Systematic taxonomy of the *Trilobatus sacculifer* plexus and descendant *Globigerinoidesella fistulosa* (planktonic foraminifera)

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The extant morphospecies of the *Trilobatus sacculifer* plexus (*T. sacculifer*, *T. quadrilobatus*, *T. immaturus* and *T. trilobus*) have widespread biogeographical distributions and long stratigraphical ranges, and are thus routinely utilized in palaeoceanographical studies. The descendant morphospecies *Globigerinoidesella fistulosa* is comparatively short-ranging (Pliocene–Pleistocene) and an important biostratigraphical marker. However, taxonomic concepts of these morphospecies are inconsistently applied between workers, leading to loss of information and incomparable datasets. We present a taxonomic appraisal of each morphospecies, including detailed taxonomic histories and refinement of their morphological concepts, using a combined population-based and typological approach. Morphometric data and scanning electron microscopy are used to illustrate morphological intergradation in the *Trilobatus sacculifer* plexus. The distinctive morphology of *Globigerinoidesella fistulosa* is shown to develop from *T. sacculifer* (as previously documented), but also from the other morphospecies in the plexus, providing the first fossil evidence demonstrating that the four morphospecies of the *T. sacculifer* plexus are the same species. Our new analyses support culturing and molecular genetic evidence from extant specimens that suggests the four *T. sacculifer* plexus morphospecies are the same biological species. However, we advocate using the four morphospecies concepts (*T. sacculifer*, *T. quadrilobatus*, *T. immaturus* and *T. trilobus*) and *G. fistulosa*, here refined, to increase their palaeoecological and biostratigraphical value.

Keywords: *Trilobatus*; *Globigerinoidesella*; morphometrics; systematic taxonomy; planktonic foraminifera

Introduction

The extant morphospecies of the planktonic foraminifera genus *Trilobatus* are part of a group called the *Trilobatus sacculifer* plexus, which consists of four morphospecies: *T. sacculifer* (Brady, 1877), *T. quadrilobatus* (d'Orbigny, 1846), *T. immaturus* (LeRoy, 1939) and *T. trilobus* (Reuss, 1850). Prior to 2015, the morphospecies were considered part of the genus *Globigerinoides*, but were then assigned to the new genus *Trilobatus* Spezzaferri *et al.* (2015), with *T. trilobus* designated as the type species. Each of the *T. sacculifer* plexus morphospecies is routinely utilized for palaeoceanographical research, as the biology and ecology of extant forms are relatively well constrained, and they are common in (sub)tropical assemblages worldwide throughout their long stratigraphical ranges (latest Oligocene/early Miocene to Recent). It is therefore imperative that the taxonomy and evolutionary relationships of this group are resolved in light of the recent implications of taxonomic changes made by Spezzaferri *et al.* (2015). Here, we use a combined typological and population-based approach in a systematic taxonomic appraisal of the

T. sacculifer plexus from Pliocene and Recent specimens, aiming to resolve taxonomic problems in this group and document morphological variation. The differences and shared morphological features between all of the *T. sacculifer* plexus morphospecies are fully discussed in the systematic taxonomy.

Historial context of the *Trilobatus sacculifer* plexus

Before the work of Spezzaferri *et al.* (2015), many previous workers recognized the polyphyletic nature of *Globigerinoides* Cushman, 1927, but the interpretations of phylogenetic relationships within the group differed among workers (e.g. Hofker 1959; Parker 1967; Takayanagi *et al.* 1979; Keller 1981; Srinivasan & Kennett 1981; Kennett & Srinivasan 1983; Jenkins 1985; Spezzaferri & Premoli Silva 1991; Spezzaferri 1994). Essentially, supplementary apertures evolved independently in more than one lineage, though numerous conflicting propositions existed as to the ancestry, early phylogeny and taxonomy of the group (see Spezzaferri *et al.* [2015] for discussion). Despite the

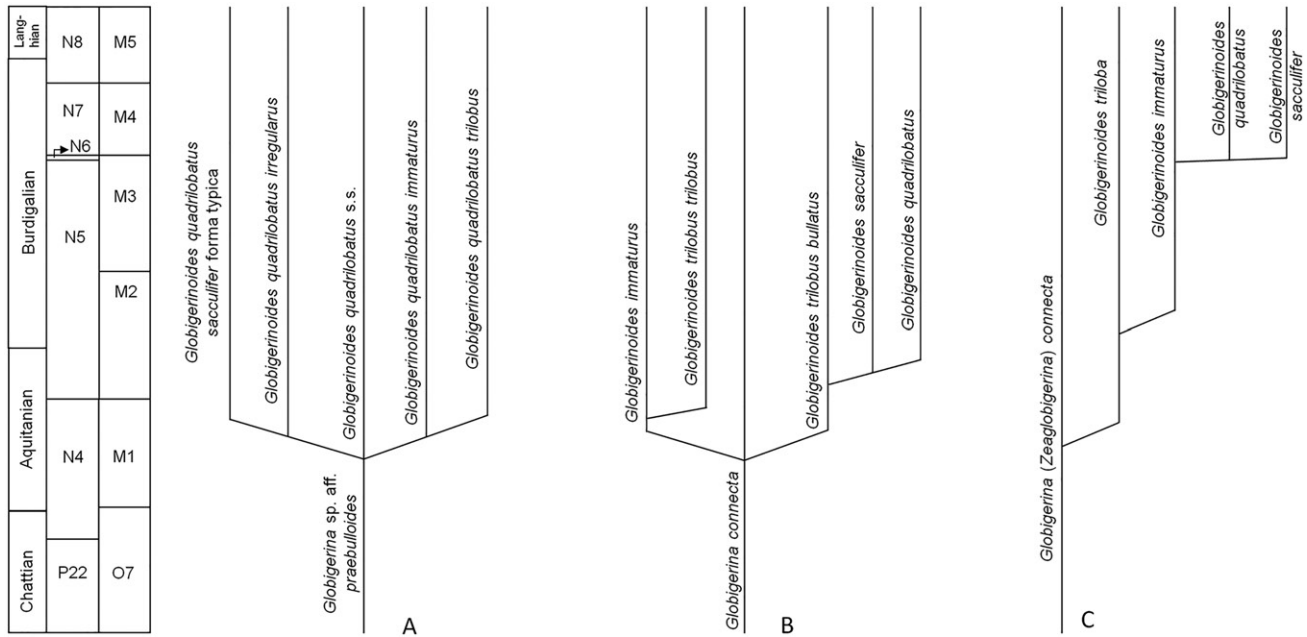*Corresponding author: Email: b.wade@ucl.ac.uk

