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## *Sphaeroidinellopsis* and *Sphaeroidinella* (planktonic foraminifera): morphological variability, wall texture and taxonomic implications

Alessio Fabbrini<sup>a,b</sup>  and Bridget S. Wade<sup>a\*</sup> 

<sup>a</sup>Department of Earth Sciences, University College London, Gower Street, London, WC1E 6BT, UK; <sup>b</sup>Department of Geography, University of Galway, Distillery Road 8, Galway, H91 CF50, Ireland

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We used biometry, multifocal optical and scanning electron microscopy to investigate the morphological variability and wall texture of the planktonic foraminifera genera *Sphaeroidinella* and *Sphaeroidinellopsis*. Our study focuses on the late Miocene to Pleistocene (Zone M11 to Subzone PT1b) from the west Pacific within the ‘warm pool’ (International Ocean Discovery Program Site U1490) and from the north-west Australian margin (International Ocean Discovery Program Site U1482). Our observations indicate a new type of wall texture that we describe and name the *disjuncta*-type, after the first morphospecies to bear it (*Sphaeroidinellopsis disjuncta*). The *disjuncta*-type wall texture is restricted to the genera *Sphaeroidinellopsis* and *Sphaeroidinella*, and it is defined by a spinose wall with extremely large pores and the ability to overgrow a thick imperforate secondary layer of calcite, known as a cortex. This type of wall is similar to the *sacculifer*-type texture, but with a larger pore size and smaller pore number per unit area. Biometric analysis of the maximum diameter and the circularity was measured on over 1100 individuals with a sample resolution of 500 kyr, to highlight the main morphological differences exhibited along this evolving lineage and to document the local phenotypic variability of both genera. We reassess the taxonomy of *Sphaeroidinellopsis kochi*, designating a neotype to accommodate the taxonomic instability surrounding this taxon. Members of the extant *Sphaeroidinella* lineage, *Sphaeroidinella dehiscens* and *Sphaeroidinella excavata*, are discussed and recognized as distinct and valid morphospecies due to their biostratigraphic potential.

**Keywords:** biometry; evolution; Pacific Ocean; planktonic foraminifera; taxonomy; Western Pacific Warm Pool

### Introduction

Micropalaeontology is based on the concept of morphospecies and their stratigraphic range. Unfortunately, the intrinsically limited data available in the fossil record prevents us from conducting genetic analysis, and requires us to separate individuals based on morphological observations. For these reasons, more objective and replicable data became necessary for defining morphospecies and applying taxonomical concepts. Advancements in technology allow the collection of quantitative data, such as biometry, which can capture the complexity of planktonic foraminifera (Fabbrini et al., 2023, 2024; Latas et al., 2023; Malmgren & Kennett, 1977; Poole & Wade, 2019; Spezzaferri et al., 2015). In the typological concept of morphospecies the variability of the phenotypes within a population will range in a limited interval of values, where ideally the holotype would represent the average. The real state of the art in taxonomy is far from the ideal conditions, especially in the past when all classifications relied on visual observation only, often from drawings. This approach has caused high uncertainty and subjectivity,

possibly over-splitting groups of organisms due to their phenotypic variability.

In order to overcome these issues, micropalaeontology has successfully implemented population-based studies combined with biometric analysis to better capture the range of variability of morphospecies thanks to the high number of individuals analysed (Fabbrini et al., 2023; Hull & Norris, 2009; Latas et al., 2023; Poole & Wade, 2019). This approach could allow more replicable and more statistically based decisions, especially for holotype and neotype selection. In this study we applied such an approach to tackle some of the uncertainties existing in *Sphaeroidinella* and *Sphaeroidinellopsis*, two genera still requiring clarifications. Hereafter, the genus *Sphaeroidinella* will be indicated as *Sa.*, and *Sphaeroidinellopsis* as *Ss.*, for simplicity.

### Biostratigraphic importance

*Sphaeroidinellopsis* spanned from the early Miocene to the Pliocene, while *Sphaeroidinella* ranges from the late

\*Corresponding author. Email: [a.fabbrini@ucl.ac.uk](mailto:a.fabbrini@ucl.ac.uk), [alessio.fabbrini@universityofgalway.ie](mailto:alessio.fabbrini@universityofgalway.ie).

Miocene to present. The group has biostratigraphic relevance, due to the extinction of one of its species (*Ss. seminulina*) marking the base of Zone PL4, and the transition to *Sphaeroidinella* (also known as the *Sphaeroidinella* event). The evolution of *Sa. dehiscens* is a diachronous event (Kučera, 1998) used to approximate the Miocene–Pliocene chronostratigraphical boundary. The ‘*Sphaeroidinella* event’ is regarded as an example of anagenesis (i.e. gradual evolution); thus, the exact appearance of *Sa. dehiscens* in the fossil record is gradual and has been strongly debated (see Kučera, 1998; Malmgren et al., 1996). Kučera (1998) extensively addressed the biostratigraphic aspects of the *Sphaeroidinella* event, providing a framework and guidelines on how to identify this evolutionary event in the stratigraphic record.

## A problematic group

*Sphaeroidinellopsis* is an extinct genus including four recognized morphospecies (*Ss. disjuncta*, *Ss. seminulina*, *Ss. kochi* and *Ss. paenedehiscens*), it was erected by Banner and Blow (1959) to accommodate all the globigerinids with no supplementary apertures and an overgrowth of calcite (cortex) covering the test. The appearance of the secondary apertures has been debated from a biostratigraphical and a genetic perspective (Spezzaferri et al., 2015), suggesting a close relationship between *Sphaeroidinellopsis* and *Globoturborotalita*. The true ancestor of *Sphaeroidinellopsis* is still controversial, but other evolutionary steps have been reassessed recently. The anagenetic transition from *Ss. disjuncta* to *Ss. kochi* was documented by Fabbrini et al. (2021), showing intermediate specimens between the two morphospecies and modifying the ancestor of *Ss. kochi* from *Ss. seminulina* to *Ss. disjuncta*.

The genus *Sphaeroidinella* is extant, with only one biological species recognized: *Sa. dehiscens*. The genus *Sphaeroidinella* was erected by Cushman in 1927, but amended by Banner and Blow in 1959 to include all globigerinids presenting a cortex and secondary openings on the spiral side. However, there are still open questions concerning its wall texture and cortex development, and taxonomical inconsistency among workers. Another riddle is to what extent phenotypic variability has influenced this taxonomic instability (see Bolli & Sanders, 1981 and Kennett & Srinivasan, 1983, among others).

The taxonomy of *Sphaeroidinella* and *Sphaeroidinellopsis* has been addressed in several studies (Banner & Blow, 1959; Bolli & Saunders, 1981; Fabbrini et al., 2021; Kennett & Srinivasan, 1983; Kučera, 1998;

Malmgren et al., 1996), but the evolution of this lineage of planktonic foraminifera remains unclear and not fully understood. Clear taxonomic guidance and extensive illustration of morphological variability are extremely important to achieve consistent identification across workers. A lack of these tools leads to taxonomic confusion, impacting the biostratigraphic schemes. To address this issue, we combine high-detail optical and scanning electron microscope (SEM) imaging with biometry to clarify the taxonomy and phylogeny of *Sphaeroidinellopsis* and *Sphaeroidinella*.

*Sphaeroidinella dehiscens* has been a problematic taxon for a long time since its original description (Parker & Jones, 1865), with contrasting views among scientists. Bé (1965) considered *Sphaeroidinella dehiscens* as an aberrant form of *Trilobatus sacculifer* occurring in deeper oceanic waters. Bandy et al. (1967) investigated the inner structure of *Sphaeroidinella* and its ancestor genus *Sphaeroidinellopsis*, both characterized by an overgrowth of a secondary layer of calcite on their tests and hiding their inner features. Bandy et al. (1967) reported how both genera contained forms similar to ‘*Globigerinoides*’, eventually defining the group *Sphaeroidinella*–*Sphaeroidinellopsis* as an example of isomorphism, or rather a human-constructed (i.e. artificial) lineage of foraminifera belonging to the genus *Globigerinoides* (species now included in the genus *Trilobatus* after Spezzaferri et al., 2015). Those findings never ignited further targeted studies, on cortex development or on such inferred isomorphism. The succeeding authors kept both genera valid, rejecting the proposed isomorphism with *Trilobatus* (Aze et al., 2011; Blow, 1979; Bolli & Saunders, 1981; Cita & Ciaranfi, 1972; Fabbrini et al., 2021; Kennett & Srinivasan, 1983; Kučera, 1998; Lam & Leckie, 2020; Malmgren et al., 1996; Pearson, 1995). Genetic studies on both *Sphaeroidinella* and *Trilobatus* ended this dispute, showing how the two genera belong to separate and distinct genetic lineages (Morard et al., 2024; Spezzaferri et al., 2015). Open questions remain on the evolution of this group of foraminifera, such as their ancestor and the development of the cortex on their tests. None of these questions can be answered without attempting to capture the morphological variability of these two genera.

## Our approach

To contribute to the taxonomy of *Sphaeroidinella* and *Sphaeroidinellopsis* we applied a population-based approach, measuring biometric parameters to distinguish morphospecies within the studied populations. This

group of planktonic foraminifera lives in equatorial to subtropical open ocean (thermocline conditions according to Aze et al., 2011). Both of these genera are predominantly distributed at low latitudes; thus, we decided to investigate their abundance and fossil range at a locality close to the equator and with good fossil preservation. We examined samples from the Western Pacific Warm Pool (WPWP) at International Ocean Discovery Program (IODP) Site U1490. Quantitative assemblage analyses indicate that *Sphaeroidinellopsis* is present in the west Pacific (0.5–4.5% of the fossil assemblage) at IODP sites U1490 and U1482 (Boscolo-Galazzo et al., 2022).

The very good fossil preservation and long fossil range continuity allowed us to study the evolution and size of both *Sphaeroidinella* and *Sphaeroidinellopsis*. Our study aims to document the range of morphological variability within this lineage and contribute to the Neogene and Quaternary Planktonic Foraminifera Working Group activity within the International Subcommission on Stratigraphy.

## Material and methods

Our study is based on IODP Site U1482 and Site U1490. The two sites represent two different locations drilled during IODP Expedition 363 (Rosenthal et al., 2018). These sites have been selected to study the evolution of *Sphaeroidinellopsis* and *Sphaeroidinella* because of the good fossil preservation (Fayolle & Wade, 2020; Rosenthal et al., 2018) and because of their geographical location (Fig. 1).

### IODP Site U1482

Site U1482 was drilled in the north-west Australian margin at 15°3.32'S, 120°26.10'E at 1466 m water depth (Rosenthal et al., 2018). The analysed interval spans from core 20HCC to 28HCC (Core Catcher), and consists of a nannofossil ooze with varying abundances of foraminifera (Rosenthal et al., 2018). This material has been used for wall texture investigations and SEM imaging.

### IODP Site U1490

Site U1490 (Eauripik Rise at 05°48.95'N, 142°39.27'E in 2341 m water depth) is located in the western equatorial Pacific Ocean in the heart of the WPWP. Sediments consist of nannofossil ooze with clay and foraminifera (Rosenthal et al., 2018). Twenty-six samples were analysed in the interval 1HCC–26HCC with an overall temporal resolution of 500 kyr, covering the

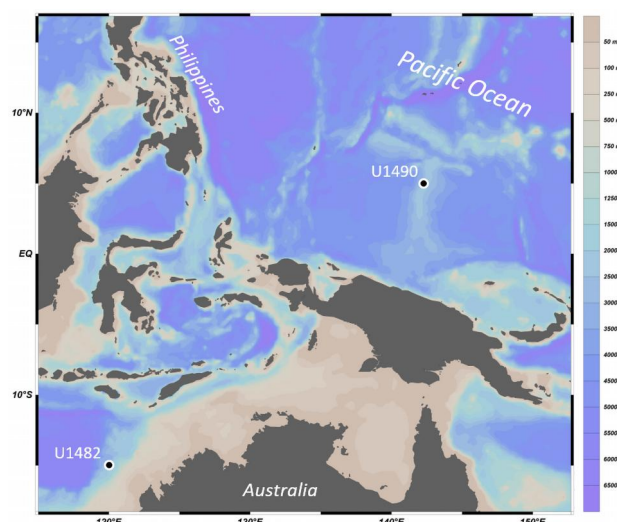


**Figure 1.** Location of the studied International Ocean Discovery Program (IODP) Sites U1482 and U1490. Water depth is indicated on the right. The figure was drawn with Ocean Data View (Schlitzer, 2018).

Pleistocene to Middle Miocene (Tortonian), based on the age model of Rosenthal et al. (2018). Throughout the entire studied section, fossil preservation is very good (Rosenthal et al., 2018). This site was used for quantitative count data and biometry.

