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Systematic taxonomy of middle Miocene *Sphaeroidinellopsis* (planktonic foraminifera)

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The taxonomy and phylogeny of the Miocene to Recent genus *Sphaeroidinellopsis* have been documented in previous studies, but the evolution of this lineage remains unclear. Some authors have debated this genus in the past, choosing a variety of parameters to discriminate the morphospecies. Here we present new scanning electron microscope analyses of specimens from Ocean Drilling Program (ODP) Site 925 (Ceara Rise, western equatorial Atlantic) and ODP Site 959 (Deep Ivorian Basin, eastern equatorial Atlantic). Our study reveals transitional individuals *Sphaeroidinellopsis disjuncta*–*Sphaeroidinellopsis kochi*, a speciation event never described previously. These transitional specimens are characterized by extreme morphological features such as elongated and sac-like final chambers, requiring amendments to the current classification and taxonomy of these morphospecies. In this paper, an alternative hypothesis is presented and discussed, to assess these new observations within the evolutionary mosaic of *Sphaeroidinellopsis*.

Keywords: *Sphaeroidinellopsis*; taxonomy; evolution; planktonic foraminifera; Miocene; Atlantic Ocean

Introduction

The genus *Sphaeroidinellopsis* ranges from the early Miocene to Pliocene. Kennett & Srinivasan (1983) considered *Sphaeroidinellopsis* to be composed of four morphospecies, *S. disjuncta*, *S. seminulina*, *S. kochi* and *S. paenedehiscens*. The genus was erected by Banner & Blow (1959) for low trochosphiral species that lacked a supplementary sutural aperture. The genus *Sphaeroidinella*, by contrast, was erected by Cushman in 1927, and amended by Banner & Blow in 1959 to include globigeriniform taxa with thick walls covered by a shiny cortex and possessing supplementary openings on the spiral side. While the two genera have been placed in a single evolutionary lineage by some authors (Banner & Blow 1959; Kennett & Srinivasan 1983; Aze *et al.* 2011; Spezzaferri *et al.* 2015, among others), Bè (1965) and Bandy *et al.* (1967) considered them bathypelagic forms of at least two different species of *Globigerinoides*. Moreover, the ancestor of these two genera is still debated. Srinivasan & Kennett (1981), Kennett & Srinivasan (1983) and Spezzaferri (1994) suggested the ancestor of *Sphaeroidinellopsis* and *Sphaeroidinella* is *Zeaglobigerina* (considered a junior synonym of *Globoturborotalita*). On the other hand, Spezzaferri *et al.* (2015) reported *Sphaeroidinella* and *Sphaeroidinellopsis* as potential

descendants of *Trilobatus* based on Small Subunit rDNA molecular data. Some fundamental questions remain open as to the origin of these taxa: Do *Sphaeroidinellopsis* and *Sphaeroidinella* belong to the same evolutionary lineage? What can we tell from the emergence of the supplementary aperture under the cortex in *Sphaeroidinella*? A deeper comprehension of each lineage is fundamental to answering these questions. Measuring and reporting morphological variability and transitional individuals are key steps in characterizing the evolution of morphospecies and the occupation of discrete parts of morphospace.

Planktonic foraminifera are characterized by large morphological variability, often making the transition from one species to another gradual. Intermediate forms have always played a fundamental role in taxonomical studies, especially when new morphospecies originated without any lineage splitting, such as in the evolution of *Sphaeroidinella* from *Sphaeroidinellopsis* (Aze *et al.* 2011). On a few occasions, the morphological change is relevant to define the appearance of a genus. One of the most important examples known in the literature is the *Sphaeroidinella* datum, a first-order biostratigraphical event, used in zonal schemes to approximate the Miocene/Pliocene boundary (Banner & Blow 1965; Blow 1969) and defined as the first occurrence of *Sphaeroidinella dehiscens*, evolving from

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Sphaeroidinellopsis paenedehiscens. Numerous authors have debated this transition over time, and a few authors have even suggested the inconsistency of the genera *Sphaeroidinella* and *Sphaeroidinellopsis* (Bandy *et al.* 1967), complicated even further by the controversial nature of the cortex. Artificially decorticated specimens of *S. dehiscens* showed in their interior *T. trilobus*- or *G. conglobatus*-like structures, lacking the characteristic supplementary aperture and thus interpreted as hidden by calcite overgrowth (Spezzaferri *et al.* 2015). Even the development of the cortex (thickened outer layer) was interpreted as an environmentally driven feature, related to bathyal waters with no taxonomical meaning (Bandy *et al.* 1967). Some specimens of *Sphaeroidinella* and *Sphaeroidinellopsis* from the Mediterranean basin do not show any cortex, an argument used to support the environmental interpretation (Parker 1958; Todd 1958; Cita *et al.* 1965; Bandy *et al.* 1967 among others). Other workers, such as Jenkins (1971) and Bè (1965), considered *Sphaeroidinellopsis* and *Sphaeroidinella* aberrant deep water variants of *T. sacculifer*, doubting the reliability of the genus itself. Kučera (1998) reported how the number of specimens bearing supplementary apertures increased in the early Pliocene in the equatorial Atlantic, marking a clear horizon that is globally recognizable and ending a long-ranging debate.

Other problems concerning the taxonomy of this complex lineage nevertheless remain open. Here we investigate the relationship among problematic taxa within *Sphaeroidinellopsis* to better understand the evolution of *Sphaeroidinellopsis* and its link to the *Sphaeroidinella* genus, focusing on the evolutionary lineage of *S. disjuncta*–*S. kochi*. In Chaisson and Leckie (1993), transitional forms of both *S. disjuncta*–*S. kochi* and *S. disjuncta*–*S. seminulina* are reported and imaged. Those transitional forms show debatable features, which are hard to interpret due to poor fossil preservation and image quality. Thus, the quest for the real ancestor of *S. kochi* served as a starting point for this paper, and our investigations potentially have implications for the whole *Sphaeroidinellopsis*–*Sphaeroidinella* plexus.

Material and methods

This study focused on the taxonomical evolution of *Sphaeroidinellopsis disjuncta* and *S. kochi* through scanning electron microscope (SEM) analyses of planktonic foraminifera in oceanic cored sediments. The microfossil specimens were examined under a light stereomicroscope and then selected for SEM imaging. The sites investigated in this paper are Ocean Drilling Program

(ODP) Leg 154 Site 925 and ODP Leg 159 Site 959 (Fig. 1). Both sites are in equatorial areas, where the genus *Sphaeroidinellopsis* showed its highest abundance during the early–middle Miocene (Srinivasan & Kennett 1981; Kennett & Srinivasan 1983). All specimens have been deposited at the Natural History Museum in London (UK), receiving a correspondent code name.

Site locations

ODP Leg 154 Site 925. Site 925 (4°12'N, 43°29'W; 3041 m water depth), located on Ceara Rise in the western equatorial Atlantic Ocean, is the shallowest site drilled in the depth transect of Leg 154. Four holes (A–D) were cored, recovering a 930 m thick sedimentary succession. The middle Miocene consists of nannofossil ooze with clay and foraminifera (Curry *et al.* 1995). Four samples have been analysed: 154/925A 4R-2 (65–67 cm), 154/925A 4R-3 (60–62 cm), 154/925A 4R-3 (73–75 cm) and 154/925A 4R-7 (60–62 cm).

ODP Leg 159 Site 959. Site 959 (3°37.659'N, 2°344.112'W; 2090 m water depth) is located on a small plateau in the southern part of the Deep Ivorian Basin, east equatorial Atlantic Ocean. It belongs to a series of four sites (Sites 959–962) drilled on Leg 159, adjacent to the continent-ocean transition along the transform passive margin of Côte d'Ivoire-Ghana. Miocene sediments consist of nannofossil ooze and foraminifera ooze with alternations of laminated and bioturbated intervals.

Eight samples were analysed: 159/959A 17H-5 (73–75 cm), 159/959A 17H-6 (37–39 cm), 159/959A 17H-6 (87–89 cm), 159/959A 17H-7 (49–51 cm), 159/959B 17H-5 (73–75 cm), 159/959B 17H-6 (37–39 cm), 159/959B 17H-6 (87–89 cm) and 159/959B 17H-7 (49–51 cm). In all samples, the >150 µm size fraction was analysed.

