycladalean algae from the Upper Cretaceous Simsima Formation. A, *Omphalocyclus macroporus* (Lamarck, 1816), MGB 59861 LP3.4, sample 2; B, *Loftusia morgani* Douvillé, 1904, MGB 59860 LP4.1, from sample 1; C, *Trinocladus radoicicae* Elliott, 1968, MGB 59861 LP6.4, from sample 2; D, *Siderolites calcitrapoides*? Lamarck, 1801, MGB 59861 LP7.1, from sample 2; E, *Pseudomphalocyclus blumenthali*? Meriç, 1980, MGB 59861 LP1.5, from sample 2; F, *Broeckina* cf. *dufrenoyi* (d'Archiac & Haime, *in* d'Archiac, 1854), MGB 59861 LP5.1, from sample 2; G, *Stomatorbina binkhorsti* (Reuss, 1862), MGB 59862 LP3.4, from sample 3; H, *Fissoelphidium operculiferum* Smout, 1954, MGB 59860 LP5.6, from sample 1. Scale bars represent 2 mm (A–B); 1 mm (D–E); 500 μm(C, F–H).
- FIG. 15. Foraminifera and green algae associated with rotaliids from the upper Danian of the Murka Formation: A, *Halimeda* sp., MGB 59870 LP1.3, from sample J5; B, *Jodotella* sp., MGB 59870 LP1.1, from sample J5; C, K. *Idalina* sp., MGB 84538 LP9.1, from sample J7; D, *Stomatorbina binkhorsti* (Reuss, 1862), MGB 84538 LP10.6 and MGB 84538 LP1.11, from samples 7 and J3, respestively; E, *Indopolia satyavanti* Pia, *in* Rao & Pia, 1936, MGB 59870 LP1.4, from sample J5; F, Bryopsidales indet., MGB 59865 LP5.31, from sample 6; G, *Valvulina triangularis* d'Orbigny, 1826, MGB 84538 LP5.25, from sample J7; H, *Gyroidina* sp., MGB 59868 LP1.8, from sample J3; I, Dasycladales indet., MGB 84538 LP14.15, from sample J7; J, *Neomeris* sp., MGB 59868 LP1.1, from sample J3; L, *Clypeina* sp., MGB 84538 LP1.11, from sample J7. Scale bars represent 1 mm (A, E), 500 μm (B–D and F–L).
- **FIG. 16.** Selandian?-early Thanetian larger foraminifera and green algae of the Abat Formation, MGB 84539, from sample 8. **A**, *Periloculina*? sp., MGB 84539 LP1.4; **B**, *Keramosphaerinopsis* sp., MGB 84539 LP1.5; **C**, *Sakesaria* sp., MGB 84539 LP1.7; **D**, *Lockhartia retiata* Sander, 1962, MGB 84539 LP1.6; **E**, *Lockhartia praehaimei* Smout, 1954, MGB 84539 LP2.1; **F**, *Kathina* cf. *major* Smout, 1954, MGB 84539 LP1.9; **G**, *Daviesina* sp., MGB 84539 LP1.8; **H**, *Cymopolia* sp., MGB 84539 LP1.3; **I**, *Periloculina*? sp. (a) and *Clypeina* sp. (b), MGB 84539 LP2.4. Scale bars represent: 1 mm (A–C, H) and 500 μm (D–G, I).

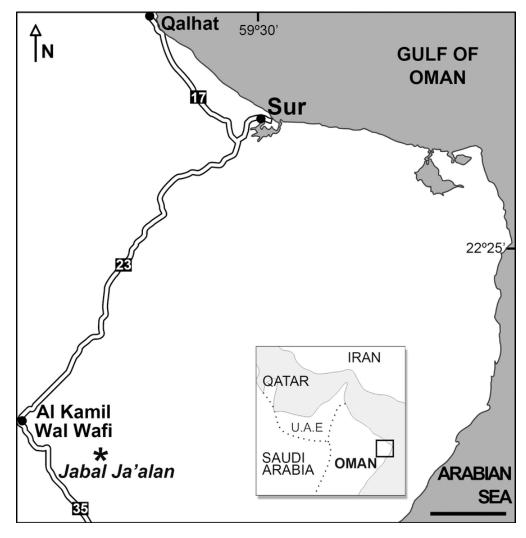


Figure 1. Geographical location of the stratigraphic section studied in Jabal Ja'alan (Oman). 17, 23, 35: roads. Scale bar represents 10 Km