## Sample preparation

Each sample consisted of 10 cm<sup>3</sup> of sediment. All samples were prepared following standard washing, drying and sieving procedures. Samples were pre-soaked in distilled water 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.

## Micropalaeontological analyses

The samples were sieved into two size fractions (>400 µm, 400–150 µm) to isolate the morphospecies under investigation, which tend to have size above 400 µm in adult specimens at these locations. Each size fraction was split twice using a microsplitter. The microfossil specimens were examined under a light stereomicroscope and then selected for SEM imaging. All unbroken specimens of *Sphaeroidinellopsis* and *Sphaeroidinella* in the size fraction >400 µm were picked and stored in microslides for imaging and biometry.

The size fraction >400 µm was used for counting exclusively individuals of *Sphaeroidinellopsis* and *Sphaeroidinella*. The size fraction 400–150 µm was

examined under the stereomicroscope for qualitative observations and biostratigraphic age control. All residues and working aliquots were weighed using a SARTORIUS Precision Lab balance. The total number of individuals picked in the size fraction  $>400\text{ }\mu\text{m}$  was standardized using the weight of the corresponding aliquot. The counts have then been expressed as the number of individuals per milligramme of sediment ( $>400\text{ }\mu\text{m}$ ). Taxonomic concepts and species identification were based on the literature (Bermúdez, 1961; Bolli & Saunders, 1981, 1985; Fabbrini et al., 2021; Fox & Wade, 2013; Kennett & Srinivasan, 1983; Lam & Leckie, 2020; Malmgren et al., 1996; Pearson, 1995; Wade et al., 2018).

### Biometry

In total 1102 specimens were measured, using the software Image Pro, and a QImaging RETIGA-2000R camera mounted on a light microscope at the Department of Earth Sciences at University College London (UCL), UK. The following two parameters were measured: area (A) ( $\mu\text{m}^2$ ) and maximum diameter (D) ( $\mu\text{m}$ ). An additional parameter to pinpoint the compactness of the specimens, circularity (C), has been calculated according to Equation (1) using A and D as follows:

$$C = A/\pi(D/2)^2 \quad (1)$$

All data were plotted using the Statistical Software PAST (Hammer et al., 2001).

### SEM and optical imaging

Specimens were selected for multifocal imaging on a Z-stacking light microscope. For SEM analyses, specimens were placed on metal stubs using double-sided sticky tape. The stubs were coated with gold and inspected using a Jeol JSM-6480LV high-performance, Variable Pressure Analytical SEM. All imaging was conducted in the Department of Earth Sciences at UCL. Imaged specimens are deposited at the Natural History Museum (NHM), London (UK). SEM images were used to measure the mean diameter of pores ( $n = 114$ ) and the total number of pores per unit area ( $2500\text{ }\mu\text{m}^2$ ) on the outside of the test in nine specimens. The close-up images (magnification  $850\times$ ) were taken on the penultimate chamber of intact, unbroken specimens.

## Results

### Biometry

Our biometric analysis ( $n = 1112$ ) conducted at IODP Site U1490 was based on six morphospecies, four

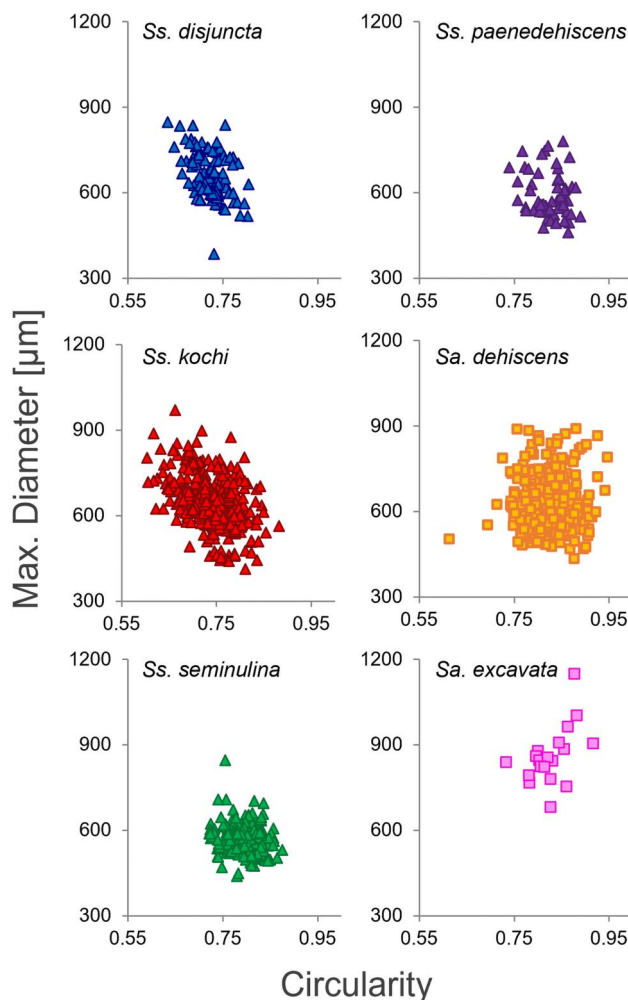


**Figure 2.** Cross plot of maximum diameter vs circularity.

belonging to the genus *Sphaeroidinellopsis* (*Ss. disjuncta*, *Ss. kochi*, *Ss. seminulina*, *Ss. paenedehiscens*) and two to the genus *Sphaeroidinella* (*Sa. dehiscens*, *Sa. excavata*). The parameters circularity and maximum diameter are plotted in Figure 2.

Circularity ranges between 0.60 and 0.94. The majority of *Sphaeroidinella dehiscens*, *Ss. paenedehiscens* and *Ss. seminulina* have circularity higher than 0.70. The highest values in circularity are reached by *Sa. dehiscens*, ranging from 0.61 to 0.94 and having an average value of circularity of 0.82, which is consistent with their sub-spherical morphology (circularity = 1 indicates a sphere). In contrast, *Ss. disjuncta* and *Ss. kochi* show lower values of circularity, below 0.88 (Fig. 2), presenting more asymmetrical and elongated individuals. *Sphaeroidinellopsis kochi* presents low values in circularity, evidence of asymmetrical tests with an average value of 0.74. *Sphaeroidinellopsis seminulina* has an average value of 0.80, while *Ss. paenedehiscens* averages 0.83

and thus is very similar to *Sa. dehiscens*. The lowest mean value of circularity is 0.72, in *Ss. disjuncta*, which then presents the least spherical and most asymmetrical tests among this group, similar to *Ss. kochi* (average circularity = 0.74). From *Sphaeroidinellopsis* to *Sphaeroidinella*, circularity increases, with individuals gradually becoming more spherical.

Maximum diameter ranges from 384  $\mu\text{m}$  to 1149  $\mu\text{m}$  (Fig. 2). *Sphaeroidinellopsis disjuncta* has a mean maximum diameter of 661  $\mu\text{m}$  ( $n = 100$ ). *Sphaeroidinellopsis kochi* reaches values close to 950  $\mu\text{m}$  in a limited number of individuals, when the ultimate chambers are extremely elongated. The mean maximum diameter of *Ss. kochi* is 648  $\mu\text{m}$  ( $n = 377$ ). Smaller values of the mean maximum diameter are evident in *Ss. paenedehiscens* 595  $\mu\text{m}$  ( $n = 56$ ) and in *Ss. seminulina* 566  $\mu\text{m}$  ( $n = 194$ ). *Sphaeroidinella dehiscens* reaches a large size, with a mean maximum diameter of 633  $\mu\text{m}$  ( $n = 366$ ) as shown in Fig. 2. A subgroup of *Sphaeroidinella* ( $n = 19$ ) presented the highest values of maximum diameter (Fig. 2) and always presented extremely open and deep sutures. We classified these individuals as *Sphaeroidinella excavata* Banner and Blow, 1965.

### Wall texture

On SEM images we measured the mean diameter of pores and the total number of pores per unit area ( $2500 \mu\text{m}^2$ ) on the tests of each morphospecies, because these two parameters have been consistently used in the literature to define wall texture in planktonic foraminifera (Bé, 1968; Hemleben et al., 1989, 2018). On average, *Sphaeroidinellopsis* and *Sphaeroidinella* present about 5 pores per unit area ( $2500 \mu\text{m}^2$ ) with a mean external diameter of 5.9  $\mu\text{m}$  (Figs 3 and 4; Table 1). We find multiple evidence of both spines and spine holes (Fig. 3).

## Discussion

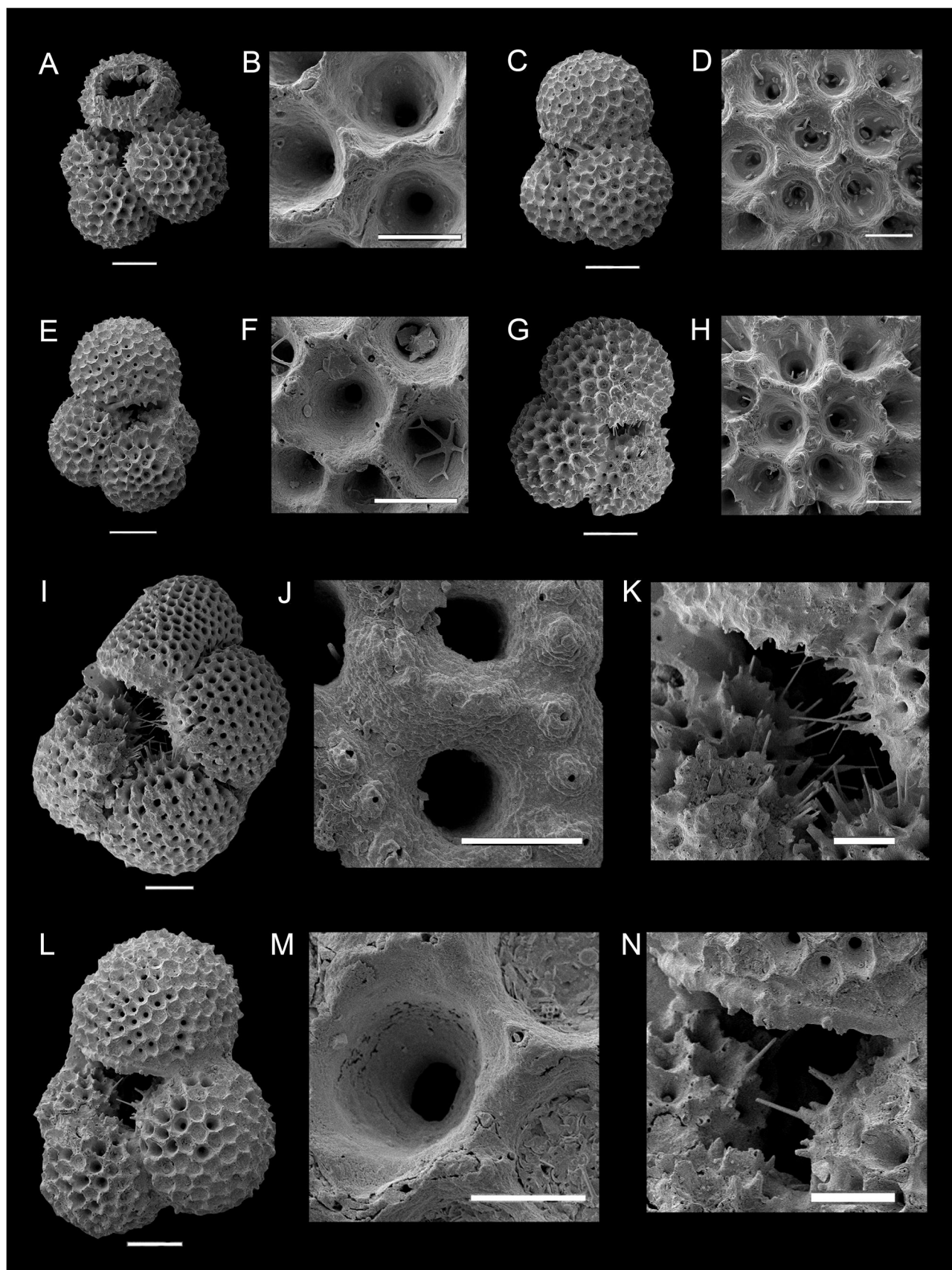
### Wall texture

**Cortex.** We compared our results for the mean diameter and pore number from *Sphaeroidinellopsis* and *Sphaeroidinella* to the wall textures of the other genera from the literature (Hemleben et al., 1989, 2018). Both *Sphaeroidinellopsis* and *Sphaeroidinella* show substantial differences from other genera in terms of porosity, and they are also characterized by a unique feature absent in other genera: a thick cortex. *Pulleniatina* is the only other living genus overgrowing a cortex on its test, which appears different in terms of thickness and transparency (Fabbrini et al., 2025; Pearson et al., 2025). The non-spinose wall of *Pulleniatina* is completely covered by a thin cortex ( $<5 \mu\text{m}$ ) sealing the small porosity of the test

(Fabbrini et al., 2025). Conversely, *Sphaeroidinellopsis* and *Sphaeroidinella* cover their tests with a thick secondary overgrowth layer of calcite without covering or sealing completely the underlying porosity on the test surface (Blow, 1969; Hofker, 1972; Kennett & Srinivasan, 1983 among others). The total surface occupied by the cortex is variable and it seems to be species dependent, but focused studies are necessary to determine the reasons for its development. Along the stratigraphic range investigated at IODP Site U1490, we observe most of the specimens had the cortex in different stages of development.