Sample preparation

All samples were prepared following standard washing, drying and sieving procedures. Each sample consisted of 20 cm³ of sediment, saving around 15% as archive. Samples were pre-soaked in ~150 mL of distillate water in order to disaggregate the sediments, and then washed with tap and distilled water, sieving the sediment through a 63 µm mesh. The residues were oven dried at 40 °C. Different size fractions were obtained through 250 µm and 150 µm dry sieves for each sample. Taxonomic concepts and species identification were based on the literature (Kennett & Srinivasan 1983; Perch-Nielsen *et al.* 1985; Aze *et al.* 2011; Fox & Wade 2013; Wade *et al.* 2018; Lam & Leckie 2020).

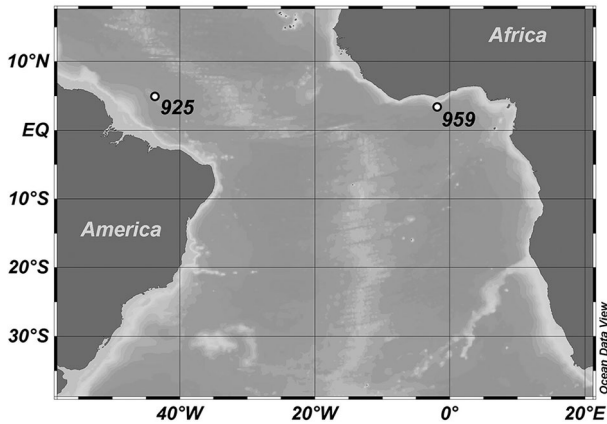


Figure 1. Locations of the Ocean Drilling Program (ODP) Sites 925 and 959 in the Atlantic Ocean. Image made using Ocean Data View (Schlitzer 2018).

Scanning electron microscope imaging

The best-preserved specimens were selected for SEM imaging. The selected specimens were stuck on metal stubs using double-sided sticky tape. The stubs were gold-coated and inspected using a Jeol JSM-6480LV high-performance Variable Pressure Analytical Scanning Electron Microscope at University College London.

Results

Preservation

The preservation in ODP Site 925 is poor to average and foraminifera show signs of dissolution and recrystallization. A moderate proportion of fragmented material is common in all samples. Planktonic foraminifera assemblages from ODP Site 959 show high diversity, while the overall preservation is moderate to good through the uppermost lower Miocene to Holocene. Fragmentation is evident, and broken individuals were numerous in a few intervals, such as in the Pleistocene, the lowermost Pliocene and the middle Miocene. Selected specimens are shown in Figure 2.

Biostratigraphy

At Site 925 planktonic foraminifera assemblages display low diversity and are dominated by warm-water tropical-subtropical species. Based on the first occurrence (FO) of *Orbulina universa* and FO of *Globorotalia peripheroacuta*, the total assemblage analysed falls into biozones M6–M7 (Wade *et al.* 2011; King *et al.* 2020; Raffi *et al.* 2020). At Site 959 the fossil assemblage is dominated by *Dentoglobigerina altispira*, *D. venezuelana*, *Trilobatus sacculifer*, *Globoquadrina dehiscens*,

Clavatorella bermudezi, *Orbulina universa* and *S. kochi*. This interval is attributed to biozone M10 (Wade *et al.* 2011; King *et al.* 2020; Raffi *et al.* 2020), confirmed by the absence of *Globorotalia fohsi* and *Globoturborotalita nepenthes*.

Systematic palaeontology

Order **Foraminiferida** d'Orbigny, 1826

Superfamily **Globigerinoidea** Carpenter, Parker & Jones, 1862

Family **Globigerinidae** Carpenter, Parker & Jones, 1862

Genus ***Sphaeroidinellopsis*** Banner & Blow, 1959

Type species. *Globigerina seminulina* Schwager, 1866 (= *Sphaeroidinella dehiscens subdehiscens* Blow, 1959).

Diagnosis. Spinose, cancellate *sacculifer*-type wall texture. The test can be totally or partially covered with a shiny, smooth cortex, which can completely obscure the cancellate texture below.

Test morphology. Test compact to slightly lobate, low to mid-trochospiral, bearing from three to five chambers in the ultimate whorl. The chambers are subspherical to radially elongated, differing among the species belonging to this genus. The aperture is umbilical to interior-marginal and may present a thick rim. No supplementary apertures are present.

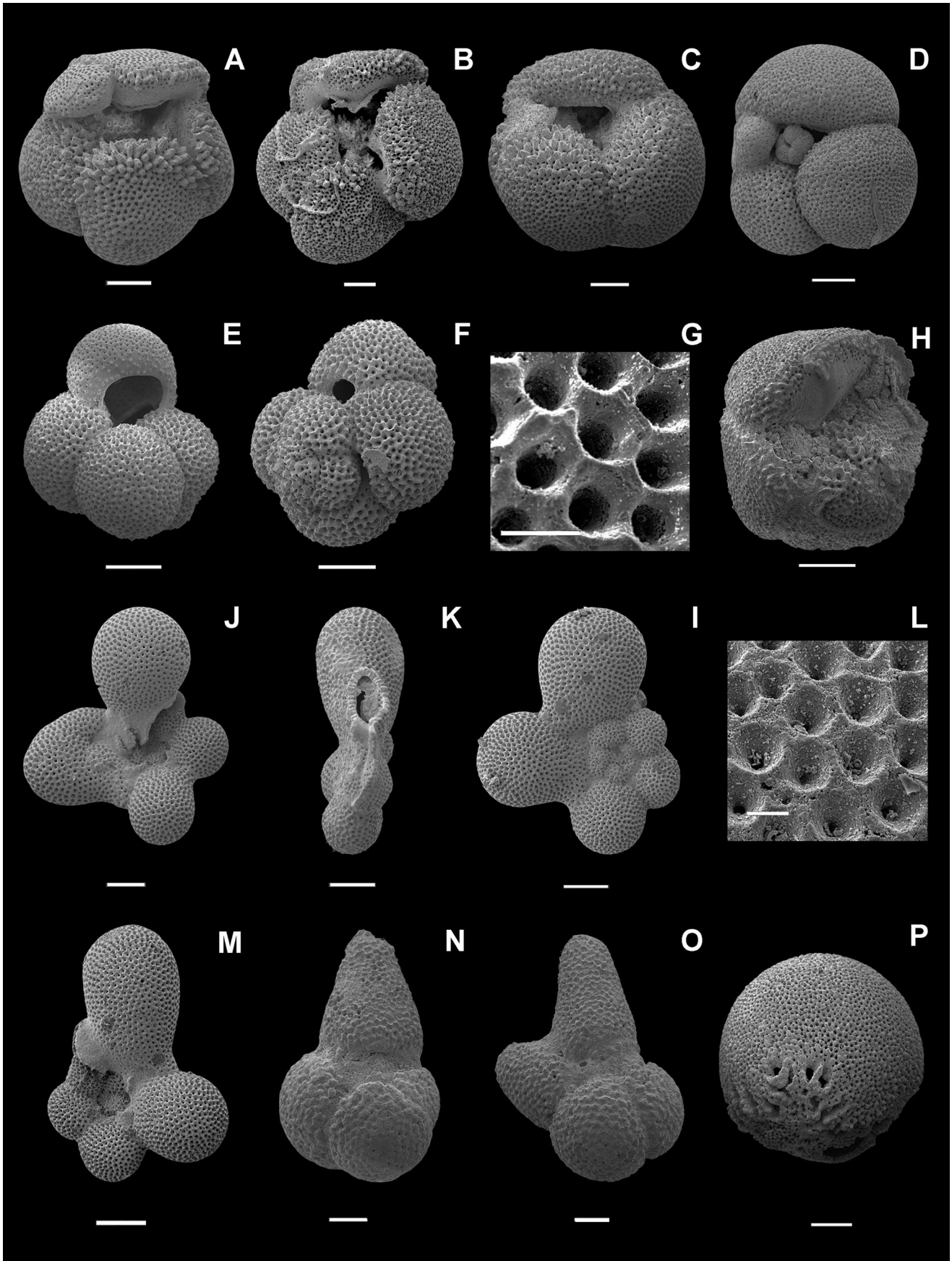
Range. Burdigalian Zone M4 (Kennett & Srinivasan 1983)–Piacenzian Zone PL4 (Kennett & Srinivasan 1983).