75x77mm (300 x 300 DPI)

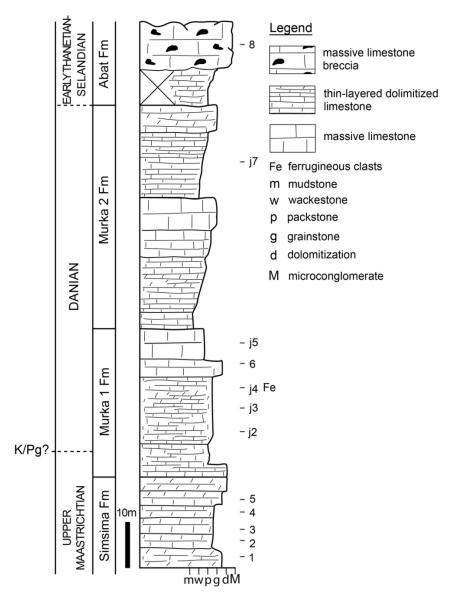


Figure 2. Lithostratigraphy of the Murka Formation in Jabal Ja'alan (Oman Mountains) and position of the samples studied.

109x125mm (300 x 300 DPI)

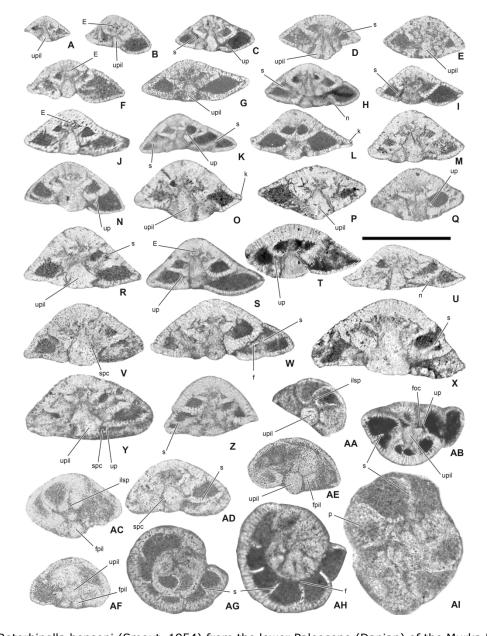


Figure 3. Rotorbinella hensoni (Smout, 1954) from the lower Paleocene (Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens A-C, E-F, H-S, U-AI from sample 6 (MGB 59865); D from sample J2 (MGB 59867); G from sample J3; and T from sample J7 (MGB 84538). A-AA, axial sections. AB-AG, oblique sections. AH-AI35, transverse sections. Scale bar represents 500 µm. Abbreviations: E: embryo; f: foramen; foc: foliar cavity or chamberlet; fpil: foliar pile; ilsp: intraseptal interlocular space; k: keel; n: notch; p: pore; s: septum; spc: spiral canal; up: umbilical plate; upil: umbilical pile or plug.

165x224mm (300 x 300 DPI)

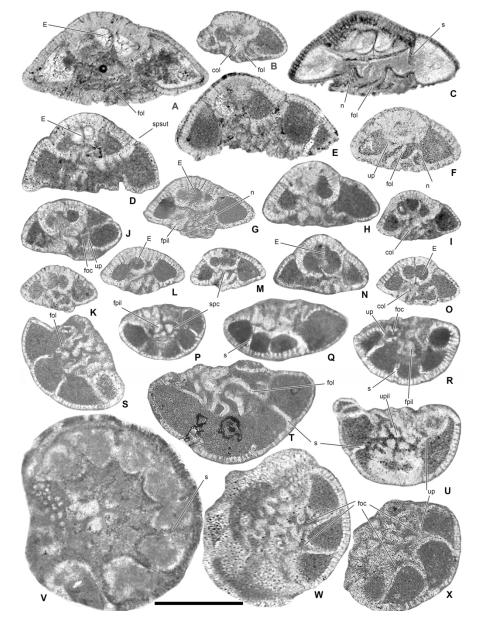


Figure 4. Rotalia cf. jacobi Sander, 1952 from the lower Paleocene (Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens A, C-D, V from sample J7 (MGB 84538); B, E-F, H-K, M-U, W-X from sample 6 (MGB 59865); and 7, L from sample J2 (MGB 59867). A-O, axial sections. P-U oblique sections. V-X transverse sections. Scale bar represents 500 µm. Abbreviations: col: columella; E: embryo; fol: folium; foc: foliar cavity or chamberlet; fpil: foliar pile; n: nocht; s: septum; spc: spiral canal; spsut: spiral suture; up: umbilical plate; upil: umbilical pile or plug.