Both Ujiié (1976) and Brönniman et al. (1988) addressed the different wall textures possessed by *Sphaeroidinellopsis* and *Sphaeroidinella* due to cortex development. Ujiié (1976) defined the new (and not valid) genus *Prosphaeroidinella* to accommodate a group of taxa identical to *Sphaeroidinellopsis*, but lacking the cortex. Ujiié (1976) commented on how *Sphaeroidinellopsis disjuncta* Finlay had a honeycomb wall structure, which is covered in the earlier chambers by the growth of an extra layer of the third lamella (Hofker, 1972); thus, *Prosphaeroidinella* accommodated all the individuals resembling *Ss. disjuncta* with a thick honeycomb wall texture but with no cortex. This wall texture was differentiated from *Globigerinoides* (and *Trilobatus*) by a “more widely spaced framework” (Ujiié, 1976). We interpret this statement as a description of the larger and sparser pores present in *Sphaeroidinella* and *Sphaeroidinellopsis* than in *Globigerinoides* and *Trilobatus*. *Prosphaeroidinella* was interpreted as a form of atavism and thus it was retained the ancestor of *Sphaeroidinellopsis*. We consider *Prosphaeroidinella* Ujiié, 1976 to be a junior synonym of *Sphaeroidinellopsis* Banner and Blow, 1959, but we acknowledge the valuable observations reported in Ujiié (1976) as an indicator of the variability of cortex development and its potential link to environmental factors. The specimens recovered by Ujiié (1976) were from temperate areas of the west Pacific Ocean (Japan archipelago), which are comparable to the specimens illustrated by Lam and Leckie (2020) that also show incomplete or even missing cortex. This suggests that environmental drivers might control or affect cortex overgrowth in planktonic foraminifera.

**Spinosity.** Our high-resolution SEM images reveal spines and spine holes (Fig. 3), indicating *Sphaeroidinellopsis* is a spinose genus, consistent with Hofker (1972), Pearson (1995) and contrary to Aze et al. (2011). Our SEM images show specimens with spines still attached to the wall in the inner portion of the aperture and on the umbilical area (Fig. 3). The extant *Sphaeroidinella dehiscens* is a spinose species and spines attached on the inside of the test were



documented and imaged by Schiebel and Hemleben (2017) in modern and recent individuals. The presence of spines in *Sphaeroidinellopsis* is thus coherent with the phylogeny of the group. We can compare our SEM images of true spines in *Sphaeroidinellopsis* (Fig. 3I, K, L, N) to those of extant *Sphaeroidinella* in plate 2.14 of Schiebel and Hemleben (2017), showing the same location of the spines on the inside of the foraminiferal test and not on the outside surface. Saito et al. (1981), Hemleben et al. (1989) and Schiebel and Hemleben (2017) discussed the possibility of *Sa. dehiscens* having spines similar to *T. sacculifer* during the juvenile stage and then shedding the spines later in life while dwelling in deeper waters. This could explain the preservation of spines inside the test and of the spine holes (Fig. 3B, F, I–K, M in this paper) under the cortex, and thus visible only in decorticated (i.e. without cortex) individuals. We observed small vertical spine-like structures (Fig. 3D, H) also reported in *Sphaeroidinella dehiscens* by Schiebel and Hemleben (2017) and classified as ‘epitactic spikes’ and thus not as true spines. These structures are thinner and more irregularly distributed on the wall, and they are shown here for comparison with the true spines recovered.

**Porosity.** Our results are consistent with Hofker (1968), who described a group of planktonic foraminifera with remarkably large pores (larger than *Globigerina sacculifera* = *Trilobatus sacculifer*) and listed them in the original paper as: *Sphaeroidinoides grimsdalei*, *Sphaeroidinoides seminulina*, *Sphaeroidinoides dehiscens* (corresponding respectively to *Ss. kochi*, *Ss. seminulina* and *Sa. dehiscens* in our classification). Moreover, Hofker (1968, 1971, 1972) discussed how the wall of *Sphaeroidinella dehiscens* and *Trilobatus sacculifer* (*Globigerina sacculifera* in the original publication) presented some differences, in terms of attachment of the spines, shape of the cross section of the pores and a lower pore density in the early chambers. Hofker (1968) measured *Sphaeroidinella dehiscens* and other planktonic foraminifera (such as *Globigerina bulloides*, *G. bradyi*, *G. pachyderma*, *G. eggeri*, *G. glutinata*, *G. inflata*, *G. rubra*, *G. conglobata* and *G. sacculifera* as named in the original publication), showing a systematic

difference in their pore diameters. Similarly, Rhumbler (1911) noticed the different porosity in the thick wall of *Sphaeroidinella dehiscens*, recognizing three layers of calcite or lamellae. The first and second lamellae of the wall were similar in both *Sphaeroidinella* and *Globigerinoides*, while the third lamella was exclusive of *Sphaeroidinella* and *Sphaeroidinellopsis* (i.e. cortex). According to Rhumbler (1911), the growth of calcite crystal constituting the third lamella would commence from ridges of the honeycomb structure of the second lamella. Eventually, the outer surface of the third lamella would overgrow, covering the underlying lamellae. The overgrowth of second and third lamellae would determine the shape of the pores, sealed by the two top-most layers. The growth of the third lamella (real ‘cortex layer’) should inevitably decrease the final pore diameter (for a more detailed discussion see Ujiié, 1976).

Our biometric measurements support the observations of both Hofker (1972) and Ujiié (1976) that the wall texture present in *Sphaeroidinellopsis* and *Sphaeroidinella* is exclusive and absent in the other genera of planktonic foraminifera, and thus we suggest the introduction of the new term *disjuncta*-type to describe this peculiar wall texture (Figs 3 and 4; Table 1). We suggest the definition of this new name due to the substantial difference in both the mean pore diameter and the number of pores per unit area (Fig. 4) and the ability to overgrow a thick glassy cortex. The features characterizing the *disjuncta*-type wall separate *Sphaeroidinellopsis* and *Sphaeroidinella* from all the other cancellate taxa such as *Trilobatus*, *Globigerinoides* and *Globoturborotalita*. The *disjuncta*-type wall is here added to the wall texture classification diagram modified from Hemleben et al. (2018) in Figure 4.

### Taxonomical confusion regarding *Ss. seminulina* and *Ss. kochi*

*Sphaeroidinellopsis kochi* is an extremely variable taxon, and criteria were suggested by Fabbrini et al. (2021) to clarify its classification and to distinguish it from *Ss. seminulina* and from its ancestor *Ss. disjuncta*. To fully unravel the taxonomical difficulty of this

**Figure 3.** SEM images of wall texture, spine holes and spines. All specimens from International Ocean Discovery Program (IODP) Site U1482 (western Pacific): **A–B**, *Ss. seminulina* (NHM PF 75414) umbilical, wall texture close-up on ultimate chamber, decorticated specimen, 20HCC, Lower Pliocene (Zone PL2); **C–D**, *Ss. seminulina* (NHM PF 75433) umbilical, spines bearing decorticated specimen, and wall close-up from penultimate chamber, 28HCC, Lower Pliocene (Zone PL1); **E–F**, *Ss. seminulina* (NHM PF 75413) spines bearing decorticated specimen umbilical, wall texture close-ups on ultimate chamber, 20HCC, Lower Pliocene (Zone PL2); **G–H**, *Ss. seminulina* (lost specimen) spines bearing decorticated specimen umbilical and wall close-ups from penultimate chamber, 25HCC, Lower Pliocene (Zone PL1); **I–K**, *Ss. kochi* (NHM PF 75424) spines bearing specimen umbilical, wall texture detail, close-up on spines, 28HCC, Lower Pliocene (Zone PL1); **L–N**, *Ss. seminulina* (NHM PF 75412) spines bearing decorticated specimen umbilical, wall texture detail, close-up on spines, 20HCC, Lower Pliocene (Zone PL2). Specimen scale bars: A, C, E, G, I, L = 100 µm; B, D, F, H, J, M = 20 µm; K, N = 5 µm.

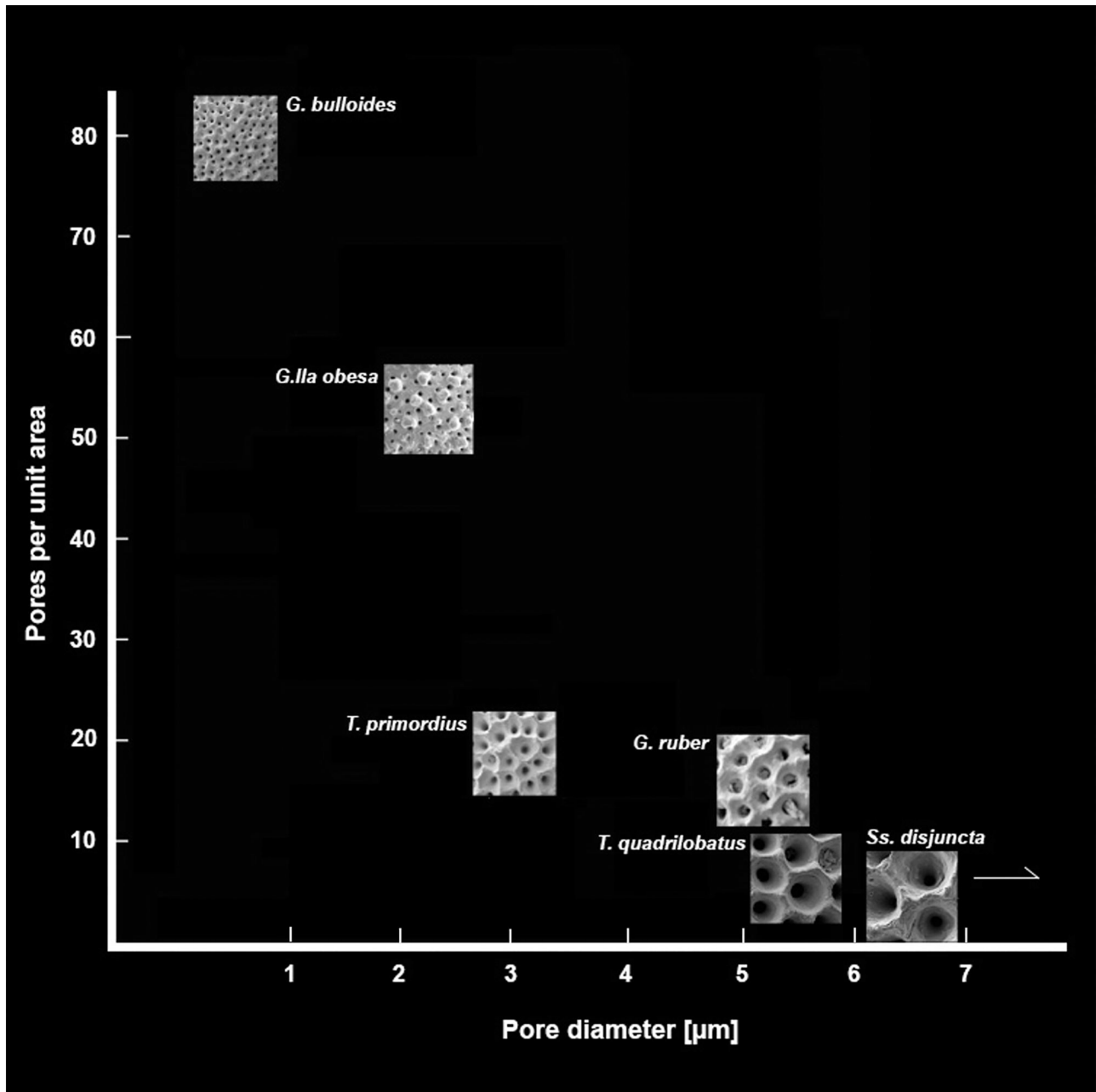


**Figure 4.** Wall texture classification diagram (not to scale) modified after Hemleben et al. (2018). The different wall textures are shown in  $2500\ \mu\text{m}^2$  surface close-up SEM images. The *disjuncta*-type wall is shown beside the *sacculifer*-type wall, with the white arrow indicating pore diameters larger than  $5.9\ \mu\text{m}$ . The species shown are *Globigerina bulloides*, *Globigerinella obesa*, *Globigerinoides ruber*, *Trilobatus primordius*, *Trilobatus quadrilobatus* and *Sphaeroidinellopsis disjuncta*.

species, here we discuss how it has been treated by previous workers and how its presence in the fossil record might have been underestimated.