Figure 1. Phylogenetic interpretations of the evolution of the *Trilobatus sacculifer* plexus. **A,** phylogeny of Banner & Blow (1960); **B,** phylogeny of Keller (1981) based on a stratophenetic investigation (average 12,000-year resolution sampling) of Deep Sea Drilling Project (DSDP) Site 292 (north-western Pacific Ocean); **C,** phylogeny of Srinivasan & Kennett (1981) and Kennett & Srinivasan (1983). Note that the original nomenclatural combinations (binomial and trinomial) used in the authors' separate phylogenies are retained for this figure.

recognized polyphyly, almost all subsequent workers continued to use the original genus concept of Cushman (1927), rather than delimit the genus into distinct, independent lineages (and hence 'true' genera).

This situation was not adequately addressed until the work of Spezzaferri *et al*. (2015); these authors used the latest Oligocene to early Miocene fossil record of the earliest representatives, and molecular genetic data from extant representatives, to re-evaluate *Globigerinoides* Cushman, 1927. Two lineages, termed the 'sacculifer group' and the 'ruber group', were found to have arisen separately, both independently evolving supplementary apertures (Spezzaferri *et al*. 2015). Therefore, a new genus, *Trilobatus* Spezzaferri, Kucera, Pearson, Wade, Rappo, Poole, Morard & Stalder 2015, was erected to accommodate the 'sacculifer group', whilst *Globigerinoides* was retained and emended for the 'ruber group' (see Spezzaferri *et al*. 2015).

One complication that arose from the erection of *Trilobatus* was the generic re-assignment of the *T. sacculifer* plexus morphospecies. Previous workers have inferred a close evolutionary relationship among all four *T. sacculifer* plexus morphospecies based on a stratophenetic approach to their earliest appearances in the latest Oligocene to early Miocene (e.g. Banner & Blow 1960, 1965; Keller 1981; Kennett & Srinivasan 1983). Whilst each of the morphospecies ranges through to Recent, the earliest stratigraphical occurrences may

show some discordance, as indicated by Kennett & Srinivasan (1983) and Keller (1981) and in the phylogeny of Aze *et al*. (2011), particularly with regards to a stratigraphically later development of a sac-like final chamber (i.e. the *T. sacculifer* morphospecies). The earliest stratigraphical ranges and phylogeny of the *T. sacculifer* plexus morphospecies are in need of evaluation by stratophenetic means, as there are different interpretations regarding which morphospecies is ancestral to the group (Fig. 1). For example, Banner & Blow (1960, 1965) considered *T. quadrilobatus* ancestral to the other *T. sacculifer* plexus morphospecies, whereas Kennett & Srinivasan (1983) regarded *T. trilobus* as ancestral to the others. There are also other interpretations of the early phylogeny of the *T. sacculifer* plexus (e.g. Keller 1981). Despite these different phylogenetic interpretations, virtually all workers consider the *T. sacculifer* plexus morphospecies to be phylogenetically related, and they have been regarded as separate morphospecies based on their differing morphology and apparently discordant stratigraphical ranges (e.g. Kennett & Srinivasan 1983).

Culturing and molecular genetic evidence from extant forms (e.g. Hemleben *et al*. 1987; André *et al*. 2013) suggests delimiting the *T. sacculifer* plexus into four distinct morphospecies is likely a taxonomic overestimation of diversity and that all four morphospecies do not simply form an evolutionary lineage, but are in fact

the same biological species. Indeed, they are regarded by most culturing workers as simply phenotypic variants, and their size and morphology may be controlled ecophenotypically (Hecht & Savin 1972; Hecht 1974; André *et al*. 2013; Schmidt *et al*. 2016) and/or related to the organism's overall fitness (e.g. Bé et al. 1982). Many studies on extant forms group all morphospecies of the *T. sacculifer* plexus as *T. sacculifer*, or discern only between *T. sacculifer* 'with-sac' (i.e. *T. sacculifer sensu stricto*) and *T. sacculifer* 'without-sac' (i.e. *T. trilobus*, *T. immaturus* and *T. quadrilobatus*). In particular, palaeoceanographical studies utilizing *T. sacculifer* often avoid specimens possessing a sac-like final chamber as they may have different geochemical signatures or add variability (e.g. Spero & Lea 1993). Equally, *T. sacculifer sensu stricto* is often used to denote only *T. sacculifer* (i.e. only forms with a sac-like final chamber), whilst *T. sacculifer sensu lato* refers to all four morphospecies of the *T. sacculifer* plexus (regardless of whether a sac-like chamber is present or not).