165x224mm (300 x 300 DPI)

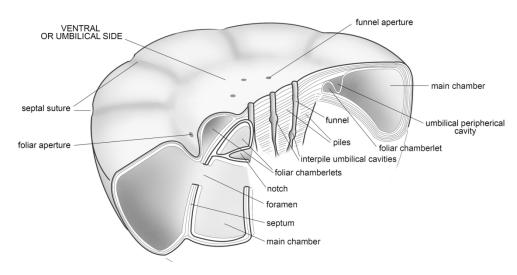


Figure 5. Basic structural model of Praelockhartia gen. nov. Transverse section of the last whorl, not to scale.

165x82mm (300 x 300 DPI)

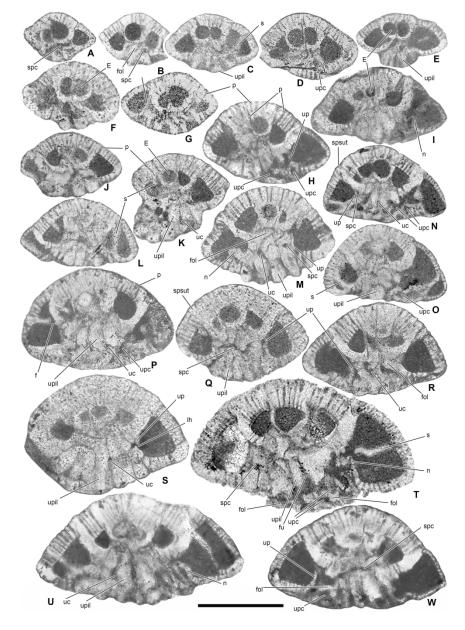


Figure 6. Praelockhartia neoakbari gen. nov. sp. nov. from the lower Paleocene (Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens A, P and R from sample J2 (MGB 59867); T from sample J7 (MGB 84538); and B-O, Q, and S-V from sample 6 (MGB 59865). Axial sections. Holotype: specimen M (MGB 59865 LP2.95). Scale bar represents 500 µm. Abbreviations: E: embryo; fol: folium; fpil: foliar pile; fu: funnel; lh: loop-hole; n: notch; p: pore; spc: spiral canal; spsut: spiral suture; uc: umbilical cavity; up: umbilical plate; upc: umbilical cavity; upil: umbilical pile.

160x224mm (300 x 300 DPI)

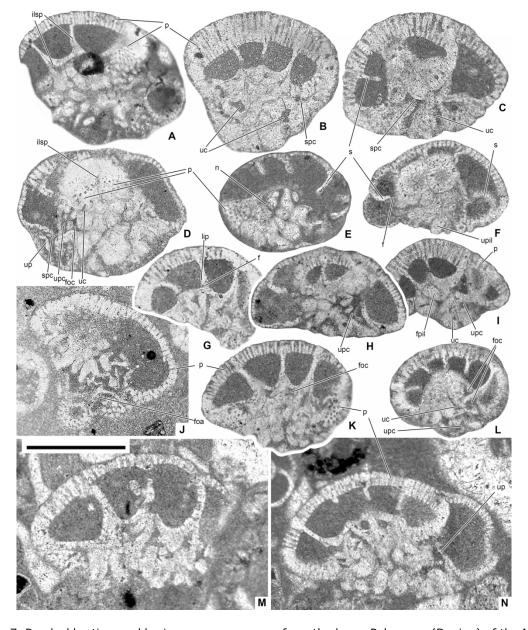


Figure 7. Praelockhartia neoakbari gen. nov. sp. nov. from the lower Paleocene (Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens from sample 6 (MGB 59865). Oblique sections. Scale bar represents 500 µm. Abbreviations: f: foramen; foa: foliar aperture; foc: foliar cavity or chamberlet; ilsp: intraseptal interlocular space; p: pore; uc: umbilical cavity; up: umbilical plate; upc: umbilical peripheral cavity; upil: umbilical pile; s: septum; spc: spiral canal.