The features which distinguish *Ss. kochi* from all the other *Sphaeroidinellopsis* are the low trochospiral

coiling mode and the elongation of the ultimate chambers. Even these two characters are subject to huge variability, with higher or lower trochospiral coiling, and a different total number of chambers in the final whorl, which in *Sphaeroidinellopsis kochi* ranges between four

**Table 1.** Summary of key wall texture types. Data for *disjuncta*-type from this study; all others from Hemleben et al. (2018).

| Type                  | Pore diameter [ $\mu\text{m}$ ] | Pores per 2500 $\mu\text{m}^2$ |
|-----------------------|---------------------------------|--------------------------------|
| <i>disjuncta</i>      | 5.9                             | 5                              |
| <i>sacculifer</i>     | >5                              | 12                             |
| <i>conglobatus</i>    | 3.5                             | 13                             |
| <i>ruber</i>          | 4.5                             | 20                             |
| <i>Globigerinella</i> | 1.8                             | 50                             |
| <i>Globigerina</i>    | 0.75                            | 82                             |

and seven chambers. This wide phenotypic variability made the classification of this taxon challenging, and thus numerous authors have suggested various alternatives. Another element which has contributed greatly to the issue is the tendency of some previous authors to subdivide or lump together morphotypes. Four morphospecies were described in the literature which have been considered junior synonyms of *Ss. kochi* (*Globigerina grimsdalei* Keijzer, 1945, *Sphaeroidinella rutschi* Cushman and Renz, 1941, *Sphaeroidinella multiloba* LeRoy, 1944, *Sphaeroidinellopsis hancocki* Bandy, 1975), with different inferred stratigraphic ranges in different regions. All the diverse classifications have increased the complexity of this group of taxa, making its identification inconsistent in successive work.

Bermudez (1961) recognized *Ss. grimsdalei* and *Sa. multiloba*, both from the middle Miocene of Jamaica and the Caribbean. Kennett and Srinivasan (1983) only recognized *Ss. kochi*, considering *Ss. multiloba* a junior synonym of it. Bolli and Saunders (1981) suggested a different phylogeny, where *Ss. multiloba* and *Ss. hancocki* were kept separated, belonging to different lineages. Bolli and Saunders (1981) considered *Ss. kochi* an invalid taxon due to the damaged holotype, and included the concept in *Ss. hancocki*. In their phylogeny, *Ss. multiloba* had an origin in the early–middle Miocene from *Ss. disjuncta*, and *Ss. hancocki* from *Ss. seminulina* in the earliest Pliocene (Bolli & Saunders, 1981). They synonymized *Sa. rutschi* with *Ss. multiloba* and *Globigerina grimsdalei* with *Ss. disjuncta*.

We think instead that *G. grimsdalei* coincides with the transitional specimens reported as the earliest *Ss. kochi* in Fabbrini et al. (2021); thus, the taxon is a junior synonym of *Ss. kochi*. We agree with Bolli and Saunders (1981) that *Sa. rutschi* might be a juvenile form of *Ss. multiloba*, which we retained as a junior synonym of *Ss. kochi* as discussed by Kennett and Srinivasan (1983) and by Fabbrini et al. (2021). Bolli and Saunders (1981, 1985) discussed the validity of the usage of *Ss. kochi*, arguing how the holotype was damaged and no paratypes were ever designated by the original author Caudri (1934). Due to the broken holotype,

Bolli and Saunders (1981, 1985) considered *Ss. kochi* a senior (but not valid) synonym of *Sphaeroidinellopsis hancocki* (Bandy, 1975). The use of a junior synonym as a substitute for the senior synonym is not necessary and it might be misleading for the palaeontological community, if the original description and illustration of the holotype are still able to clarify and to bear a clear concept. According to the International Code of Zoological Nomenclature (ICZN), article 73.1.4, “Designation of an illustration of a single specimen as a holotype is to be treated as designation of the specimen illustrated; the fact that the specimen no longer exists or cannot be traced does not of itself invalidate the designation” (Ride et al., 1999, p. 80). This case is applicable to the original drawing of *Ss. kochi* in Caudri (1934). Bolli and Saunders (1981) indeed referred to the original drawing of *Ss. kochi* to support the synonymy with *Ss. hancocki*. In our opinion, the use of *Sphaeroidinellopsis kochi* is advisable, due to the vast practice of applying this name among previous workers and the rules of ICZN not preventing it.

At Site U1490 the four morphospecies *Globigerina grimsdalei* Keijzer, 1945, *Sphaeroidinella rutschi* Cushman and Renz, 1941, *Sphaeroidinella multiloba* LeRoy, 1944 and *Sphaeroidinellopsis hancocki* Bandy, 1975 can be recognized, and they all coexist for most of their range. Our morphometric data indicate that these morphotypes merge into one another in a continuous spectrum (Fig. 2). We adopted the criteria described in Fabbrini et al. (2021) and grouped all individuals (*Ss. hancocki*, *Sa. multiloba* and *Sa. rutschi*) in *Ss. kochi*. The biometric data make evident the huge variability of *Ss. kochi*, in terms of circularity (Fig. 2). Such variation in circularity is explained by the elongation of the penultimate or ultimate chamber in the last whorl. This variability coincides with the morphological differences described in *Ss. hancocki*, *Ss. multiloba* and *Sa. rutschi*.

Biometric data ascribed to *Ss. kochi* shows a wide variation (0.6–0.88) in terms of circularity (Fig. 2), which can be explained by the number of chambers in the final whorl, ranging in this morphospecies between four and seven (Fig. 2). All individuals attributed to *Ss. kochi* share the same key features: elongation of the ultimate chamber(s) and very low trochospiral coiling. Thus, low values of circularity and long maximum diameter best characterize *Ss. kochi*. This taxon must be regarded as extremely variable and plastic, with the different types not bearing any reliable biostratigraphic significance. More studies and data are necessary to fully understand the function and the mechanism which promote such plasticity in species like *Ss. kochi*.

In our biometric results (Fig. 2), *Ss. seminulina* occupies a more similar morphospace to *Ss. paenedehiscens*

than to *Ss. kochi*, pinpointing the substantial and consistent difference in morphology between *Ss. seminulina* and *Ss. kochi*, and the evident shape gradation between *Ss. seminulina* into *Ss. paenedehiscens*. The two morphospecies (*Ss. seminulina* and *Ss. kochi*) occupy a different morphospace (Fig. 2), due to their dissimilar coiling, exemplified by a lower trochospire and a flatter spiral side in *Ss. kochi* and eventually by the degree of elongation of the final jutting chambers in *Ss. kochi*. The height of the trochospire in conjunction with elongated chambers gives a distinctive morphology to *Ss. kochi* in contrast to the more compact and ovoid shape of *Ss. seminulina*, leading to different circularity and maximum diameter values (Fig. 2). These observations help to differentiate the two taxa, and they support that *Ss. seminulina* and *Ss. kochi* are distinct morphospecies and potentially belong to parallel phyletic lineages both evolved from *Ss. disjuncta* (Fabbrini et al., 2021).

In order to stabilize the taxonomical concept of *Sphaeroidinellopsis kochi*, we selected a specimen with average values of circularity and maximum diameter for this species as a neotype (NHM PF 75444), which retains similar features to the original drawing from Caudri (1934), such as an elongated final chamber, flat spiral side and cortex covering the test. The specimen was selected from IODP Hole U1490A 9HCC, from Zone PL1 (Lower Pliocene).

### The genus *Sphaeroidinella*

The *Sphaeroidinella* event is considered by some authors as an example of punctuated anagenesis (Kučera, 1998; Malmgren et al., 1996). Punctuated anagenesis can be seen as the unpredictable and inconstant evolution of two populations, with the disappearance of the ancestor species through a gradual transition to the descendant species. The transition *Ss. seminulina*–*Ss. paenedehiscens*–*Sa. dehiscens* (the *Sphaeroidinella* event) is a phenomenon described globally and occurring with a slight diachroneity between 3.60 and 3.47 Ma (as per Kučera, 1998; Malmgren et al., 1996). The whole argument revolves around the secondary apertures on the spiral side, in terms of their size and number. Adopting the punctuated anagenesis framework would consider *Ss. seminulina*–*Ss. paenedehiscens*–*Sa. dehiscens* as chronospecies, i.e. populations with constant characters in a certain time interval, then disappearing gradually via anagenesis. Malmgren et al. (1996) documented the full transition occurring during the Pliocene and considered *Ss. paenedehiscens* the intermediate form between *Ss. seminulina* and *Sa. dehiscens*. Kučera (1998), on the other hand, did not retain the concept of *Ss. paenedehiscens*, only classifying *Ss. seminulina*, *Sa. dehiscens* and *Sa. dehiscens* forma immatura. The latter included the earliest individuals of *Sa. dehiscens* with a small secondary aperture on the

spiral side. These specimens were interpreted as transitional forms between *Ss. seminulina* and *Sa. dehiscens*. We identify *Ss. paenedehiscens* as the intermediate taxon leading to the evolution of the genus *Sphaeroidinella*. In our biometric analyses (Fig. 2), *Ss. paenedehiscens* plots in a section of morphospace occupied by *Ss. seminulina* and *Sa. dehiscens*. This supports the interpretation of the gradual morphological transition occurring in the lineage described by Malmgren et al. (1996). The different stratigraphic range exhibited by the three morphospecies reflects how they can be seen as separated populations, co-occurring for a limited time (Fig. 5). The extinction of the genus *Sphaeroidinellopsis* might indicate the success of the secondary supplementary aperture in improving the fitness of *Sphaeroidinella*.

The gradual morphological transition (triangular–ovoidal–sub-spherical) occurring along the *Sphaeroidinella* lineage is captured in Figure 2. The variability within *Sphaeroidinella* stands out, having a large range in maximum diameter (between 400 and 1150 µm) and circularity values generally above 0.75 and up to 0.95. This extreme variability is caused by different chamber shapes, height of the trochospire and number of chambers in the final whorl. For these reasons, we reassess some of the morphospecies described in the literature to capture the variability of *Sa. dehiscens* in its stratigraphic record. Within this variability falls *Sphaeroidinella excavata* (Banner & Blow, 1965) which was described as a variant of *Sa. dehiscens*, presenting deeper and more incised apertures revealing the inner part of the test.