To summarize the current knowledge of the *T. sacculifer* plexus: whilst culturing and molecular genetic evidence suggest that all four morphospecies are the same biological species, the morphospecies are regularly differentiated in palaeoceanographical, evolutionary and biostratigraphical studies.

Globigerinoidesella fistulosa

Similar to the *T. sacculifer* plexus, *G. fistulosa* has also undergone taxonomic change following Spezzaferri *et al*. (2015). *Globigerinoidesella fistulosa* had previously been termed *Globigerinoides fistulosus* under the traditional concept of *Globigerinoides*. However, Spezzaferri *et al*. (2015) re-introduced the genus *Globigerinoidesella* El-Naggar, 1971, to separate forms with extended projections from *Trilobatus*.

Globigerinoidesella fistulosa is a short-ranging morphospecies (mid-Pliocene to early Pleistocene). The restricted biostratigraphical range of *G. fistulosa* makes it a useful zone fossil in tropical assemblages worldwide, and its last appearance is used to define the base of Zone PT1 (Wade *et al*. 2011). Its ancestral stock is the *T. sacculifer* plexus and it is inferred to have arisen gradually from *T. sacculifer* (e.g. Parker 1967; Kennett & Srinivasan 1983; Chaisson & Pearson 1997). *Globigerinoidesella fistulosa sensu stricto* is characterized by its ornate, digitate morphology, often with numerous protuberances on a single chamber. It is therefore easy to identify and distinguish from other taxa, including its ancestor *T. sacculifer*. *Trilobatus sacculifer* regularly possesses an extended final chamber, but is typically not digitate. *Trilobatus sacculifer sensu stricto* is indeed strikingly disparate from *G. fistulosa sensu*

stricto; the latter possesses one or more elongated projections from at least one of the final chambers. However, there exists a complete morphological intergradation between the *T. sacculifer* plexus and *G. fistulosa sensu stricto*, impeding objective delimitation and thus constraining its first (and last) stratigraphical occurrences. The presence of such intermediate or 'transitional' forms with progressively more developed protuberances towards the rise of *G. fistulosa sensu stricto* has been observed by Chaisson & Pearson (1997) from Ocean Drilling Program (ODP) Site 925 (Ceara Rise, western equatorial Atlantic Ocean).

Transitional forms are most common during the stratigraphical range of *G. fistulosa sensu stricto*, which also co-exists with all morphospecies of the *T. sacculifer* plexus. In other words, *G. fistulosa* does not replace *T. sacculifer*, but co-exists with it until the last stratigraphical occurrence of *G. fistulosa* in the early Pleistocene. Following the last occurrence of *G. fistulosa*, all morphospecies of the *T. sacculifer* plexus persist to the present day. However, it is demonstrated here that transitional forms with incipient protuberances also range to the Recent. It is unsatisfactory for these forms to be termed *G. fistulosa*, as then all biostratigraphical utility is lost. They are typically regarded as extreme morphological variants of *T. sacculifer*. In this study, we use the occurrence of such transitional forms in Pleistocene to Recent cores from the GLOW cruise (Kroon & Scientific Participants 2010) to form a morphological basis for delimiting the gradual transition between *T. sacculifer* and *G. fistulosa* in the mid-Pliocene to early Pleistocene. This delimitation is used to refine the morphological concept of *G. fistulosa* in a systematic taxonomic appraisal presented herein.

Typological and population-based taxonomic principles

Heavy reliance on holotypes and typological taxonomy to exemplify a morphospecies' morphology may lead to loss of information about population variation (Emiliani 1969; Scott 2011). The combined effects of typological taxonomy and gradual morphological intergradation between morphospecies inherently lead to artificial subdivision into 'species' (e.g. see Fordham 1986; Pearson 1992, 1993, 1996, 1998; Scott 2011). Although finer taxonomic splitting may better describe the morphological variation within a given lineage, and certainly facilitate greater biostratigraphical resolution, it does not necessarily convey any evolutionary meaning regarding speciation or extinction (Fordham 1986; Pearson 1992, 1998; Scott 2011).

Morphological trait variation for a species, at a given time and site, is at least hypothetically normally
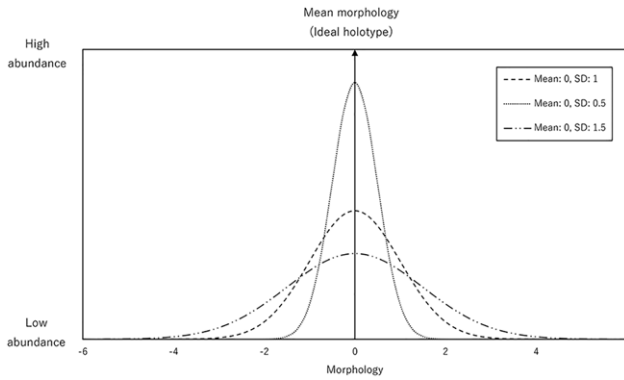
Figure 2. Hypothetical visualization of morphology in a single dimension. Trait morphology is normally distributed, whereby the mean morphology (solid vertical arrow) should form the type specimen. Morphospecies with high intraspecific variation may be represented by the dot-dashed distribution curve. Conversely, morphospecies with moderate and low intraspecific variation are represented by the dashed and dotted distribution curves, respectively. Finer taxonomic splitting results in more morphospecies with a narrow (dotted line) distribution curve. SD: standard deviation.
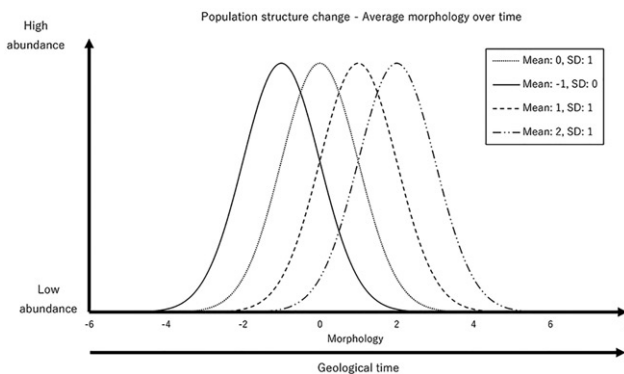