165x200mm (300 x 300 DPI)

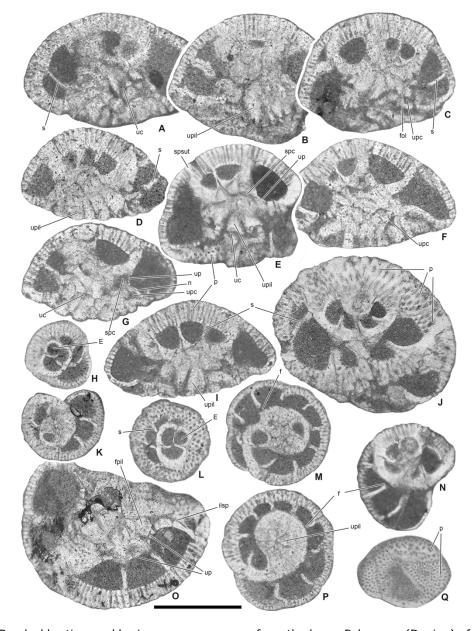
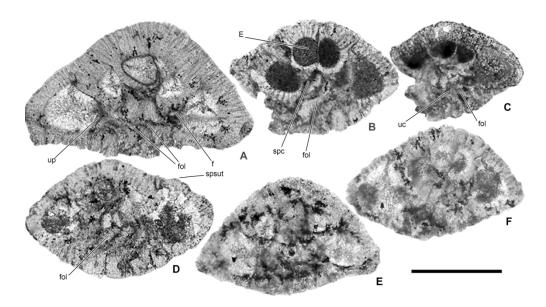


Figure 8. Praelockhartia neoakbari gen. nov. sp. nov. from the lower Paleocene (Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens A-F, H-Q from sample 6 (MGB 59865); and specimen G from sample J2 (MGB 59867). Oblique sections. Scale bar represents 500 µm. Abbreviations: E: embryo; f: foramen; fo: folia; ilsp: intraseptal interlocular space; n: notch; p: pore; s: septum; spc: spiral canal; uc: umbilical cavity; up: umbilical plate; upc: umbilical peripheral cavity; upil: umbilical pile.

165x226mm (300 x 300 DPI)



umbilical plate; upc: umbilical peripheral cavity; upil: umbilical pile. Figure 9. Rotospirella conica (Smout, 1954) from the lower Paleocene (Danian) of the Murka 2 Formation, Jabal Ja'alan, Oman Mountains. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens A-F from sample J7 (MGB 84538). Scale bar represents 500 µm. Abbreviations: E: embryo; f: foramen; fol: folium; spc: spiral canal; spsut: spiral suture; uc: umbilical cavity; up: umbilical plate.

165x91mm (300 x 300 DPI)

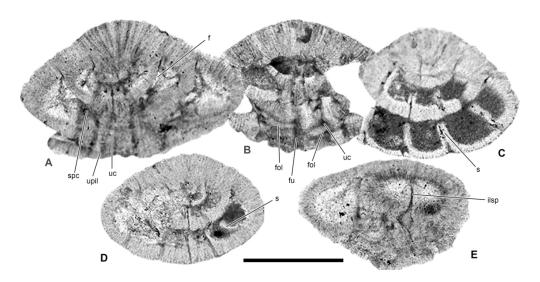


Figure 10. Lockhartia aff. conditi (Nuttall, 1926) from the lower Paleocene (Danian) of the Murka 2 Formation, Jabal Ja'alan, Oman Mountains. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens A-E from sample J7 (MGB 84538). Scale bar represents 500 µm. Abbreviations: f: foramen; fol: folium; fu: funnel; ilsp: intraseptal interlocular space; s: septum; spc: umbilical spiral canal; uc: umbilical cavities.

165x82mm (300 x 300 DPI)