In this study the abundance of both *Sa. dehiscens* and *Sa. excavata* peaks at around 2 Ma, thus showing an analogous occurrence (Fig. 5). The coeval maximum abundance suggests how these two taxa most likely belong to the same biological species (Brunner & Kučera, 2022). At Site U1490 *Sa. excavata* is rarer than *Sa. dehiscens*, and with a shorter stratigraphic range (Zone PT1 in this study). Pearson (1995) reported a high abundance of *Sa. excavata* in the Marshall Islands group (Ocean Drilling Program Leg 144) and distinguished it from *Sa. dehiscens* due to the different stratigraphic range. Wang (2000) and Numberger et al. (2009) documented how distinct morphologies within *Globigerinoides ruber* correspond to diverse ecological conditions and to separate genotypes. Among the objectives of micropalaeontology is recording and storing all the possible useful information archived in the fossil record. In such a framework, the real significance of the different morphologies and their function is not recognized, but since some species (as *G. ruber*) seem to bridge this gap of knowledge, the most conservative approach is recording the distinct morphospecies, where numerical

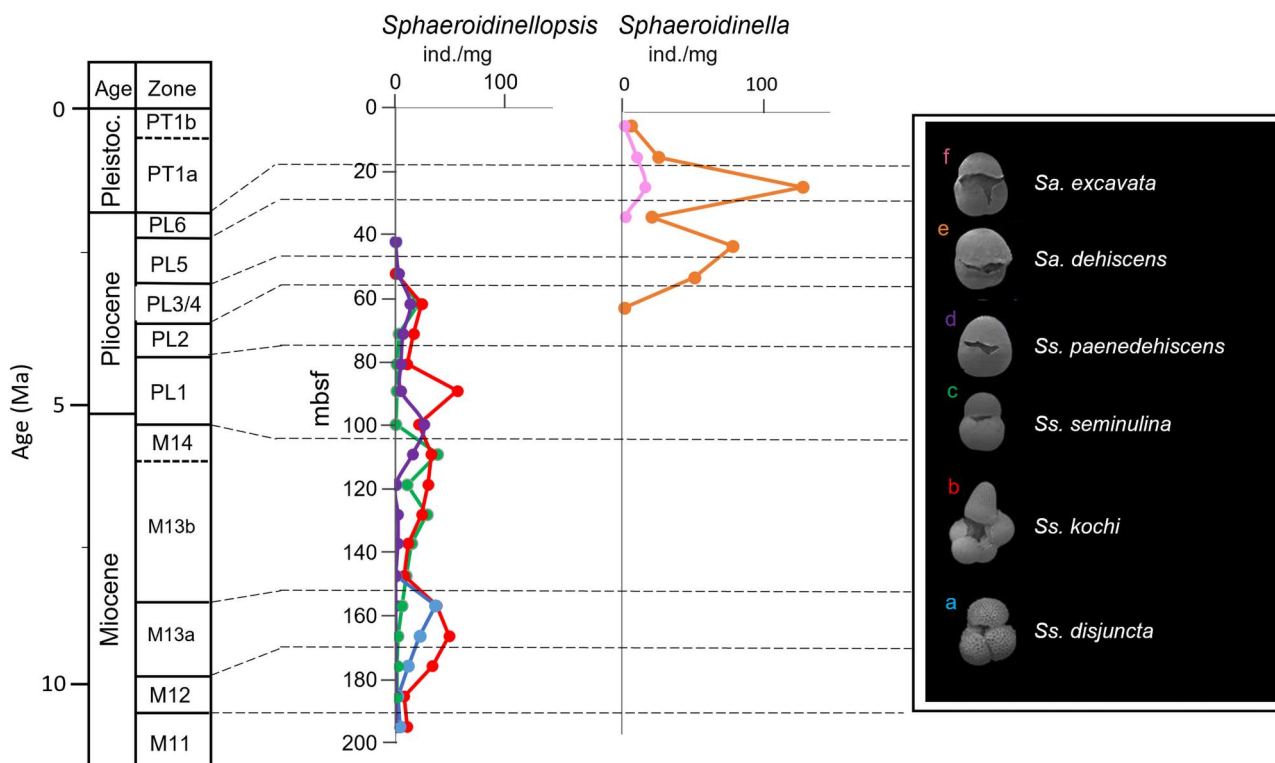


**Figure 5.** Distribution plot of individuals in the size fraction >400 µm. The x-axis shows the number of individuals per milligramme. The vertical axis represents depth in mbsf (metres below seafloor). The six morphospecies are shown on the right of the panel, and illustrated with different colours and letters. SEM images of each morphospecies are shown for reference. On the left panel the chronostratigraphic chart and the biozonal scheme (Wade et al., 2011) are reported for correlation to the biostratigraphy from shipboard studies (Rosenthal et al., 2018).

and objective data can support the split. Other subspecies or variants – *Sa. ionica*, *Sa. ionica evoluta*, and *Sa. excavata* – deserve a reinvestigation of the original descriptions and concepts. Herein, we recognized *Sphaeroidinella excavata* as a valid morphospecies and kept it separated from *Sa. dehiscens* in our counting, following Pearson (1995). We consider *Sa. ionica evoluta* a junior synonym of *Sa. excavata*, as the former falls within the latter’s range of morphological variability. In our opinion, *Sa. ionica* might represent kummerform individuals of *Sa. dehiscens*; thus, this taxon is here considered a *nomen inquirendum* awaiting further investigations from the Neogene and Quaternary Planktonic Foraminifera Working Group.

## Systematic palaeontology

Order **Foraminiferida** d’Orbigny, 1826  
Superfamily **Globigerinoidea** Carpenter,  
Parker and Jones, 1862

Family **Globigerinidae** Carpenter, Parker and Jones, 1862  
Genus *Sphaeroidinellopsis* Banner and Blow, 1959

**Type species.** *Globigerina seminulina* Schwager, 1866.

**Diagnosis.** Spinose, cancellate *disjuncta*-type wall texture. The test can be totally or partially covered with a shiny, smooth cortex obscuring completely the underlying texture. On the surface of the cortex wide pores can be present (Fig. 3), most commonly in the ultimate chamber.

**Test morphology.** Test compact to lobate, low to mid trochospiral, bearing from three to seven chambers in the ultimate whorl. The chambers are sub-spherical to radially elongated, varying strongly between morphospecies. The aperture is umbilical to interiomarginal, and it may present a thick rim or lip, or a flap generated by the secondary cortex where present. No true supplementary apertures are present, while the cortex on the spiral side can be thin and crenulated.

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

**Remarks.** This genus is distinguished from *Sphaeroidinella* because of the absence of secondary apertures on the spiral side. *Sphaeroidinellopsis* can be

**Table 2.** Taxonomic key summarizing all the species discussed in this study.

| Species                   | Primary aperture            | Sec. aperture       | Chambers (Ch)     | Ch/whorl | Trochospire    | Cortex             |
|---------------------------|-----------------------------|---------------------|-------------------|----------|----------------|--------------------|
| <i>Ss. disjuncta</i>      | Umbilical, low arch         | No                  | Subglobular       | 3–4      | Low to medium  | Absent to partial  |
| <i>Ss. kochi</i>          | Umbilical to spiroumbilical | No                  | Subglob-elongated | >3.5     | Low            | Absent to complete |
| <i>Ss. paenedehiscens</i> | Umbilical, slit-like        | No                  | Subsphaerical     | 3–4      | High           | Complete           |
| <i>Ss. seminulina</i>     | Umbilical, low              | No                  | Subglobular       | 3–4      | Medium to high | Absent to complete |
| <i>Sa. dehiscens</i>      | Umb-interiomarginal         | Spiral side         | Subglobular       | 3–4      | High           | Complete           |
| <i>Sa. excavata</i>       | Umb-interiomarginal         | Spiral side-sutural | Subglobular       | 3–4      | High           | Complete           |

distinguished from *Globoturborotalita* because of the 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 in the latter genera and for its typical wall texture, showing wider pores (*disjuncta*-type) or covered by a glassy and thick cortex (Table 2).

***Sphaeroidinellopsis disjuncta* (Finlay, 1940)**  
(Fig. 6)

- 1940 *Sphaerodinella disjuncta* Finlay: pl. 67, figs 224–228.  
 1973 *Sphaerodinella disjuncta* Kennett: pl. 21, figs 12–15.  
 1983 *Sphaeroidinellopsis disjuncta* Kennett and Srinivasan: pl. 51, figs 3–5.  
 1993 *Sphaeroidinellopsis disjuncta* Chaisson and Leckie: pl. 10, fig. 16.  
 1994 *Sphaeroidinellopsis disjuncta* Spezzaferri: pl. 10, fig. 4a–c.  
 2013 *Sphaeroidinellopsis disjuncta* Fox and Wade: figs 17.6–17.8, 19.  
 2014 not *Sphaeroidinellopsis disjuncta* Sanchez et al.: pl. 3, figs 1–8 = *Ss. kochi*  
 2020 *Sphaeroidinellopsis disjuncta* Lam and Leckie: pl. 10, figs 11–12.  
 2021 *Sphaeroidinellopsis disjuncta* Fabbrini et al.: fig. 3A–H.

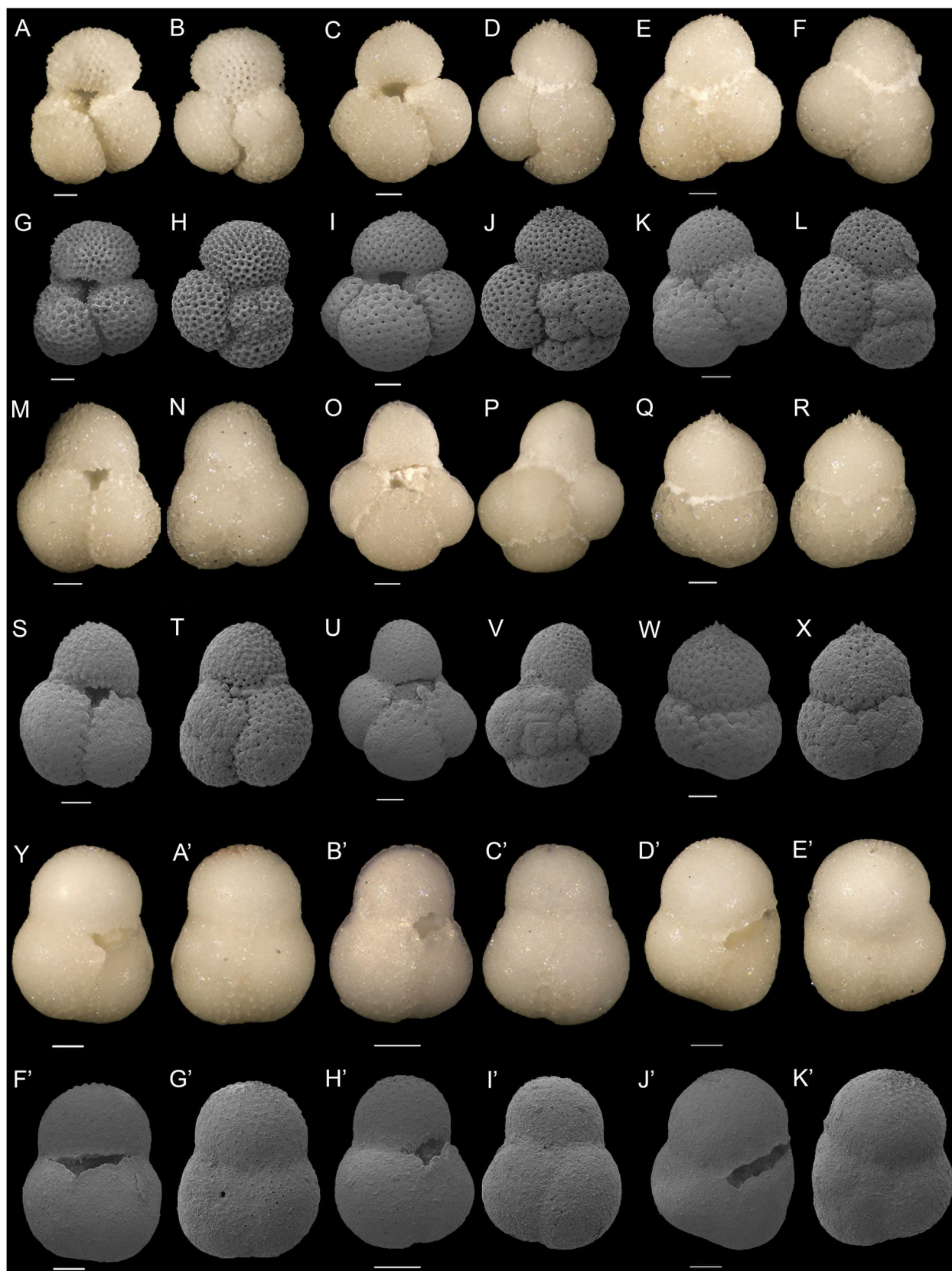
**Test morphology.** Test compact and mid trochospiral. Wall strongly cancellate, *disjuncta*-type texture. In umbilical view sutures deeply incised and radial, umbilicus narrow and deep with a low arched umbilical aperture bordered by a thick rim. In spiral view two whorls are visible for a total of 6–7 chambers, separated by incised straight sutures. In edge view profile rounded and slightly triangular, chambers from previous whorls visible in the low trochospire. The last whorl presents  $3\frac{1}{2}$ –4 sub-globular chambers slowly growing in size as added.

**Range.** Burdigalian Zone M3 (Zone N6 in Kennett & Srinivasan, 1983)–Tortonian Subzone M13a (Kennett & Srinivasan, 1983; this study). The base of *Ss. disjuncta* is reported within Zone M3 in the North Atlantic IODP Site U1406 (Fabbrini et al., 2019; Fabbrini & Foresi, 2020). The extinction of this taxon is reported in Zone N17 (Zone ~M13/M14) in Bolli and Saunders (1981), while in Zone N11 (Zone M8) in Kennett and Srinivasan (1983). The latest specimens reported in this study are from Subzone M13a.

**Remarks.** *Sphaeroidinellopsis disjuncta* can be distinguished from *Ss. kochi* by having a maximum of four chambers in the final whorl and lacking the peculiar elongation (sac-like) in the final or penultimate chamber (Table 2). *Sphaeroidinellopsis disjuncta* can be distinguished from *Ss. seminulina* in having  $3\frac{1}{2}$ –4 chambers in the ultimate whorl and for its deeply incised sutures and less compact coiling. This taxon also has a more open umbilicus than *Ss. seminulina* and a wider, higher aperture compared with the slit-like aperture characterizing *Ss. seminulina*. *Sphaeroidinellopsis disjuncta* differs from *Globoturborotalita woodi* by the different wall texture (*disjuncta*-type), by a lower aperture bordered with a rim, and by the usually smaller jutting final chamber. The wall of *Ss. disjuncta* can be covered partially by a shiny secondary cortex.