Remarks. This genus is distinguished from *Sphaeroidinella* based on the absence of secondary apertures on the spiral side and the incomplete development of the cortex. *Sphaeroidinellopsis* can be distinguished from *Globoturborotalita* because of its more robust cancellate wall texture and the potential presence of the cortex or a thickened wall in certain species. The genus *Sphaeroidinellopsis* is easily distinguished from *Trilobatus* and *Globigerinoides* due to the absence of supplementary apertures on the spiral side and by its typical wall texture, showing wider pores generally; some species are covered by a glassy and thick cortex.

Sphaeroidinellopsis disjuncta (Finlay, 1940)

1958 Non *Sphaeroidinella cellata* Subbotina Bykova: pl. 11, figs 4, 5.

1983 *Sphaeroidinellopsis disjuncta* Kennett & Srinivasan: pl. 51, figs 3–5.



1994 *Sphaeroidinellopsis disjuncta* Spezzaferri: pl. 10, fig. 4a–c.

2020 *Sphaeroidinellopsis disjuncta* Lam & Leckie: pl. 10, figs 11, 12.

Test morphology. Test compact and mid-trochospiral. In umbilical view, sutures are slightly incised and radial, umbilicus is narrow and deep with a low-arched umbilical aperture bordered by a thick rim. The final chamber tends to be smaller than or the same size as the penultimate chamber. In spiral view two whorls are visible for a total of six to seven chambers, separated by incised straight sutures. In edge view, the profile is rounded and slightly triangular due to the reduced size of the final chamber, chambers from previous whorls visible in the low trochospire. The last whorl presents 3½ to 4 sub-globular chambers slowly growing in size as added.

Range. Burdigalian Zone M4 (Kennett & Srinivasan 1983) to Tortonian Zone M13 (Kennett & Srinivasan 1983). The extinction of this taxon is reported in Zone N17 in Bolli & Saunders (1981), and in Zone N11 in Kennett & Srinivasan (1983). The latest specimens reported here, in this study, are from Zone M10 (= Zone N13).

Remarks. *Sphaeroidinellopsis disjuncta* can be distinguished from *S. kochi* by having only four chambers in the final whorl and lacking the peculiar elongation in the final or penultimate chamber. *Sphaeroidinellopsis disjuncta* can be distinguished from *S. seminulina* in having 3½ to 4 chambers in the ultimate whorl instead of three. This taxon also has a more open umbilicus than *S. seminulina* and a wider, higher aperture compared with the slit-like aperture characterizing *S. seminulina* sensu Schwager 1866. *Sphaeroidinellopsis disjuncta* differs from *Globoturborotalita woodi* by showing a lower aperture bordered with a rim, and by the usually smaller jutting final chamber. The wall shows wider pores and frequently it is covered totally or partially by a shiny cortex. It is distinguished from *G. druryi* due to the less pronounced apertural rim and the

coarser wall texture with cortex development, a feature totally absent in *Globoturborotalita*.

Sphaeroidinellopsis kochi (Caudri, 1934)

1923 *Globigerina* sp. Koch: 351, fig. 8a, b.

1934 *Globigerina kochi* Caudri: fig. 8a, b.

1945 *Globigerina grimsdalei* (Keijzer, 1945): taf. 33a, c.

1959 *Sphaeroidinella seminulina kochi* (Caudri); Blow: pl. 12, figs 78, 79.

1960 *Sphaeroidinellopsis seminulina* Banner & Blow: pl. 7, fig. 2.

1983 *Sphaeroidinellopsis kochi* (Caudri) Kennett & Srinivasan: pl. 52, figs 1–3.

1985 *Sphaeroidinellopsis multiloba* (LeRoy, 1944); Bolli & Saunders: pl. 38, figs 15, 16.

1993 *Sphaeroidinellopsis kochi* Chaisson & Leckie: pl. 10, figs 10, 14, 18.

2013 *Sphaeroidinellopsis disjuncta* Fox & Wade: fig. 17.8.

2014 *Sphaeroidinellopsis disjuncta* Sanchez, Berggren & Liska: pl. 3, figs 1–8.

2020 *Sphaeroidinellopsis kochi* Lam & Leckie: pl. 11, figs 1–4, 6–7.

Test morphology. Low trochospiral and slightly lobate profile. Four to six chambers in the final whorl, often characterized by a radial elongation of the final chamber. This feature might be observable both in kummerforms and normalforms. In umbilical view, four to six chambers are present, and the umbilicus is open, with a low, arched umbilical-extraumbilical aperture. The aperture always presents a thick rim. The final chamber is commonly sac-like and it can be strongly elongated and tilted towards the previous chambers. In spiral view, up to 12 chambers are visible, arranged in three whorls, sutures radial and deeply incised. In edge view, spiral side flat with a low trochospire, with the final sac-like chamber often tilted towards the umbilicus or more rarely towards the spire.

Figure 2. A–H, *Dentoglobigerina altispira*; A, NHMUK PM PF 75178; B, NHMUK PM PF 75179, umbilical view from sample 159/959B 17H-6 (87–89 cm), Zone M10 middle Miocene, east equatorial Atlantic; *Dentoglobigerina venezuelana*: C, NHMUK PM PF 75180; D, NHMUK PM PF 75181, from sample 159/959B 17H-6 (36–38 cm), Zone M10 middle Miocene, east equatorial Atlantic; *Globigerinoides* cf. *altiaperturus*: E, NHMUK PM PF 75182; F, G, NHMUK PM PF 75183, umbilical, spiral views and wall detail on 50 × 50 µm, from sample 154/925A 4R-2 (65–67 cm), Zone M7 middle Miocene, western equatorial Atlantic; *Globoquadrina dehiscens*: H, NHMUK PM PF 75184, umbilical view, from sample 154/925A 4R-2 (65–67 cm), Zone M7 middle Miocene, western equatorial Atlantic; *Clavatorella bermudezi*: J, NHMUK PM PF 75185; K, NHMUK PM PF 75186; L, M, NHMUK PM PF 75187; N, NHMUK PM PF 75188, umbilical, edge and spiral views, and wall detail; from sample 154/925A 4R-2 (65–67 cm), Zone M7 middle Miocene, western equatorial Atlantic; *Sphaeroidinellopsis disjuncta*–*Sphaeroidinellopsis kochi*: O, NHMUK PM PF 75189, transitional specimen umbilical view from sample 154/925A 4R-2 (65–67 cm), Zone M7 middle Miocene, western equatorial Atlantic; *Sphaeroidinellopsis kochi*: P, NHMUK PM PF 75190, umbilical view from sample 154/925A 4R-2 (65–67 cm), Zone M7 middle Miocene, western equatorial Atlantic; *Orbulina suturalis*: Q, NHMUK PM PF 75191, from sample 159/959B 17H-6 (87–89 cm), Zone M10 middle Miocene, east equatorial Atlantic. Scale bars: A–F, H–L, N–Q = 100 µm; G, M = 10 µm.

Range. Langhian (Kennett & Srinivasan 1983)–Zanclean Zone PL1 (Wade *et al.* 2011).

Remarks. This taxon is easily distinguishable from *Sphaeroidinellopsis disjuncta* due to the elongation of the last chamber, or of the final two chambers. It differs from *S. seminulina* in having four to six chambers in last whorl, having the final chamber elongated and sac-like, often tilted, and presenting a wider umbilicus and a looser coiling. It can be distinguished from *Trilobatus sacculifer* by the absence of supplementary apertures on the spiral side and the potential development of a partial or full glassy cortex. *Sphaeroidinellopsis kochi* differs from *Globoturborotalita druryi* in its higher number of chambers in the final whorl, the elongation in the final chambers, a looser coiling mode and the potential development of the cortex. This species is also the only one within *Sphaeroidinellopsis* bearing more than four chambers. A full investigation of the probable synonymies of *S. multiloba* and similar taxa with *S. kochi* will be conducted by the Neogene Planktonic Foraminifera Working Group. Also questionable is the synonymy proposed in Bolli & Saunders (1981) with *S. hancocki* Bandy 1975, a species described from the Pliocene of the eastern Indian Ocean and presenting some features not compatible with *S. kochi* as originally described.