Figure 3. Overlapping morphological clusters. As the mean morphology of a population changes gradually on a temporal scale, morphospecies are challenging to delimit, and arbitrary morphospace sectors are required for taxonomic units. SD: standard deviation.

distributed (see Healy-Williams *et al.* 1985, figs 1–3; Hull & Norris 2009, p. 21224). However, molecular genetic evidence suggests that cryptic diversity (i.e. the presence of distinct genetic types, often inferred to be equivalent to biological species) is prevalent in modern planktonic foraminifera morphospecies (see Darling & Wade [2008] for a review). The revealed pattern is a taxonomic underestimation of modern species diversity, and this is likely to translate to morphospecies concepts in the fossil record. Some genetic types within modern morphospecies can be delimited morphologically using various morphometric approaches (e.g. in *Orbulina universa*; Morard *et al.* 2009), but this is time consuming. In most cases, cryptic diversity is likely masked or undetected in the fossil record, partly due to the apparent gradual (anagenetic) morphological change which is recognized along many lineages, and because cryptic speciation may occur with negligible morphological change. If detected, cryptic diversity and speciation events (cladogenetic branching) may be the cause of trait polymodality that is sometimes observed in single recognized morphospecies.

Here, species morphology is hypothetically represented in a single dimension for illustrative purposes (Figs 2, 3). In reality, any species should be visualized as occupying a multidimensional morphospace, within which the holotype should be defined based on the mean morphology (e.g. Pearson 1992, 1998). In a (hypothetical) normally distributed morphospecies population, the majority of specimens should fall close to a mean morphology, with decreasing abundances of more extreme morphotypes that are distal from the mean (Fig. 2). By this theory, a standard morphospecies concept should, by definition, only encompass specimens demonstrating morphological variability within the limits of normal distribution (e.g. Hull & Norris 2009). Any co-existing species displaying divergence outside of these limits no longer exhibits intraspecific variation, but is regarded a distinct species. Depending on the degree of intraspecific variation recorded in a morphospecies, the bell curve may be flatter or narrower (Fig. 2). For example, any morphospecies that exhibits significant morphological variation will have a large abundance of morphotypes that are morphologically distant from the typical species concept, which in theory should be the type specimen.

On a temporal scale, morphospecies populations may be dynamic in their morphological change. Gradual morphological change (anagenesis) is characteristic of many Cenozoic planktonic foraminiferal lineages (Malmgren & Kennett 1981; Arnold 1983; Malmgren *et al.* 1983, 1984; Hunter *et al.* 1988; Biolzi 1991; Pearson & Ezard 2014). Many lineages form morphological clines (i.e. within-lineage intergradation), which inexorably results in coinciding distribution curves of morphological variation (overlapping morphological clusters; Fig. 3). This has led to difficulties in assessing broader evolutionary relationships and bioevents, as morphospecies populations often grade into a distinct population rather than indicating any clear cladogenetic branching (Pearson 1998; Aze *et al.* 2011; Fordham *et al.* 2018). Cenozoic planktonic foraminifera have an excellent fossil record, which in some respects is a double-edged sword as morphological clines are particularly apparent and make morphospecies delimitation challenging.
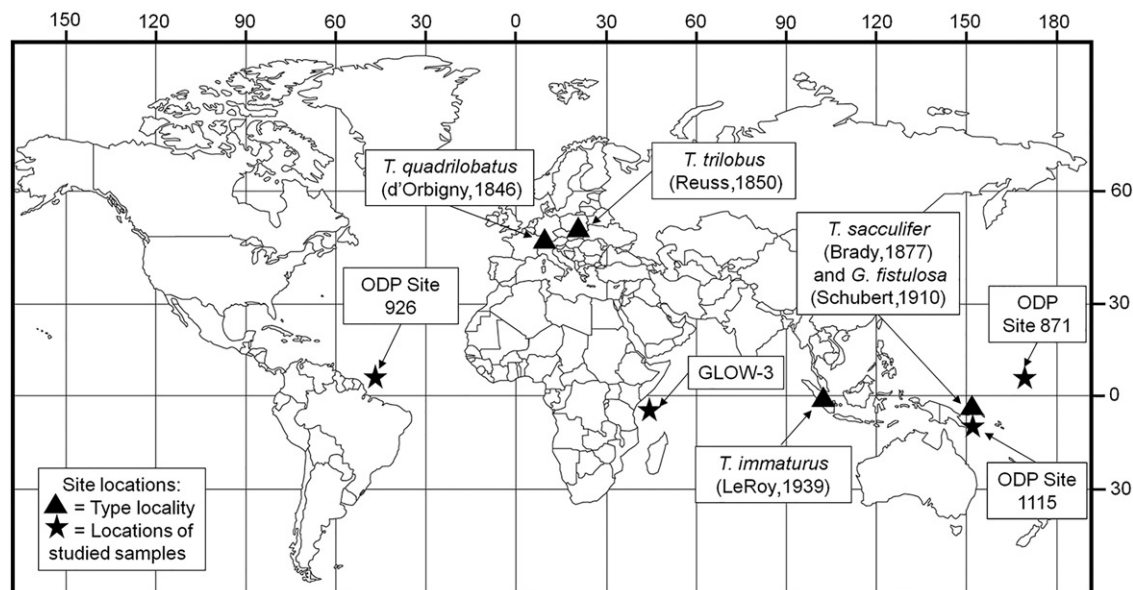
Figure 4. Site location map. Location map showing sites from this study (black star symbols) and the type localities (black triangle symbols) for the investigated morphospecies.