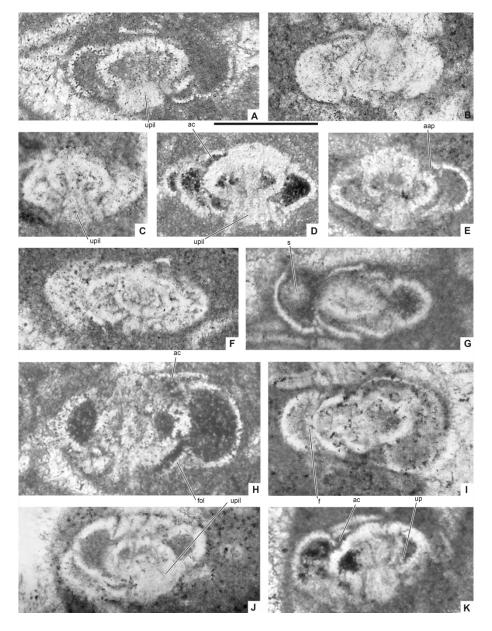


Figure 11. Rotaliidium parvum, gen. nov. sp. nov. from the lower Paleocene (Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens from sample 6 (MGB 59865). Holotype: specimen D (MGB 59865 LP6.134). Axial, subaxial and oblique sections. Scale bar represents 200 µm. Abbreviations: sch: supplementary chamberlets; sap: f: foramen; fol: folia; s: septum; up: umbilical plate; upil: umbilical pile or plug.

165x218mm (300 x 300 DPI)

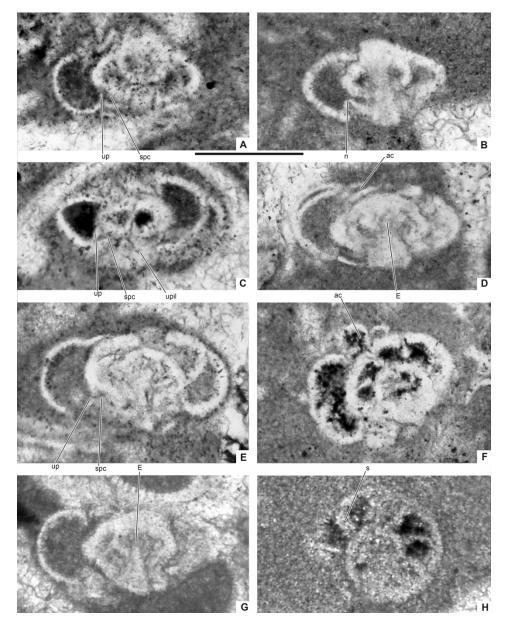


Figure 12. Rotaliidium parvum, gen. nov. sp. nov. from the lower Paleocene (Danian) of the Murka Formation, Jabal Ja'alan, Oman Mountains. Megalospheric generation. Transmitted light photographs of thin sections of cemented carbonate rocks. Specimens from sample 6 (MGB 59865). Scale bar represents 200 µm. Axial, oblique and transverse sections. Abbreviations: sch: supplementary chamberlets; E: embryo; n: notch; spc: spiral canal; up: umbilical plate; upil: umbilical pile or plug.

165x209mm (300 x 300 DPI)

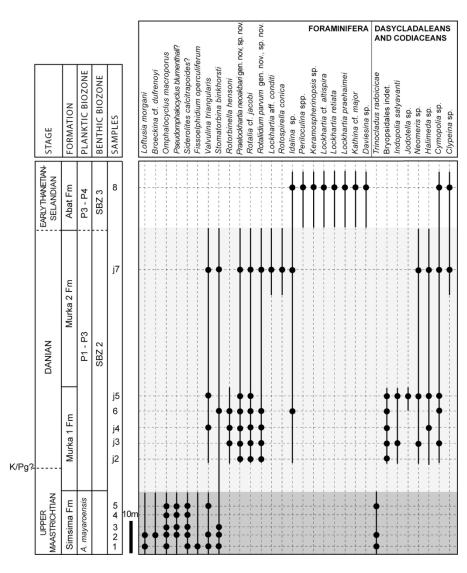


Figure 13. Larger foraminiferal and green algae biostratigraphy in the west flank of Jabal Ja'alan (Oman Mountains) (data of planktic foraminifera extracted from Roger et al. 1998 and Serra-Kiel et al. 2016).

156x167mm (300 x 300 DPI)