Sphaeroidinellopsis seminulina (Schwager 1866)

- 1866 *Globigerina seminulina* Schwager: fig. 142.
 1959 *Sphaeroidinella dehiscens subdehiscens* Blow: pl. 12, fig. 71a–c.
 1960 non *Sphaeroidinellopsis disjuncta* Banner & Blow: pl. 7, fig. 2.
 2009 *Sphaeroidinellopsis seminulina* Hokuto, Ayayu, Toshiaki, Hayashi & Tanaka: 549, pl. 3, fig. 2a–c.

Test morphology. Low trochospiral, compact, equatorial periphery broadly ovate to slightly trilobulate. The ultimate whorl presents three subglobular chambers, with sutures obscured by a heavy cortex. In umbilical view, the umbilicus is narrow with a low umbilical aperture bordered by a thickened crenulated rim (Kennett & Srinivasan 1983). In spiral view, previous chambers' whorls tend to be hidden under the cortex. When visible, the sutures are straight and incised. In edge view, rounded margin and compact outline with a flat trochospire.

Range. Tortonian (Zone M13)–Piacenzian (Zone PL3). According to Kennett & Srinivasan (1983) this taxon appeared in the early Miocene in Zone N7 (= M4), but this datum might be affected by the misconception caused by the neotype erected by Banner & Blow (1960).

Remarks. This species can be distinguished from *S. disjuncta* by having a fully developed cortex, giving this species the typical glossy appearance shared with its descendant in the *Sphaeroidinella* lineage. *Sphaeroidinellopsis seminulina* is distinguished from *S. kochi* by its higher trochospire and having three chambers in the ultimate whorl and a fully developed cortex, often absent in *S. kochi*. Possible synonymies requiring further investigation are *Prosphaeroidinella valleriae* Bronniman, Whittaker & Parisi 1988 and *Sphaeroidinella spinulosa* Subbotina in Bykova 1958. *Sphaeroidinellopsis seminulina* can be distinguished from *Globoturborotalita connecta* by its fully developed cortex, or in uncovered specimens (lacking a cortex) by its coarser honeycomb wall texture. It differs from *G. woodi* in having three chambers in the ultimate whorl, a more compact coiling, the lower aperture, the narrower umbilicus and the secondary crystallization of the cortex. It can be distinguished from *Sphaeroidinella dehiscens* due to the lack of a supplementary aperture on the spiral side and the trilobate overall shape, compared with the bilobate appearance of *S. dehiscens*.

Taxonomic history. Schwager (1866) described this species from the lower Pliocene of Car Nicobar Island (Srinivasan & Sharma 1974), but the holotype and primary paratypes have been lost, requiring the definition of neotypes. Banner & Blow (1960) indicated that *S. disjuncta* was a junior synonym of *S. seminulina*, an argument strongly debated by Jenkins (1971) and Kennett & Srinivasan (1983). This synonymy is not retained as valid today. The absence of the holotype motivated Banner & Blow (1960) to re-examine the metatype material at the Natural History Museum, London, describing and illustrating a controversial neotype. Despite the majority of the metatypes having three chambers in the ultimate whorl, as did the holotype illustrated by Schwager (1866), Banner & Blow (1960) selected an atypical four-chambered specimen as the neotype. This has since given the impression that *S. seminulina* is typically a four-chambered taxon (Stainforth *et al.* 1975). In Blow (1959), a new species was erected, *S. subdehiscens*, considered different from *S. seminulina* due to having three chambers in the ultimate whorl. Srinivasan & Kennett (1981) considered *S. subdehiscens* a junior synonym of *S. seminulina* and consequently re-designated *S. seminulina* (Schwager 1866) to be the genotype of *Sphaeroidinellopsis* (Kennett & Srinivasan 1983), after comparing the original topotypes of *S. seminulina* from Car Nicobar Island with *S. subdehiscens* (Blow 1959). No significant differences in terms of chamber number, structure of the cortex or in the apertural characters were identified by Srinivasan & Kennett (1981).

In the original description of Schwager (1866), *Sphaeroidinellopsis seminulina* is described as having three and seldom four chambers in the ultimate whorl, while the cortex may fully or partially cover the test, but no supplementary apertures are present. *Sphaeroidinellopsis seminulina* is retained as the ancestor of *S. paenedehiscens*, which led to the origin of *Sphaeroidinella dehiscens*, adding supplementary apertures and developing a full cortex (Blow & Banner 1962; Kennett & Srinivasan 1983; Kučera 1998; Aze *et al.* 2011). The relationship between *S. seminulina* and *S. disjuncta* is still unclear, and some morphological overlap between these taxa is common. Lam & Leckie (2020) reported transitional specimens between these two species in the north-west Pacific Ocean.

Discussion

Distinguishing features

The primary feature described in the original definition of *S. kochi* in Caudri (1934) was the elongation of the last chamber; hence, we suggest this must be retained as a crucial feature to discriminate this morphospecies within the genus, together with the number of chambers in the last whorl. In this study, all specimens showing an elongation in the final chamber or in the last two chambers have been allocated to *S. kochi*. For the same reason, in our opinion, the *S. seminulina* neotype Banner & Blow (1960) and consequently *S. multiloba* LeRoy, 1944 should be also synonymized with *S. kochi*, making this species more common in the fossil record than previously reported in literature. An example of the influence of Banner & Blow's (1960) neotype is found in Chaisson *et al.* (1993), where transitional *S. disjuncta*–*S. seminulina* are debated. In our opinion, these specimens more closely resemble *S. kochi* kummerforms (Fig. 5). The anomalous *S. seminulina* neotype of Banner & Blow (1960) probably led to a biased identification of *S. seminulina*, with a morphological overlap with *S. kochi* and thus influencing the opinion of various workers. For these reasons and to avoid more confusion, we suggest using the elongation of the final chamber and the sac-like morphology as the key characteristic of *S. kochi*, along with more than 3½ chambers in the final whorl. In Lam & Leckie (2020), *S. kochi* from the north Pacific Ocean exhibits a less pronounced elongation in the final chamber and atypical features, as usually happens when planktonic foraminifera are pushed to the edge of their niche. We also suggest that the supposed intermediate specimens *S. disjuncta*–*T. sacculifer* (Bé 1965; Bandy *et al.* 1967) should be