Distinguishing between morphospecies is often characterized by subjectivity, and arbitrary delimitation of morphospecies can cause problems in assessing true evolutionary relationships in the fossil record. Species-level delimitation is obviously necessary for intergrading morphospecies, not only for biostratigraphical purposes, but because without such a procedural basis, whole lineages lasting millions of years and exhibiting significant morphological change would be represented by a solitary species (see Pearson 1992; Pearson *et al*. 2006, p. 17). Thus, a Linnean-style typological taxonomy, albeit with its limitations with regards to 'true' evolutionary classification as discussed above, is still necessary in planktonic foraminifera (e.g. Pearson *et al*. 2006; Pearson & Wade 2015), although see Fordham (1986) for an alternative evolutionary classification of Cenozoic planktonic foraminifera.

Material and methods

Site locations
We combine typological and population-based methods in order to investigate the type morphology for the *T. sacculifer* plexus morphospecies and identify the morphological variability surrounding these types. For the *T. sacculifer* plexus, populations were investigated from two time intervals and multiple ocean basins. The time intervals are late Pleistocene to Recent, and Pliocene to early Pleistocene. The late Pleistocene to Recent samples are from box core sediments recovered

from the GLObal Warming cruise, known as the GLOW Cruise (Kroon & Scientific Participants 2010). The GLOW-3 box core sample was recovered from offshore Tanzania, western tropical Indian Ocean (Fig. 4). The second time interval of Pliocene to early Pleistocene consists of material from multiple ODP sites in the Atlantic and Pacific Oceans. This includes ODP Site 1115 (offshore Papua New Guinea, western tropical Pacific Ocean), which was used for the biometric and morphometric analyses of *Globigerinoidesella fistulosa*. Site 1115 is also proximal to the type localities of both *T. sacculifer* (Brady 1877) and *G. fistulosa* (Schubert 1910) (Fig. 4). Additional scanning electron microscope (SEM) images were obtained from *T. sacculifer* plexus and *G. fistulosa* populations from supplementary ODP Sites 871 (Marshall Islands, western tropical Pacific Ocean) and 926 (Ceara Rise, western tropical Atlantic Ocean) (Fig. 4).

Morphometrics and biometrics
The morphological characters that define the *T. sacculifer* plexus are primarily the *sacculifer*-type wall texture, and multiple supplementary apertures (one per chamber). This means that genus-level identification was straightforward and the genus was not confused with broadly similar genera or lineages. Samples were dry-sieved at the 250-μm size fraction before being split into a suitable aliquot (using a micro-splitter) to ensure a representative population of the *T. sacculifer* plexus was picked. Brummer *et al*. (1987) found that the onset of the adult ontogenetic stage in *T. sacculifer* is
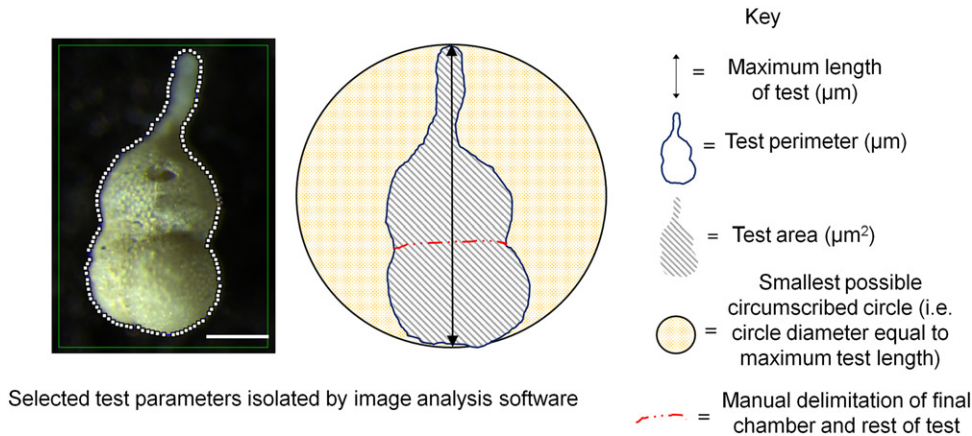
Figure 5. Visual representation of image analysis software and measured morphometric and biometric parameters (see text for details of parameter equations).

confined to a narrow size range centred around 200 μm, and therefore some adult specimens may be less than 250 μm in size and thus not retained in the ≥ 250 μm fraction. However, in this study, our biometric investigation primarily focused upon maximum test sizes. All specimens identified as one of the four morphospecies of the *T. sacculifer* plexus were picked for morphometric and biometric analysis. In the case of the GLOW-3 box core sample, this amounted to more than 450 specimens, and the coiling direction was also noted for each specimen. More than 200 specimens of *G. fistulosa* were also picked from three closely spaced samples in core 10H of Site 1115, which were pooled for biometric and morphometric analysis.