***Sphaeroidinellopsis kochi* (Caudri, 1934)**  
(Fig. 7)

- 1923 *Globigerina* sp. Koch: fig. 8a–b.  
 1934 *Globigerina kochi* Caudri: fig. 8a–b.  
 1941 *Sphaeroidinella rutschi* Cushman and Renz: pl. 4, fig. 5a–b.  
 1944 *Sphaeroidinellopsis multiloba* Le Roy: pl. 4, figs 7–9.  
 1945 *Globigerina grimsdalei* Keijzer: fig. 33a–c.  
 1959 *Sphaeroidinella seminulina kochi* hypotype Blow: pl. 12 figs 78–79.  
 1960 not *Sphaeroidinellopsis seminulina* Banner and Blow: pl. 7, fig. 2.



- 1969 *Sphaeroidinellopsis seminulina kochi* Blow: pl. 30, fig. 8.  
 1972 *Sphaeroidinellopsis seminulina* Cita and Ciaranfi: pl. 74, figs 3–4.  
 1975 *Sphaeroidinellopsis hancocki* Bandy: pl. 1, figs 3–7.  
 1975 *Sphaeroidinellopsis seminulina* Stainforth et al.: fig. 142, specimens 1–6.  
 1976 *Prosphaeroidinella parkerae* Ujiie: pl. 4, fig. 1a–c.  
 1983 *Sphaeroidinellopsis kochi* Kennett and Srinivasan: pl. 52, figs 1–3.  
 1985 *Sphaeroidinellopsis multiloba* Bolli et al.: pl. 38, figs 15–16.  
 1993 *Sphaeroidinellopsis kochi* Chaisson and Leckie: pl. 10, figs 10, 14, 18.  
 1995 *Sphaeroidinellopsis kochi* Pearson: pl. 5, fig. 8.  
 2014 *Sphaeroidinellopsis disjuncta* Sanchez et al.: pl. 3, figs 1–8.  
 2020 *Sphaeroidinellopsis kochi* Lam and Leckie: pl. 11, figs 1–4, 6–7.  
 2021 *Sphaeroidinellopsis kochi* Fabbrini et al.: figs 4–7.

**Neotype.** NHM PF 75444

**Type locality.** IODP Site U1490, Eauripik Rise (west Pacific Ocean).

**Type sample.** IODP Hole U1490A 9HCC.

**Type age.** Zanclean (Lower Pliocene), Zone PL1.

**Test morphology.** Wall cancellate, *disjuncta*-type wall texture, fully or partially covered by a glassy cortex. Low trochospiral and slightly lobate profile. Four to seven chambers in the final whorl, often characterized by a radial elongation of the final chamber. This feature may be observable in both kummerforms and normal-forms. In umbilical view, four to seven chambers, the umbilicus is open with a low arched umbilical-extraumbilical aperture. The aperture may present a rim. In individuals with more than five chambers the aperture can become interiomarginal to spiroumbilical. 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 visible arranged in three

whorls, sutures radial and deeply incised. The cortex can be thinner on the sutures of the spiral side, even leading to openings exposing the underlying wall texture. In edge view, flat spiral side with a low trochospire, the final sac-like chamber is often tilted towards the umbilicus or more rarely towards the spire.

**Range.** Langhian, Zone M6 (Kennett & Srinivasan, 1983)–Zanclean, Zone PL2 (this study).

**Remarks.** This taxon is distinguished from *Ss. disjuncta* by the elongation of the last or of the final two chambers. It differs from *Ss. seminulina* in having more than four chambers in the last whorl, having the final chamber elongated and sac-like, often tilted and presenting a wider umbilicus and a lower trochospire (Table 2). 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 a full glassy cortex, and by the *disjuncta*-type wall texture. *Sphaeroidinellopsis kochi* remains a variable taxon requiring further data and analysis to comprehend fully its variability and the relation between the different morphotypes falling under its umbrella name (see Discussion). This extensive variability coincides with the morphological differences described in the morpho-species *Ss. hancocki*, *Ss. multiloba* and *Sa. rutschi*, which are all considered here junior synonyms of *Ss. kochi*.

### *Sphaeroidinellopsis seminulina* (Schwager, 1866) (Fig. 6)

1866 *Globigerina seminulina* Schwager: fig. 142.

1958 *Sphaeroidinella spinulosa* Subbotina in Bykova et al.: pl. 11, figs 6a–c.

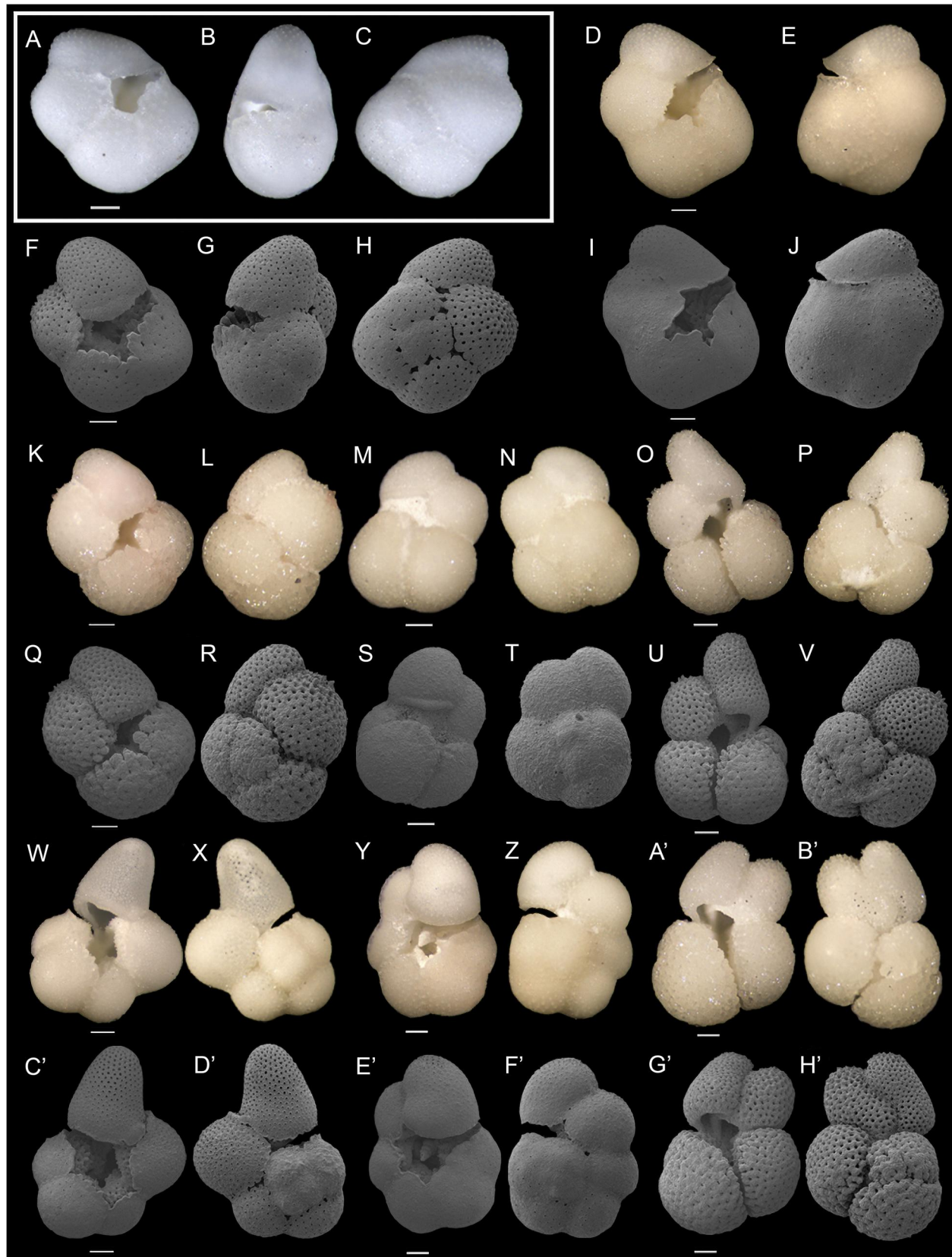
1959 *Sphaeroidinella dehiscens subdehiscens* Blow: pl. 12, fig. 71a–c.

1969 *Sphaeroidinellopsis seminulina* Blow: pl. 30, fig. 7.

1988 *Prosphaeroidinella valleriae* Brönnimann, Whittaker and Parisi: pl. 1, figs 1–8.

1996 *Sphaeroidinellopsis seminulina* Malmgren et al.: pl. 8, figs 7, 10.

**Figure 6.** Light microscope and SEM images of selected specimens of *Sphaeroidinellopsis disjuncta* and *Sphaeroidinellopsis seminulina*. All specimens are from International Ocean Discovery Program (IODP) Site U1490: **A–B, G–H**, *Ss. disjuncta* (NHM PF 75406) umbilical, spiral view, 17HCC, Upper Miocene (Subzone M13a); **C–D, I–J**, *Ss. disjuncta* (NHM PF 75407) umbilical, spiral view, 17HCC, upper Miocene (Subzone M13a); **E–F, K–L**, *Ss. disjuncta* (NHM PF 75408) umbilical, spiral view, 19HCC, upper Miocene (Zone M12); **M–N, S–T**, *Ss. disjuncta* (NHM PF 75409) umbilical, spiral view, 19HCC, upper Miocene (M12); **O–P, U–V**, *Ss. disjuncta* (NHM PF 75410) umbilical, spiral view, 21HCC, Upper Miocene (Zone M11); **Q–R, W–X**, *Ss. seminulina* (NHM PF 75429) umbilical, spiral view, 17HCC, Upper Miocene (Subzone M13a); **Y–A', F'–G'**, *Ss. seminulina* umbilical, spiral view, 17HCC, Upper Miocene (Subzone M13a); **B'–C', H'–I'**, *Ss. seminulina* (NHM PF 75428) umbilical, spiral view, 17HCC, Upper Miocene (Subzone M13a); **D'–E', J'–K'**, *Ss. seminulina* (specimen lost) umbilical, spiral view, 13HCC, Pliocene (Zone PL3/4). Scale bars: 100 µm.



2009 *Sphaeroidinellopsis seminulina* Hokuto et al.: 549, pl. 3, fig. 2a–c.

2020 *Sphaeroidinellopsis seminulina* Lam and Leckie: pl. 10, figs 13–20.

**Test morphology.** Wall spinose *disjuncta*-type, often covered with a shiny secondary cortex. Low trochospiral, compact, equatorial periphery broadly ovate to slightly trilobate. The ultimate whorl presents 3–4 sub-globular chambers, with sutures obscured by heavy cortex. In umbilical view, umbilicus narrow with an umbilical low aperture bordered by a thickened crenulated rim (Kennett & Srinivasan, 1983). In spiral view, previous whorls of chambers 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.** Burdigalian (Zone M4)–Zanclean (Zone PL3). Its extinction marks the base of Zone PL4 (Wade et al., 2011).