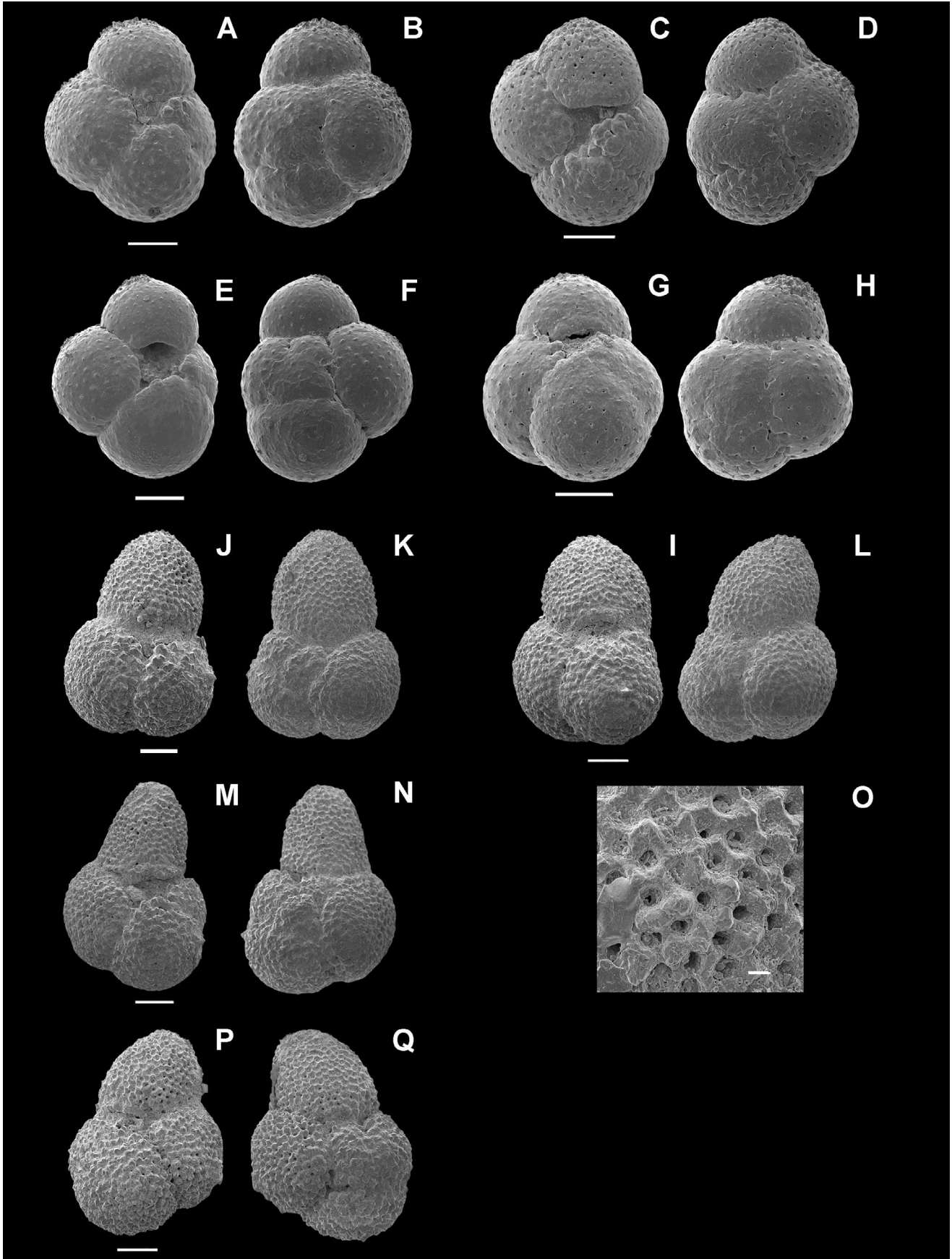
compared to *S. disjuncta*–*S. kochi* transitional specimens presented here (Fig. 3J–Q).

Wall texture

The wall texture of *Sphaeroidinellopsis* is highly variable. All the specimens in this study present a cancellate *sacculifer*-type wall texture. Even though spine holes have not been identified in this study, or in the few detailed wall texture images available in the literature (e.g. Fox & Wade 2013), the inferred phylogeny from a spinose ancestor (Kennett & Srinivasan 1983; Spezzaferri *et al.* 2015; this study) prevents us from considering the *Sphaeroidinellopsis* wall texture as non-spinose as reported in Aze *et al.* (2011). Comprehensive study of the wall texture is often complicated by the overgrowth of the secondary cortex. The thickness of this secondary layer can vary between chambers and between parts of chambers on the same specimen, potentially fully covering the test and hiding the underlying honeycomb texture (Fig. 3A–H). In the decorticated specimens, the wall texture seems to be quite variable in terms of pore diameter and pore number per unit area (Bé 1965; Hemleben *et al.* 2018). The data presented here indicate that the genus *Sphaeroidinellopsis* has a *sacculifer*-type wall texture (Fig. 4P).

The cortex can cover portions of the test or, ultimately, the entire surface. Specimens of *S. disjuncta* can present a cortex on the whole test (Fig. 3A–H) acquiring a shiny and glassy aspect with a marked reduction or total disappearance of pores. In contrast, all the transitional specimens of *S. disjuncta*–*S. kochi* (Fig. 3J–Q) do not present the development of the secondary cortex. On the other hand, *S. kochi* shows large variability, having no cortex (Figs 4A–C, E–G, I–K, M–O; 5), presenting a secondary calcite or partial cortex development (Figs 4D, 6C, G–L, 7C, E, J) or having the test fully covered (Figs 5A, E, M–P, 6A, G, I). In specimens with a partial cortex, recrystallization in the form of intergrown rhombohedrons is commonly evident in the early chambers of the ultimate whorl. This crystalline outer crust has also been identified in species of *Neogloboquadrina* and *Paragloborotalia* (Olsson 1976; Wade *et al.* 2016).

Another element to note is the different development of the cortex through time. In these assemblages, specimens from Zone M6 and M7 (Langhian, middle Miocene) do not show any evidence of the development of a cortex (Figs 3J–Q, 4A, E–O, 5, 7M–P). All the specimens presenting a full or a partial cortex all belong to Zone M10 (Serravallian, middle Miocene). Bolli & Saunders (1985) also reported how, during the late Miocene and Pliocene, the development of the cortex is



more common, even though it is still variable within the same population.

A different phylogeny

In the phylogeny presented by Kennett & Srinivasan (1983) and subsequently incorporated into Aze *et al.* (2011) and the Mikrotax online portal (Huber *et al.* 2016), *Globoturborotalita woodi* is the ancestor of the *Sphaeroidinellopsis* lineage, with *S. disjuncta* evolving from *G. woodi* in the early Miocene (Fig. 8). Kennett & Srinivasan (1983) indicated that *S. disjuncta* gave rise to *S. seminulina* in the early Miocene, and then *S. seminulina* gave rise to *S. kochi* in the middle Miocene. The *Sphaeroidinella* lineage evolves from *S. seminulina* in the late Miocene. This well-established phylogeny is not supported by our new records from the Atlantic Ocean. We find a very close relationship between *S. disjuncta* and *S. kochi*, and suggest that *S. kochi* evolved from *S. disjuncta* and not from *S. seminulina* (Fig. 3J–Q). No specimens intermediate between *S. seminulina* and *S. kochi* occur in our assemblages or in the literature. Microphotographs showing specimens named *S. seminulina*, but more closely resembling *S. kochi* – with a full-grown cortex, with four chambers and with the last chamber elongated – are evident in the literature (Kase *et al.* 2008).

Sphaeroidinellopsis kochi is retained as a descendant of *S. seminulina* (Kennett & Srinivasan 1983; Bolli & Saunders 1985; Aze *et al.* 2011), but all of these *S. seminulina* must be directly compared to the neotype of Banner & Blow (1960). Bolli & Saunders (1985) considered *S. multiloba* to be a descendant of *S. disjuncta*, and belonging to a different plexus than *S. kochi*. Kučera (1998) identified *S. seminulina* specimens with three chambers in the ultimate whorl and a fully developed cortex as more closely resembling *S. dehiscens* forma *immatura* and *S. subdehiscens* Blow, 1959. On the other hand, Jenkins (1971) considered *S. seminulina* as bearing either three or four chambers in the ultimate whorl. Due to this morphologic variability, a different phylogeny and classification of the group is proposed. *Sphaeroidinellopsis disjuncta* has the lowest occurrence within Zone M3 (Zone N6 in Kennett & Srinivasan 1983), the oldest among species of the genus, and it

shows features intermediate with *Globoturborotalita*. Specimens possessing four chambers clearly resemble *G. druryi* or *G. labiacrassata* with a thickened test and more strongly cancellate texture. No fully developed cortex is reported in *S. disjuncta*, suggesting an environmental origin of the cortex later on in the lineage. Srinivasan & Kennett (1981) reported *G. woodi* as the ancestor of *S. disjuncta*, but further studies would be required to exclude the evolution of *S. disjuncta* from *G. labiacrassata* (Spezzaferri, 1994) or *G. druryi*. In absence of intermediate forms of *G. druryi*–*S. disjuncta*, we provisionally retain *G. woodi* as the questionable ancestor of *S. disjuncta*.

According to our data, an alternative phylogeny can be hypothesized for *Sphaeroidinellopsis* (Fig. 8). This hypothesis describes two lineages originating from *S. disjuncta* in the early Miocene: >3½ chambered specimens transitioning to *S. kochi*, and three-chambered specimens evolving into *S. seminulina*, ancestral to *Sphaeroidinella* during the late Miocene through *S. panaedelescens*.

Following the *G. woodi*-ancestor hypothesis (Fig. 8), the four-chambered specimens with any elongation in the final chambers should be named *S. kochi*. The cortex would be an environmentally driven feature, thus not having any taxonomical importance. Instead, the three-chambered specimens should be considered *S. seminulina* (compare to *S. subdehiscens* [Blow 1960]). Lam & Leckie (2020) reported transitional individuals of *S. disjuncta*–*S. seminulina*, which could support the scenario described in this paper.