Once picked, specimens were positioned in umbilical view and imaged for morphometric and biometric analysis. Each specimen was photographed using a camera mounted on a binocular microscope. Image analysis software (Image-Pro Premier®, publisher: MediaCybernetics®) was used to analyse the binocular microscope images. All separate images were taken at the same magnification, which is calibrated in the software before image analysis. Individual specimen outlines were isolated in a semi-automated procedure using brightness threshold tools. The translucent/white foraminifera outlines were easily discerned from the black background by the software (Fig. 5). Multiple specimens were photographed simultaneously (i.e. numerous specimens per image) and the image analysis software was able to isolate numerous specimens for simultaneous morphometric and biometric analysis. Specimens were analysed initially as whole tests (e.g. maximum diameter of the test), but the software was also subsequently used to manually delimit between the final chamber and rest of the test which enabled split measurements (e.g. area of the final chamber). Multiple parameters were

measured for each individual specimen, and those used in this study are listed below (see also Fig. 5):

1. Maximum diameter of whole test (μm). Tests positioned in umbilical view, diameter generated from the two-dimensional view of the test.
2. Test area (μm^2) and final chamber area (μm^2) generated from the two-dimensional view of the umbilical side of the test.
3. Circularity: a numerical representation for how circular the outline of the whole test is (here used as a measure of lobateness). A circularity value is generated by using two parameters: the two-dimensional test surface area (μm^2) and the maximum diameter (μm) of a specimen. It is calculated as the ratio of the area of an object (the foraminifera) against a circle whose diameter is equal to the object's maximum diameter (see Fig. 5 for visual representation of parameters measured). The value is between 0 and 1 (where 1 represents a perfect circle). It is calculated using the following equation:

$$\text{Circularity} = \left(4 * \text{Area}\left[\text{of Foraminifera; } \mu m^2\right]\right)/ \left(\pi * \text{MaxDiameter}^2\right) \tag{1}$$

4. Curvature: A numerical value generated based on the relationship between the perimeter length of the specimen and the surface area of the specimen (here used as a measure of lobateness). It was calculated using the following equation:

$$\text{Curvature} = \left(\text{perimeter}^2\right)/(4.\pi.\text{area}) \tag{2}$$

Curvature is most sensitive to the angularity or 'texture' of the specimen outline, and therefore morphospecies

such as *G. fistulosa*, which possess protuberances, should generate the highest values. Higher curvature values represent more lobate specimens. Notes: (a) the above-employed definition is a non-standard definition of 'curvature'; (b) the curvature and roundness values are used in combination as a measure of the 'lobateness' of a specimen. It has recently been demonstrated that whilst planktonic foraminifera test lengths and aspect ratios show good repeatability when measured using image analysis software, perimeter and roundness, conversely, regularly do not show repeatability (Brombacher *et al*. 2017), and thus these metrics must be interpreted with caution.

5. Final chamber dominance ratio: A ratio between the surface area of the final chamber and the surface area of the remaining test. Morphospecies with dominant final chambers, such as *T. trilobus*, should generate high final chamber dominance ratios. One of the key distinguishing characters between *T. trilobus* and *T. immaturus* is the dominance of the final chamber in comparison to the rest of the test. In *T. trilobus*, the final chamber is larger than all of the preceding chambers combined (see systematic taxonomy and concept used by Bolli 1957). Thus, it is possible to objectively delimit *T. trilobus* from *T. immaturus* by quantifying the surface area of the final chamber relative to the rest of the test. In this study, a strict quantitative morphospecies concept was used for *T. trilobus*, as a threshold final chamber dominance ratio of ≥ 1 was required in order to assign a specimen to *T. trilobus*.

Systematic palaeontology overview

One of the primary aims of this work is not only to demonstrate exemplar morphology in a typological fashion, but also to highlight the morphological intergradation between each pair of morphospecies using a population-based approach. We present multiple figures (Figs 6–17) highlighting the intra- and inter-specific variation in the plexus, and provide clarifications regarding the working taxonomic concepts of each morphospecies. The morphological concepts of each morphospecies are detailed in the systematic taxonomy and also illustrated in Figures 6–17. Although the 'typical' forms are figured, much emphasis is also placed upon illustrating the wide range of morphological variation in the *T. sacculifer* plexus (particularly in *T. sacculifer sensu stricto*) and in *Globigerinoidesella fistulosa*. Figured specimens are arranged with the primary aperture (in umbilical view) or largest supplementary aperture (in spiral view) facing upward as the reference point. Although standard taxonomic practice is to orientate the specimen based on the position of the final

chamber, the sac-like final chamber of *T. sacculifer* can extend in a variety of directions from the preceding chamber. Consistency is maintained in using the largest aperture as the reference point and it also further highlights the variability in the sac-like final chamber position and growth direction, rather than solely morphological variation.