**Remarks.** *Sphaeroidinellopsis seminulina* can be distinguished from *Ss. disjuncta* by having a fully developed cortex, giving to *Ss. seminulina* the typical glossy appearance, shared with its descendant *Ss. paenedehiscens* and in the *Sphaeroidinella* lineage (Table 2). *Sphaeroidinellopsis seminulina* is distinguished from *Ss. kochi* by its higher trochospire and having less than four chambers in the ultimate whorl and a fully developed cortex, often absent in *Ss. kochi*. Possible synonymies requiring deeper investigations are *Prosphaeroidinella valleriae* Brönnimann, Whittaker and Parisi (1988) and *Sphaeroidinella spinulosa* Subbotina in Bykova (1958). *Sphaeroidinellopsis seminulina* can be distinguished from *Globoturborotalita connecta* thanks to its fully developed cortex and, in uncovered specimens, to its coarser *disjuncta*-type wall texture. It differs from *Globoturborotalita woodi* thanks to a more compact coiling, the lower aperture, the narrower umbilicus and the secondary crystallization of the cortex. It can be distinguished from *Ss. paenedehiscens* by its less spherical test and smaller aperture, not presenting a flange, and

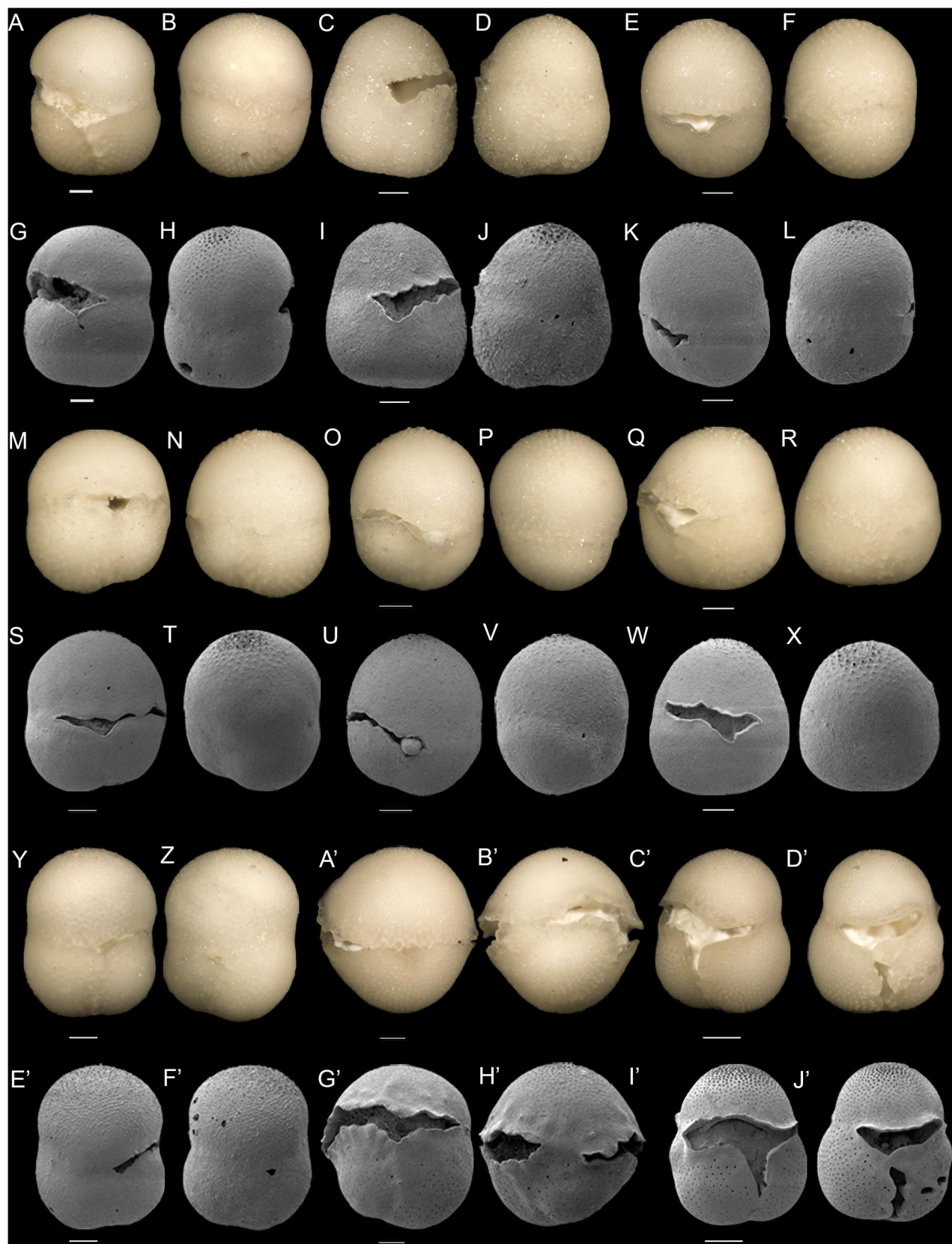
from *Sa. dehiscens* due to the lack of supplementary aperture on the spiral side.

### Taxonomic history

Schwager (1866) described this species from the lower Pliocene of Car Nicobar Island (Srinivasan & Sharma, 1974), but the holotype and primary paratypes were lost, requiring the definition of neotypes. In 1960 Banner and Blow indicated that some specimens described as *Ss. disjuncta* in Finlay (1940) might be referable to *Ss. seminulina*, due to the strong morphologic similarities. This argument was strongly debated by both Jenkins (1971) and Kennett and Srinivasan (1983). The absence of the holotype motivated Banner and Blow (1960) to reexamine the metatype material at the British Museum of Natural History, describing and illustrating a controversial neotype. Despite the majority of the metatypes having three chambers in the ultimate whorl like the holotype illustrated by Schwager (1866), Banner and Blow (1960) selected an atypical four-chambered specimen as the neotype. This has since given the impression that *Ss. seminulina* is typically a four-chambered taxon (Stainforth et al., 1975). In the original description of Schwager (1866), *Sphaeroidinellopsis seminulina* is described as having three and seldom four chambers in the ultimate whorl; also, the cortex may be fully or partially covering the test, but no supplementary apertures are present. In Blow (1959) a new species was erected, *S. subdehiscens*, considered different from *Ss. seminulina* by having three chambers in the ultimate whorl. Srinivasan and Kennett (1981) considered *Ss. subdehiscens* a junior synonym of *Ss. seminulina* and consequently redesignated *Ss. seminulina* (Schwager) to be the type species of *Sphaeroidinellopsis* (Kennett & Srinivasan, 1983), after comparing the original topotypes of *Ss. seminulina* from Car Nicobar Island with *Ss. subdehiscens* Blow (1959). No significant differences in terms of chamber number or structure of the cortex or in the apertural characters were identified by Srinivasan and Kennett (1981).

*Sphaeroidinellopsis seminulina* is retained as the ancestor of *Ss. paenedehiscens*, which led to the origin of

**Figure 7.** Light microscope and SEM images of selected specimens of *Sphaeroidinellopsis kochi*. All specimens from International Ocean Discovery Program (IODP) Site U1490. **A–C**, *Sphaeroidinellopsis kochi* neotype (NHM PF 75444), umbilical, side and spiral view, 9HCC, Lower Pliocene (Zone PL1); **D–E**, **I–J**, *Ss. kochi* (NHM PF 75421) umbilical, spiral view, 7HCC, Lower Pliocene (Zone PL2); **F–H**, *Ss. kochi* (specimen lost) umbilical, peripheral, spiral view, 7HCC, Lower Pliocene (Zone PL2); **K–L**, **Q–R**, *Ss. kochi* (NHM PF 75418) umbilical, spiral view, 17HCC, Upper Miocene (Subzone M13a); **M–N**, **S–T**, *Ss. kochi* (NHM PF 75415) umbilical, spiral view, 21HCC, Upper Miocene (Zone M11); **O–P**, **U–V**, *Ss. kochi* (NHM PF 75417) umbilical, spiral view, 17HCC, Upper Miocene (Subzone M13a); **W–X**, **C'–D'**, *Ss. kochi* (NHM PF 75419) umbilical, spiral view, 10HCC, Lower Pliocene (Zone PL1); **Y–Z**, **E'–F'**, *Ss. kochi* (NHM PF 75420) umbilical, spiral view, 10HCC, Lower Pliocene (Zone PL1); **A'–B'**, **G'–H'**, *Ss. kochi* (NHM PF 75416) umbilical, spiral view, 17HCC, Upper Miocene (Subzone M13a). Note the spiroumbilical aperture in specimens W–X, C'–D' and Y–Z, E'–F'. Scale bars: 100 µm.



*Sphaeroidinella dehiscens*, adding supplementary apertures and developing a full cortex (Aze et al., 2011; Blow & Banner, 1962; Kennett & Srinivasan, 1983; Kučera, 1998). The relationship between *Ss. seminulina* and *Ss. disjuncta* is still unclear and some morphological overlap between these taxa is common (Fig. 2). Lam and Leckie (2020) reported transitional specimens between these two species in the north-west Pacific Ocean.

***Sphaeroidinellopsis paenedehiscens* (Blow, 1969)**  
(Fig. 8)

- 1969 *Sphaeroidinellopsis sphaeroides* Lamb: pl. 1, figs 1–5; pl. 2, figs 1–3.  
 1969 *Sphaeroidinella subdehiscens paenedehiscens* Blow: pl. 30, figs 4, 5, 9.  
 1981 *Sphaeroidinellopsis sphaeroides* Bolli and Saunders: pl. 2, figs 14–17.  
 1983 *Sphaeroidinellopsis paenedehiscens* Kennett and Srinivasan: pl. 52, figs 4–6.  
 1993 *Sphaeroidinellopsis paenedehiscens* Chaisson and Leckie: pl. 10, fig. 9.  
 1998 *Sphaeroidinellopsis paenedehiscens* Norris: pl. 5, fig. 3.  
 2020 *Sphaeroidinellopsis paenedehiscens* Lam and Leckie: pl. 11, figs 5, 8–15.

**Test morphology.** Test large, rounded or ovoidal, consisting of an unknown number of chambers arranged in a trochospiral coiling mode, with three chambers in the final whorl and an overall ovate shape. Wall cancellate *disjuncta*-type, completely covered with a shiny cortex, sometimes bearing large pores on the last chamber. The cortex hides the structure of the test and the early chambers, while the sutures can be completely obscured or lightly marked. The chambers are embracing and inflated, sub-globular and increasing rapidly as added. The primary aperture is an elongate, slit-like opening extending from the umbilicus to almost over the dorsal peripheral shoulder. The aperture follows the line of the intercameral sutures between the last and first chamber of the final whorl and is bordered by a crenulate flap. No supplementary aperture on the spiral side.

**Range.** Miocene, Subzone M13b (Kennett & Srinivasan, 1983)–Pliocene, Zone PL3/4 (Kennett & Srinivasan, 1983; this study).

**Remarks.** *Sphaeroidinellopsis paenedehiscens* is distinguished from *Sphaeroidinella dehiscens* due to the lack of supplementary aperture on the spiral side. *Sphaeroidinellopsis paenedehiscens* is distinguished from *Ss. seminulina* thanks to its ovate shape, tendentially bigger size and a wider and more irregular primary aperture in umbilical view (Table 2). Transitional forms between *Ss. seminulina* and *Ss. paenedehiscens* make their classification difficult in certain intervals. Stainforth et al. (1975) first reported *Ss. paenedehiscens* Blow, 1969 as the senior synonym of *Ss. sphaeroides* Lamb, 1969. The continuous spectrum of morphologies between *Ss. seminulina* and *Ss. paenedehiscens* testifies to their ancestor–descendant phylogenetic relationship (Fig. 9).

Genus ***Sphaeroidinella*** Cushman, 1927, emend.  
 Banner and Blow, 1959

***Sphaeroidinella dehiscens* (Parker & Jones, 1865)**  
(Fig. 8)

- 1865 *Sphaeroidina bulloides* var *dehiscens* Parker and Jones: pl. 19, fig. 5.  
 1919 *Sphaeroidina dehiscens immatura* Cushman: pl. 14, fig. 2.  
 1967 *Sphaeroidinella dehiscens* Bandy et al.: pl. 1, figs 1–6.  
 1969 *Sphaeroidinella dehiscens* Blow: pl. 29, figs 6–9.  
 1973 *Sphaeroidinella dehiscens* Kennett: pl. 21, figs 2–6.  
 1983 *Sphaeroidinella dehiscens* Kennett and Srinivasan: pl. 51, fig. 2; pl. 52, figs 7–9.  
 1985 *Sphaeroidinella dehiscens* Bolli et al.: pl. 39, fig. 1a–b.  
 1995 *Sphaeroidinella dehiscens* Pearson: pl. 5, fig. 9.  
 1996 *Sphaeroidinella dehiscens* Malmgren et al.: figs 8.3–8.4.  
 1998 *Sphaeroidinella dehiscens* Kučera: fig. 1.  
 2017 *Sphaeroidinella dehiscens* Schiebel and Hemleben: pl. 2.2, figs 1–3, 6.

**Figure 8.** Light microscope and SEM images of selected specimens of *Sphaeroidinellopsis paenedehiscens*, *Sphaeroidinella dehiscens* and *Sphaeroidinella excavata*. All specimens from International Ocean Discovery Program (IODP) Site U1490: **A–B, G–H**, *Ss. paenedehiscens* (NHM PF 75436) umbilical, spiral view, 11HCC, Lower Pliocene (PL1); **C–D, I–J**, *Ss. paenedehiscens* (NHM PF 75435) umbilical, spiral view, 7HCC, Lower Pliocene (Zone PL2); **E–F, K–L**, *Ss. paenedehiscens* (NHM PF 75438) umbilical, spiral view, 11HCC, Lower Pliocene (Zone PL1); **M–N, S–T**, *Ss. paenedehiscens* (NHM PF 75439) umbilical, spiral view, 7HCC, Lower Pliocene (Zone PL2); **O–P, U–V**, *Ss. paenedehiscens* (NHM PF 75440) umbilical, spiral view, 7HCC, Lower Pliocene (Zone PL2); **Q–R, W–X**, *Ss. paenedehiscens* (NHM PF 75442) umbilical, spiral view, 7HCC, Lower Pliocene (Zone PL2); **Y–Z, E'–F'**, *Ss. paenedehiscens* (specimen lost) umbilical, spiral view, 7HCC, Lower Pliocene (Zone PL2); **A'–B', G'–H'**, *Sa. dehiscens* (NHM PF 75441) umbilical, spiral view, 6HCC, Pliocene (Zone PL3/4 undifferentiated); **C'–D', I'–J'**, *Sa. excavata* (NHM PF 75443) umbilical, spiral view, 2HCC, Pleistocene (Zone PL6/PT1 undifferentiated). Scale bars: 100 µm.