A rigorous study of *S. disjuncta* populations will help us understand the phenotypic variability of this species, unravelling the possibility of a polyphyletic genus. The ancestor of the genus must be investigated, taking into account all the specimens of *S. seminulina* bearing supplementary apertures, such as *S. cellata* (Subbotina in Bykova, 1958). The nature and precise time of appearance of these secondary apertures should be investigated to clarify whether *Globoturborotalita*, or *Trilobatus/Globigerinoides* as supposed by Bè (1965), Bandy *et al.* (1967), Jenkins (1971), was the ancestor of these populations. Specimens bearing dorsal supplementary apertures have also been reported in Lam & Leckie (2020), even though their origin could be a diagenetic feature.

Figure 3. *Sphaeroidinellopsis disjuncta*: **A, B**, NHMUK PM PF 75143; **C, D**, NHMUK PM PF 75144; **E, F**, NHMUK PM PF 75145; **G, H**, NHMUK PM PF 75146, umbilical and spiral views from sample 159/959B 17H-6 (87–89 cm), Zone M10 middle Miocene, east equatorial Atlantic; **G, H**, from sample 159/959B 17H-6 (36–38 cm), Zone M10 middle Miocene, east equatorial Atlantic; *Sphaeroidinellopsis disjuncta*–*Sphaeroidinellopsis kochi*: **J, K**, NHMUK PM PF 75147; **I–L**, NHMUK PM PF 75148; **M–O**, NHMUK PM PF 75149; **P, Q**, NHMUK PM PF 75150, transitional individuals from sample 154/925A 4R-3 (60–62 cm), Zone M6 middle Miocene, western equatorial Atlantic; **O**, wall texture detail in 50 × 50 µm surface of specimen shown in **M, N**. Scale bars: **A–N, P, Q** = 100 µm; **O** = 10 µm.

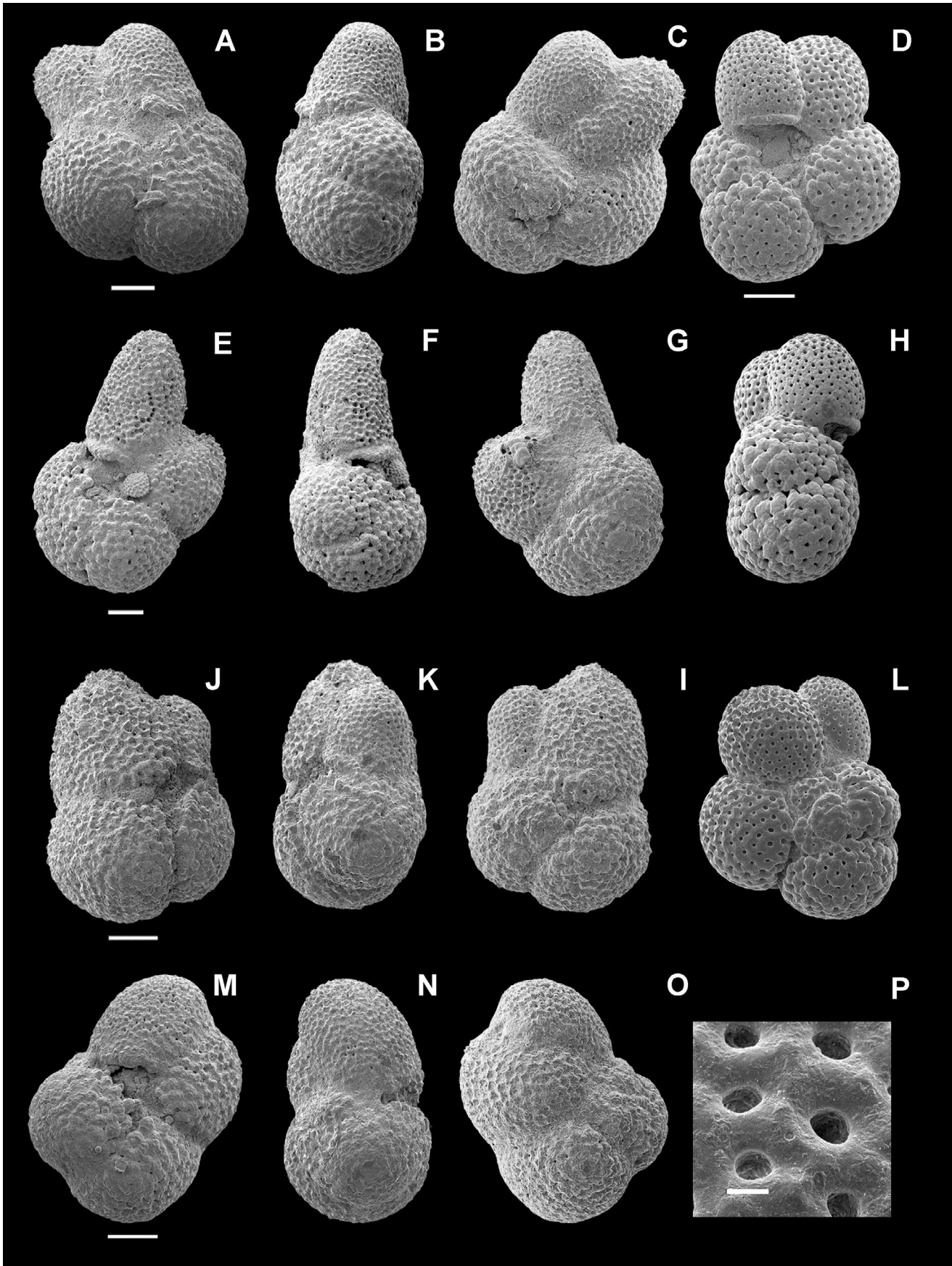


Figure 4. *Sphaeroidinellopsis kochi*: A–C, NHMUK PM PF 75151, umbilical, edge and spiral views from sample 154/925A 4R-3 (60–62 cm), Zone M6 middle Miocene, western equatorial Atlantic; D, H, L, NHMUK PM PF 75152, from sample 159/959B 17H-6 (36–38 cm), Zone M10 middle Miocene, east equatorial Atlantic; P, wall texture detail in $50 \times 50 \mu\text{m}$ surface from specimen D; E–G, NHMUK PM PF 75153; J–I, NHMUK PM PF 75154; M–O, NHMUK PM PF 75155, from sample 154/925A 4R-2 (65–67 cm), Zone M7 middle Miocene, western equatorial Atlantic. Scale bars: A–O = $100 \mu\text{m}$; P = $10 \mu\text{m}$.