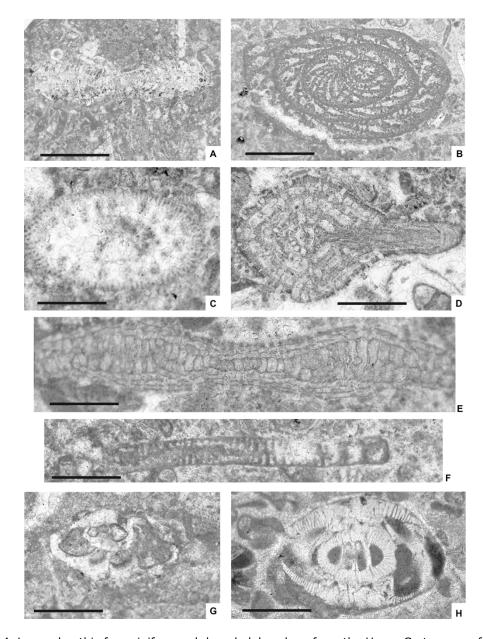


Figure 14. Larger benthic foraminifera and dasycladales algae from the Upper Cretaceous of Simsima Formation. A, Omphalocyclus macroporus (Lamarck, 1816); B, Loftusia morgani Douvillé, 1904; C, Trinocladus radoicicae Elliott, 1968; D, Siderolites calcitrapoides? Lamarck, 1801; E, Pseudomphalocyclus blumenthali? Meriç, 1980; F, Broeckina cf. dufrenoyi (d'Archiac & Haime in d'Archiac, 1854); G, Stomatorbina binkhorsti (Reuss, 1862); H, Fissoelphidium operculiferum Smout, 1955. Scale bars represent 2 mm (A-B); 1 mm (D-E); 500 µm (C, F-H).

165x225mm (300 x 300 DPI)

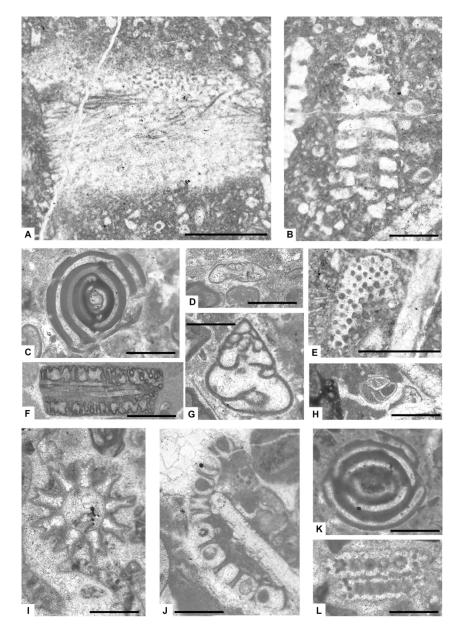


Figure 15. Foraminifera and green algae associated with rotaliids from the Danian of Murka Formation: A, Halimeda sp.; B, Jodotella sp.; C and K. Idalina sp.; D, Stomatorbina binkhorsti (Reuss, 1862); E, Indopolia satyavanti Pia in Rao & Pia, 1936; F, Bryopsidales indet.; G, Valvulina triangularis d'Orbigny, 1826; H, Gyroidina sp.; I, Dasycladales indet.; J, Neomeris sp.; K, Clypeina sp. Scale bars represent 1 mm (A and E), 500 µm (B-D and F-L).

158x225mm (300 x 300 DPI)

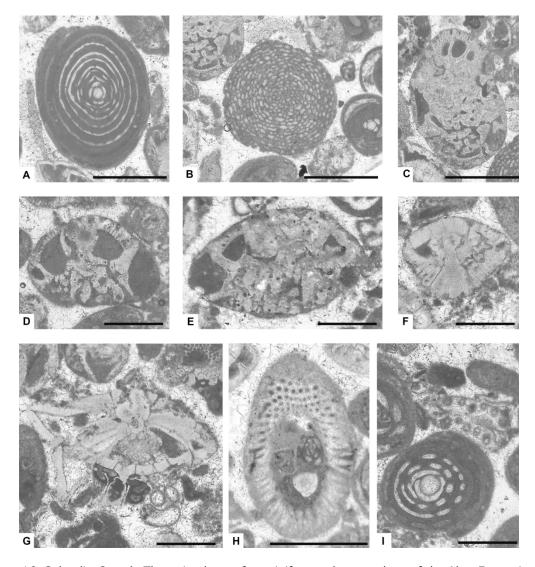


Figure 16. Selandian?-early Thanetian larger foraminifera and green algae of the Abat Formation. A, Periloculina? sp.; B, Keramospherinopsis sp.; C, Lockhartia cf. altispira Smout, 1954; D, Lockhartia retiata Sander, 1962; E, Lockhartia praehaimei Smout, 1954; F, Kathina cf. major Smout, 1954; G, Daviesina sp.; H, Cymopolia sp.; I, Periloculina? sp. (a) and Clypeina sp. (b). Scale bars represent: 1 mm (A-C, H) and 500 μm (D-G, I).

165x176mm (300 x 300 DPI)