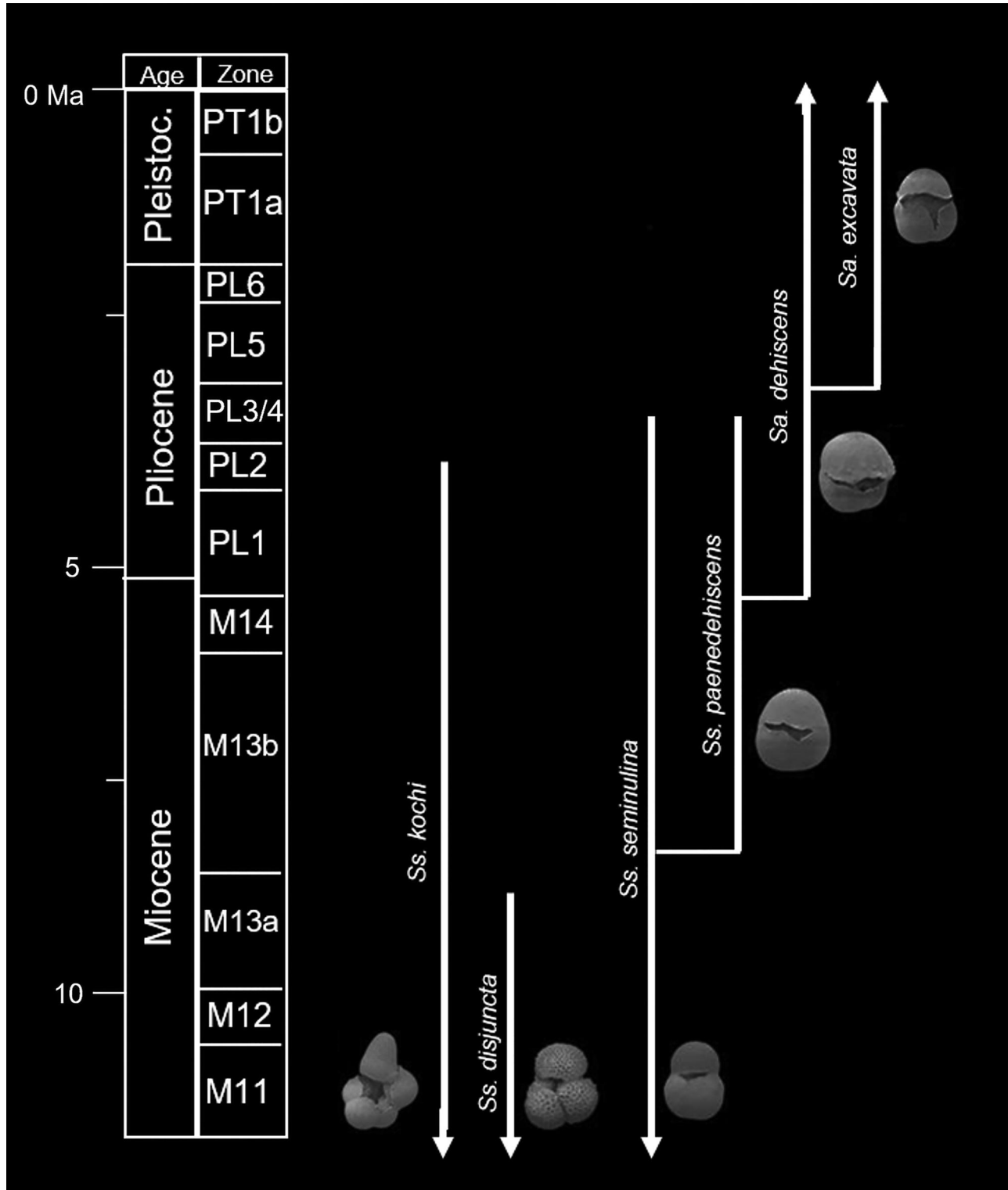


**Figure 9.** Phylogenetic summary of the genera *Sphaeroidinellopsis* and *Sphaeroidinella* at International Ocean Discovery Program (IODP) Site U1490 from Zone M11 to Zone PT1 (biozones from Wade et al., 2011).

2017 not *Sphaeroidinella dehiscens* Schiebel and Hemleben: pl. 2.2, fig. 5.

2020 *Sphaeroidinella dehiscens* Lam and Leckie: pl. 11, figs 16–19.

**Test morphology.** Large globose to sub-spherical involute test. The chambers are sub-spherical, inflated, partially embracing, rapidly enlarging in trochospiral coiling. The wall texture is cancellate *disjuncta*-type, completely covered by the cortex. Sutures are broadly depressed, and the periphery of the test is compact. The primary aperture is umbilical to interiomarginal. One or more supplementary apertures are present on the spiral side. The apertures are furnished with thick flange-like flaps generated by the overgrowth of the cortex on the original apertural rim. The flanges extend around the umbilical margins of the chambers and on both sides of the supplementary aperture. The sutures appear to be deeply incised in the vicinity of the apertures, and the flanges border these incisions throughout their length and in part bridge them. Large pores can be present on the cortex, more commonly on the last chamber.

**Range.** Zanclean, Zone PL1–Extant. Its origination is a secondary marker within Zone PL1 (Wade et al., 2011).

**Remarks.** *Sphaeroidinella dehiscens* can be distinguished from *Ss. paenedehiscens* by the supplementary aperture on the spiral side. Brummer and Kučera (2022) and Schiebel and Hemleben (2017) state that only one genotype exists for *Sa. dehiscens* (André et al., 2014), suggesting that this constitutes only one biological species. Consequently, the coexistence of *Sa. dehiscens* with *Sa. excavata* suggests that the latter must be interpreted as an extreme morphotype of *Sa. dehiscens* (see the following section).

***Sphaeroidinella excavata* Banner and Blow, 1965 (Fig. 8)**

1965 *Sphaeroidinella dehiscens excavata* Banner and Blow: pl. 7, fig. 3.

1967 *Sphaeroidinella dehiscens excavata* Banner and Blow: pl. 4, fig. 5.

1972 *Sphaeroidinella excavata* Hofker; pl. 7, figs A–D, p. 133

1972 *Sphaeroidinella ionica evoluta* Cita and Ciaranfi: 701–702, pl. 76, figs 1–4.

1975 *Sphaeroidinella dehiscens excavata* Stainforth et al.: fig. 161, specimens 6–7.

1981 *Sphaeroidinella excavata* Saito et al.: pl. 20, fig. 1a–c, p. 73

1995 *Sphaeroidinella excavata* Pearson: pl. 5, fig. 10.

2017 *Sphaeroidinella dehiscens* Schiebel and Hemleben: pl. 2.2, fig. 5.

**Test morphology.** Large, globose with three or four sub-spherical chambers in the last whorl, completely covered by a cortex. The chambers are inflated, partially embracing, rapidly enlarging and in trochospiral coiling mode. The sutures are wide open and depressed. The primary aperture is interiomarginal, umbilical. The dorsal supplementary aperture is large and follows the sutures. Extra apertures might be present along any sutural portion. All apertures are furnished with thick flange. The wall texture is cancellate *disjuncta*-type. On the cortex large pores can be common especially on the last chamber.

**Range.** Piacenzian, Zone PL4 (Pearson, 1995)–Extant.

**Remarks.** *Sphaeroidinella dehiscens excavata* was introduced as a subspecies of *Sa. dehiscens* by Banner and Blow (1965). However, the taxon was not included in the Ellis and Messina catalogue due to a mistake in the original paper where the specimen was referred to as a paratype. In the NHM catalogue the specimen is deposited and listed correctly as holotype; thus, the morphospecies concept is valid. Kennett and Srinivasan (1983) described *Sphaeroidinella excavata* as an advanced form within the *Sphaeroidinella* lineage, and it has been regarded as a discrete species by Pearson (1995), occurring more commonly in the upper part of Zone N22 (= Zone PT1), having its lowest occurrence in Zone N21 (= PL4) at Site 873 (Pearson, 1995). On the other hand, Brummer and Kučera (2022) synonymized this taxon with *Sphaeroidinella dehiscens*. *Sphaeroidinella excavata* is here considered a valid morphospecies to highlight its biostratigraphic potential following Pearson (1995) and confirming the stratigraphic range (Fig. 9).

*Sphaeroidinella excavata* can be distinguished from *Sa. dehiscens* by its deeply excavated sutures exposing the inner whorls, its wide-open test, and the different total number of chambers (Table 2). *Sphaeroidinella excavata* can have more than four chambers in the final whorl, where often the last chamber is smaller and slightly elongated (Saito et al., 1981). Cita and Ciaranfi (1972) described a new subspecies named *Sphaeroidinella ionica evoluta*, sharing numerous similarities with *Sphaeroidinella dehiscens excavata* Banner and Blow, 1965. Cita and Ciaranfi (1972) discussed the occurrence of similar specimens in Hofker (1972), depicted as *Sa. excavata* in recent sediments from the Caribbean, and they commented that the occurrence of *Sa. ionica evoluta* outside of the Mediterranean would make this taxon a junior synonym of *Sphaeroidinella excavata* Banner and Blow, 1965. We found specimens similar to *Sphaeroidinella ionica evoluta* Cita and Ciaranfi, 1972 in the samples investigated for this study (IODP Site U1490) in the intervals where *Sa. excavata* is present and more abundant. For these reasons, we consider *Sa. ionica evoluta*

a junior synonym of *Sa. excavata*, in line with what was stated by Cita and Ciaranfi (1972) about the potential extra-Mediterranean occurrences.

## Conclusions

These biometric data and images further our understanding of *Sphaeroidinellopsis* and *Sphaeroidinella*, documenting the wide range of phenotypic variability within this group of foraminifera. We have shown how *Sphaeroidinellopsis* and *Sphaeroidinella* are both spinose and possess the same cancellate wall texture. This wall texture has been compared to the other types known in the literature, showing unique features such as the large pore size and the lowest concentration of pores per unit area. We named this structure *disjuncta*-type, based on the first morphospecies to bear it and setting it apart from its probable ancestor genus *Globoturborotalita*. The *disjuncta*-type wall includes another exclusive feature: the possibility to overgrow a thick imperforate calcite cortex covering the test. Our data, combining images and biometrics, documents the constant presence of the cortex in *Sphaeroidinellopsis* and *Sphaeroidinella*, but with different stages of development along the lineage, especially in *Ss. kochi* and *Ss. seminulina*. Our biometric data also highlights how the morphological differences between *Sphaeroidinellopsis* and *Sphaeroidinella* are not limited to the wall texture, but extend also to other key taxonomic features. They indicate similarities between phylogenetically linked species within each genus, e.g. *Ss. disjuncta*–*Ss. kochi* and *Ss. seminulina*–*Sa. dehiscens* lineages. *Sphaeroidinellopsis kochi* presents the widest range of variability in its characters, as exemplified by its complex taxonomical history. Our data do not support the splitting of *Ss. kochi* into different morphospecies as previous authors have suggested. For these reasons, we illustrate and acknowledge the variability of *Ss. kochi*, preserving the original concept and suggesting the designation of a neotype to consolidate its taxonomic status. We discussed here another variable and problematic taxon, *Sphaeroidinella dehiscens*, and recognize its descendant *Sphaeroidinella excavata*.

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## Author contributions

CRediT: **Alessio Fabbrini**: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing; **Bridget S. Wade**: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

## ORCID

Alessio Fabbrini  <http://orcid.org/0000-0002-4190-6429>

Bridget S. Wade  <http://orcid.org/0000-0002-7245-8614>

## Data availability statement

The data that support the findings of this study are openly available from figshare. Biometric data can be found at <https://doi.org/10.6084/m9.figshare.30851180> (Fabbrini & Wade, 2025), wall texture data can be found at <https://doi.org/10.6084/m9.figshare.32592168> (Fabbrini & Wade, 2026a) and abundance counts can be found at <https://doi.org/10.6084/m9.figshare.32592099> (Fabbrini & Wade, 2026b).

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