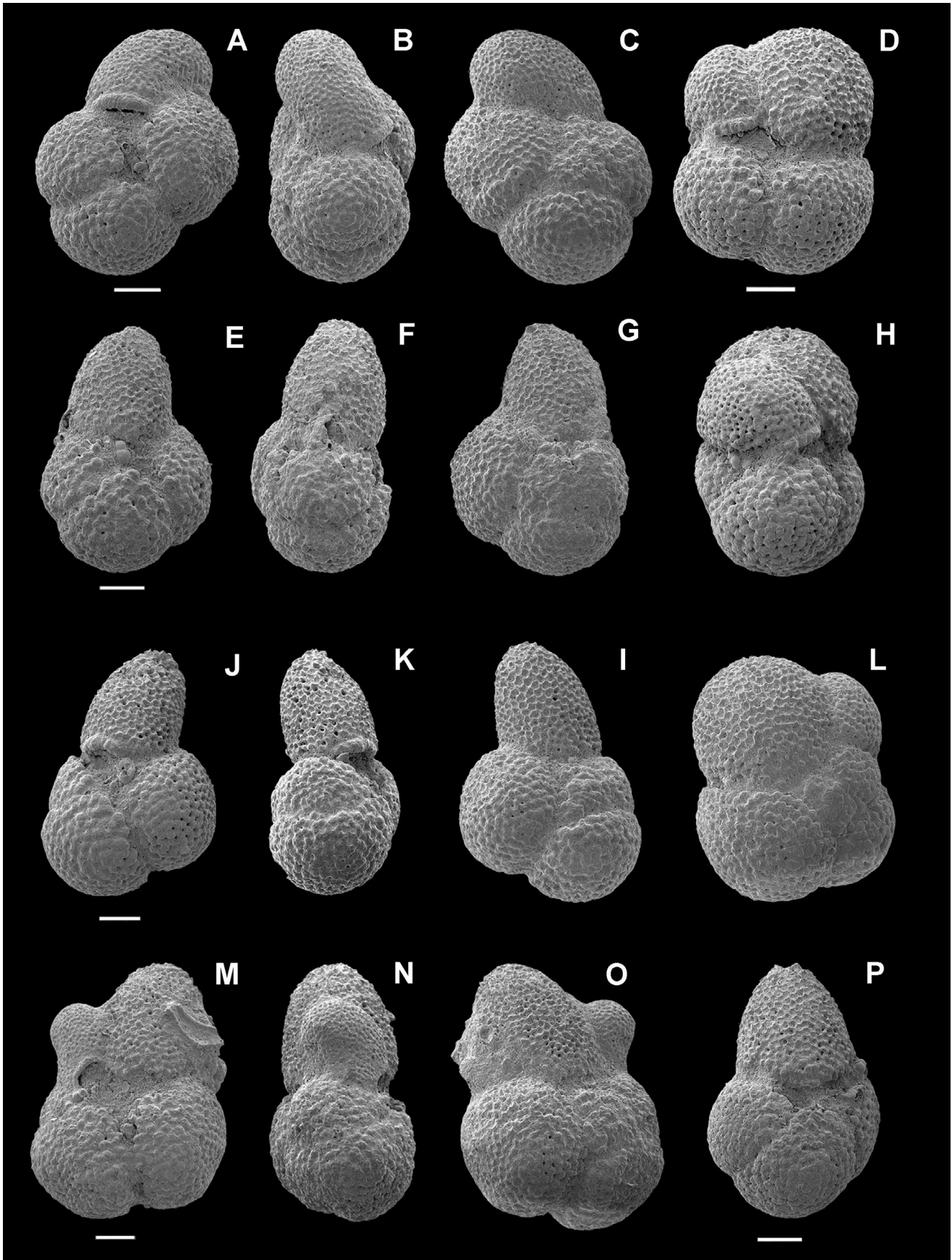


Figure 5. *Sphaeroidinellopsis kochi*: A–C, NHMUK PM PF 75156; D, H, L, NHMUK PM PF 75157; E–G, NHMUK PM PF 75158; J–I, NHMUK PM PF 75159; M–O, NHMUK PM PF 75160; P, NHMUK PM PF 75161, from sample 154/925A 4R-2 (65–67 cm), Zone M7 middle Miocene, western equatorial Atlantic; D, H, L, P from sample 154/925A 4R-3 (60–62 cm), Zone M6 middle Miocene, western equatorial Atlantic. Scale bars = 100 μ m.

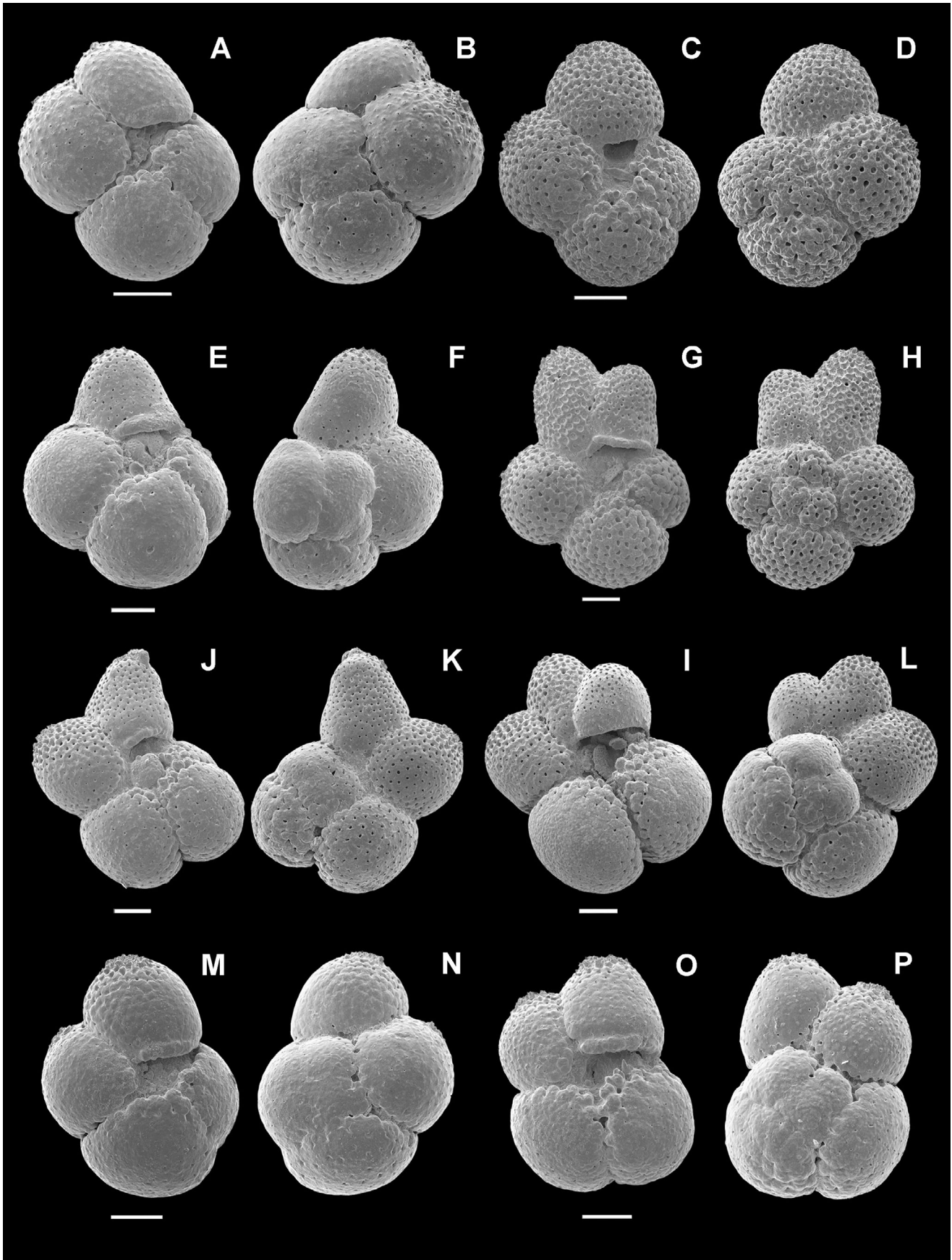
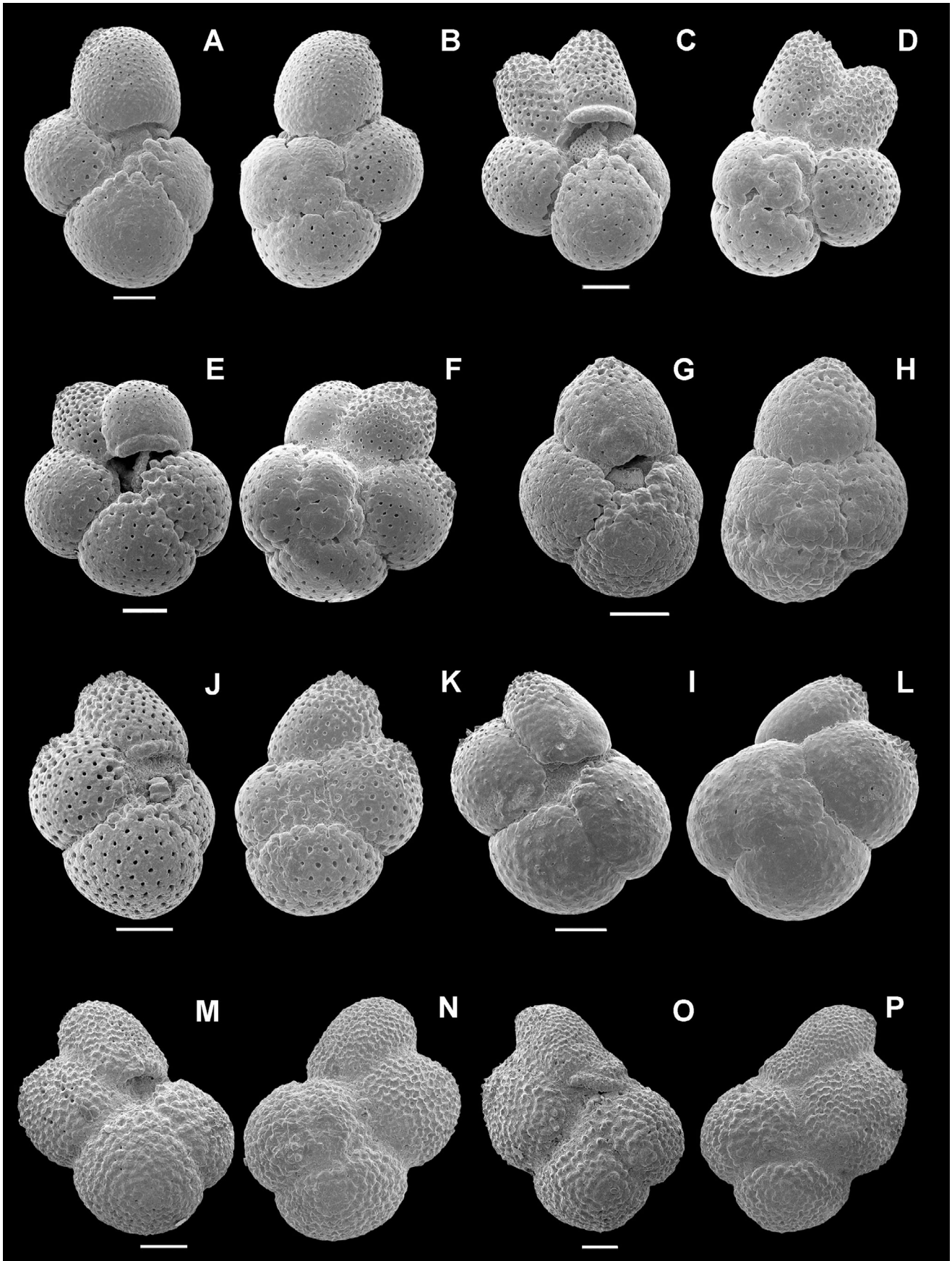