Wall structure and texture

The wall texture of planktonic foraminifera is of primary phylogenetic and taxonomic importance (Lipps 1966; Fleisher 1974, 1975; Steineck & Fleisher 1978; Benjamini & Reiss 1979; Cifelli 1982; Hemleben *et al*. 1991; Olsson *et al*. 1992; Spezzaferri 1994, p. 25, fig. 26). Planktonic foraminifera are also classified on whether they were spinose (i.e. possessed spines) or non-spinose during life. Unfortunately, spines are typically shed/lysed towards the end of the life cycle (e.g. Hemleben *et al*. 1989; Schiebel & Hemleben 2017), and so indirect evidence is usually required to determine spinosity. Remnants of spines, and/or spine cavities, can sometimes be seen in the cross-section of the wall when well-preserved tests are dissected, but one of the key assessments is to look for 'spine holes' on the test surface (see Pearson & Wade 2015; pp. 5–6 for discussion). Spine holes are smaller than normal pores and are typically situated between pores where interpore ridges adjoin, and are often atop small topographic highs (spine bases) on the surface. Good evidence for spinosity consists of "abundant and systematically distributed spine holes", but even in modern morphospecies that are known to be spinose, secondary calcite or corrosion may obscure spine holes completely (Pearson & Wade 2015, p. 6).

The *T. sacculifer* plexus morphospecies are all extant and are known to be unequivocally spinose (e.g. Hemleben *et al*. 1989). The fact that many fossil and Recent forms have spine bases and spine holes that are masked by secondary calcification is of importance when determining whether other fossil groups are spinose or not. For example, whether the genus *Dentoglobigerina* Blow, 1979 is spinose, non-spinose or contains both types is currently under discussion (see Wade *et al*. 2018b). In their taxonomic and phylogenetic appraisal of *Dentoglobigerina*, Olsson *et al*. (2006) stated that the genus was non-spinose. However, evidence for spinosity has been identified in multiple morphospecies (*D. baroemoenensis*, *D. binaiensis*, *D. eotripartita*, *D. galavisi*, *D. juxtabinaiensis*, *D. larmeui*, *D. pseudovenezuelana*, *D. taci*, *D. tapuriensis*; Fox & Wade 2013; Pearson & Wade 2015; Wade *et al*. 2018b). It is imperative that well-preserved specimens are utilized for evaluating spinosity. Yet even in the
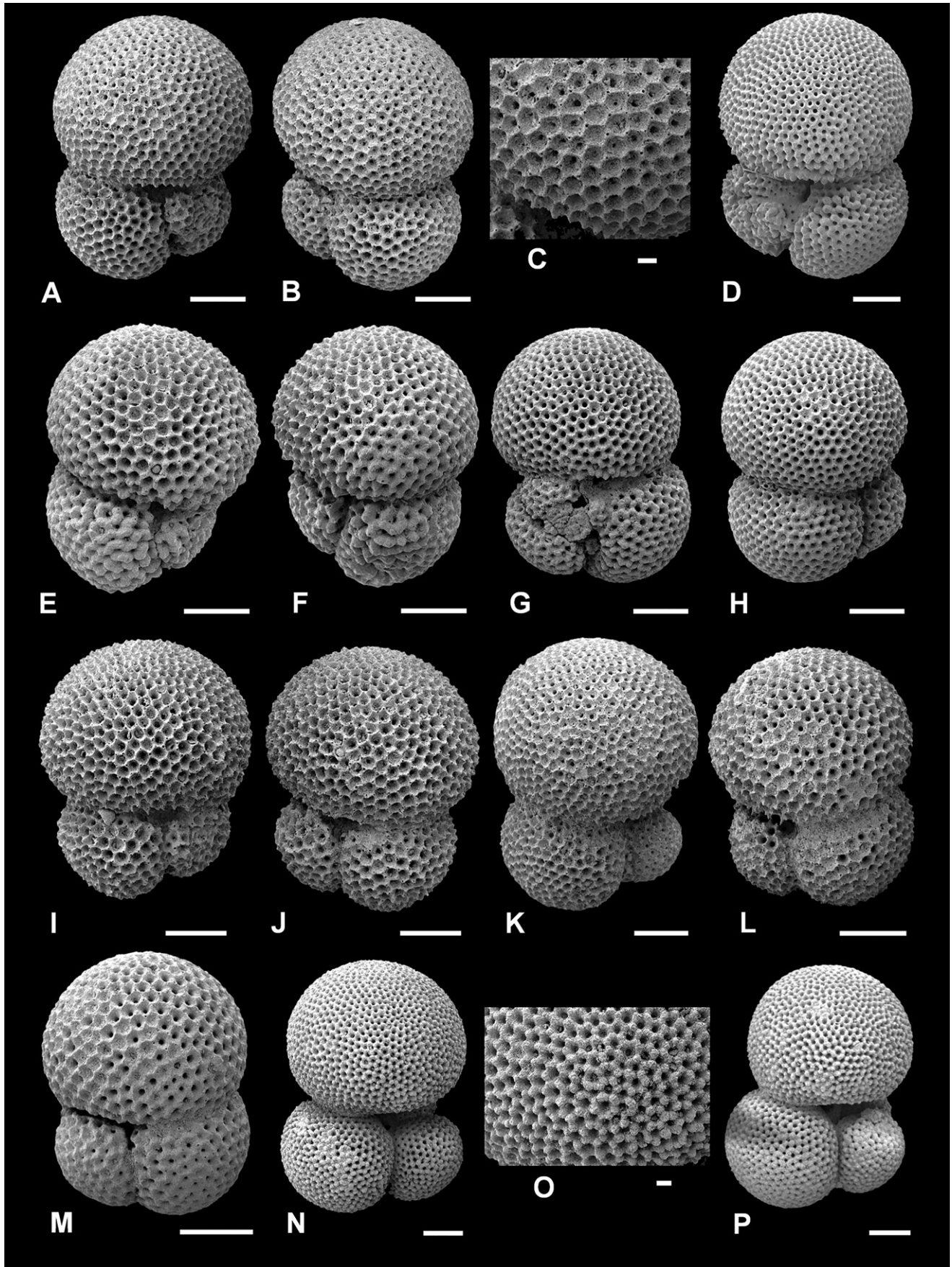
well-preserved GLOW-3 material studied here, morphospecies of the *T. sacculifer* plexus, which are known to be spinose (as each morphospecies is extant), often have their spine holes completely obscured for the entire test. Equally, there may be a patchy distribution or an almost total coverage of spine holes (e.g. Fig. 7N), highlighting the importance of assessing populations rather than individuals. All *T. sacculifer* plexus specimens in each of the investigated samples were likely heavily spinose, just like their recent counterparts, but they exhibit a large amount of variability in spine hole coverage across the test.