Figure 6. *Sphaeroidinellopsis kochi*: **A, B**, NHMUK PM PF75162; **C, D**, NHMUK PM PF 75163; **E, F**, NHMUK PM PF 75164; **G, H**, NHMUK PM PF 75165; **J, K**, NHMUK PM PF 75166; **I-L**, NHMUK PM PF 75167; **M, N**, NHMUK PM PF 75168; **O, P**, NHMUK PM PF 75169, umbilical and spiral views from sample 159/959B 17H-6 (87–89 cm), Zone M10 middle Miocene, east equatorial Atlantic. Scale bars = 100 μ m.



These hypotheses must also be verified by investigating the wall structure in order to clarify the real nature of these secondary apertures and thus the possible synonymy of *S. cellata* with *S. dehiscens*.

Phylogeny

Ancestral specimens with a thinner or partial cortex were informally designated as ‘*Sphaeroidinellopsis*’ in Spezzaferri (1994), where three different morphotypes and their most probable ancestor were identified as follows: (1) ‘*Sphaeroidinellopsis*’ *disjuncta* probably evolved from *G. labiacrassata*; (2) ‘*Sphaeroidinellopsis*’ aff. *disjuncta* probably evolved from *G. woodi* in the late Oligocene; and (3) ‘*Sphaeroidinellopsis*’ sp. 1 may have evolved from *G. connecta*. Based on modern taxonomical concepts, such an interpretation would determine a polyphyletic genus. Extending the stratigraphical range of *Sphaeroidinellopsis* to the upper Oligocene and determining the definition of a new genus for *S. seminulina* and ‘*Sphaeroidinellopsis*’ sp. 1 Spezzaferri (1994) still has no support to the present day.

In Spezzaferri *et al.* (2015), *Sphaeroidinellopsis* and *Sphaeroidinella* are inferred to be descendants of *Trilobatus*, but here, in this study, no evidence of supplementary apertures has been observed. Since supplementary apertures are retained as phylogenetic characters, we support the origin of *Sphaeroidinellopsis* from *Globoturborotalita* and not from *Trilobatus*. The real ancestor of *Sphaeroidinellopsis* is still problematic. *Globoturborotalita druryi* or *G. labiacrassata* might be studied as the possible ancestor rather than *G. woodi*, but more data are necessary to support this hypothesis.

Conclusions

Our study and the new SEM images have ramifications for the phylogeny of *Sphaeroidinellopsis*. The observation of transitional *S. disjuncta*–*S. kochi* individuals allowed us to hypothesize a different phylogeny for the genus *Sphaeroidinellopsis*. Our data suggest that *S. seminulina* and *S. kochi* could not be directly linked as previously reported in the literature. The transition *S. disjuncta*–*S. kochi* can be identified using two main features: the elongation of the final chamber and having more than 3½ chambers in the ultimate whorl. No

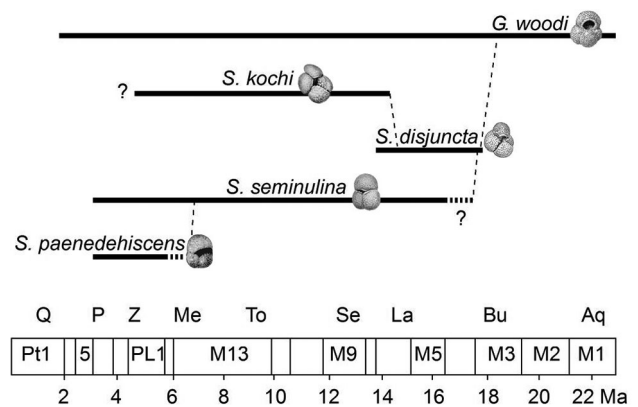


Figure 8. *Sphaeroidinellopsis* phylogeny. *Sphaeroidinellopsis disjuncta* appeared from *Globoturborotalita woodi* in the early Miocene, giving rise to two different lineages. With a progressive elongation of the last chamber, the transition to *S. kochi* took place at the end of the early Miocene. The second lineage arose from the three-chambered populations giving rise to *S. seminulina*, leading to the *Sphaeroidinella* lineage. *Globoturborotalita woodi* is provisionally retained as the ancestor according to the literature and in the absence of transitional individuals between *G. druryi* or *G. labiacrassata* and *S. disjuncta*.

intermediate individuals of *S. seminulina*–*S. kochi* are reported in the literature, invalidating the origin of *S. kochi* from *S. seminulina*. The problematic *S. seminulina* neotype erected by Banner & Blow (1960) may have been the cause of the taxonomical confusion of the group and its ancestry. Our findings, integrated with data and observations from the literature, allowed us to revise the phylogeny, indicating that *Sphaeroidinellopsis kochi* and *S. seminulina* represent two different lineages within the same genus, *Sphaeroidinellopsis*, having their common ancestor in *S. disjuncta*, which evolved from *G. woodi* (Fig. 8); this is also supported by the transitional specimens of *S. disjuncta*–*S. seminulina* (Lam & Leckie 2020). Further population and morphometric studies on key transitional taxa will clarify the ancestor–descendent relationships.

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Figure 7. *Sphaeroidinellopsis kochi*: **A, B**, NHMUK PM PF 75170; **C, D**, NHMUK PM PF 75171, umbilical and spiral views from sample 159/959B 17H-6 (87–89 cm), Zone M10 middle Miocene, east equatorial Atlantic; **E, F**, NHMUK PM PF 75172; **G, H**, NHMUK PM PF 75173; **J, K**, NHMUK PM PF 75174; **I, L**, NHMUK PM PF 75175, from sample 159/959B 17H-6 (36–38 cm), Zone M10 middle Miocene, east equatorial Atlantic; **M, N**, NHMUK PM PF 75176; **O, P**, NHMUK PM PF 75177, from sample 154/925A 4R-2 (65–67 cm), Zone M7 middle Miocene, western equatorial Atlantic. Scale bars = 100 µm.

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