The original wall texture is identical for all morphospecies investigated here (*G. fistulosa*, *T. sacculifer*, *T. quadrilobatus*, *T. immaturus* and *T. trilobus*), though see the discussion of the *T. quadrilobatus* wall texture. They are all spinose, normal perforate foraminifera, possessing a cancellate 'sacculifer-type' wall texture (*sensu* Hemleben & Olsson 2006). The *sacculifer*-type wall texture is common to all members of the *T. sacculifer* plexus and is a key diagnostic feature of the newly erected genus *Trilobatus*. *Globigerinoides*, on the other hand, has a *ruber*- or *ruber/sacculifer* type wall texture (Spezzaferri *et al.* 2015), which is cancellate but less symmetrical than the *sacculifer*-type wall texture (see Hemleben & Olsson [2006] for full distinguishing features and illustrations).

The classification schemes are generally adequate for assigning a wall texture type to any given specimen of good preservation. However, the wall texture may be obscured by secondary 'gametogenic' calcite (Bé 1980), altered by dissolution (e.g. Berger 1970; Caron *et al.* 1990), and modified by other interrelated diagenetic alteration processes (e.g. inorganic calcite overgrowth and secondary recrystallization; see Pearson & Burgess 2008). These combined processes do not usually affect gross morphology, but may affect the wall texture dramatically, such that wall texture classification may be encumbered. This is particularly the case for the *T. sacculifer* plexus.

Some specimens in our study exhibit secondary recrystallization and gametogenic calcite to varying degrees, which to some extent masks the original *sacculifer*-type wall texture (see Figs 6–17 and Discussion).

However, irrespective of preservation, the general morphology is not affected in any of the samples, and the specimens were therefore suitable for biometric and morphometric analysis.

Ontogeny

Whilst wall texture is a key diagnostic character in planktonic foraminifera, the earliest ontogenetic stages, which are often concealed or indistinguishable using light microscopy, are typically not considered in systematic taxonomy and morphospecies identification. Nevertheless, several authors have championed the importance of the whole ontogenetic series in taxonomy, citing the ability to discern differences and highlight shared characteristics at the species and genus level (e.g. Huang 1981; Brummer *et al.* 1986, 1987). Like many trochospiral planktonic foraminifera, the earliest juvenile stages of *T. sacculifer* plexus morphospecies exhibit a relatively conservative, near-planispiral, 'globorotaliid' coiling (Parker 1967, 1973; Huang 1981; Sverdlove & Bé 1985; Brummer *et al.* 1986, 1987; Schmidt *et al.* 2013; Caromel *et al.* 2016, 2017). These early stages do not possess the typically cancellate, *sacculifer*-type wall texture as seen in the adult, because it develops later in ontogeny (Brummer *et al.* 1987; Schmidt *et al.* 2013; Caromel *et al.* 2016). It is likely that *G. fistulosa* has analogous embryonic and juvenile ontogenetic stages to *T. sacculifer*, as until the final chambers the neanic-adult ontogeny appears equivalent. The following systematic descriptions consider only the chambers viewable under a binocular microscope, as is standard taxonomic practice, but also because the morphospecies-level morphological differences in the *T. sacculifer* plexus only occur in the adult stages.

Synonymized taxon lists

All members of the *T. sacculifer* plexus are common constituents of (sub)tropical planktonic assemblages throughout their similarly long stratigraphical ranges, and have thus been recorded countless times in previous works. The names here treated in the list of synonymized taxa are by no means exhaustive, but rather concentrate on the original descriptions, key taxonomic

Figure 6. Typical *Trilobatus trilobus* and intergradation with *Trilobatus immaturus*. **A–O,** *Trilobatus trilobus* (Reuss, 1850); **P,** *Trilobatus immaturus* (LeRoy, 1939). **A–K,** GLOW-3, south-west Indian Ocean (**A, D, E, G, I,** spiral view, in **D** note no spine holes are visible due to gametogenic calcite; **B, F, H, J, K,** umbilical view, in **F** note thick gametogenic calcite obscuring *sacculifer*-type wall texture on penultimate chamber; **C,** detail of coarse *sacculifer*-type wall texture and abundant spine holes at intersections of interpore ridges); **L, M,** ODP Site 926, Ceara Rise, western tropical Atlantic, 11H/04/50–52 cm (umbilical view); **N, O,** ODP Site 871, Limalok Guyot, Marshall Islands, equatorial Pacific 3H/03/60–62 cm (**N,** umbilical view; **O,** detail of gametogenic calcite, no spine holes visible). **P,** ODP Site 871, Limalok Guyot, Marshall Islands, equatorial Pacific 3H/03/60–62 cm (umbilical view; note final chamber not dominant over previous chambers, compare with **A–O**). Scale bars = 100 µm, except for close-up images **C** and **O,** where scale bars = 20 µm.
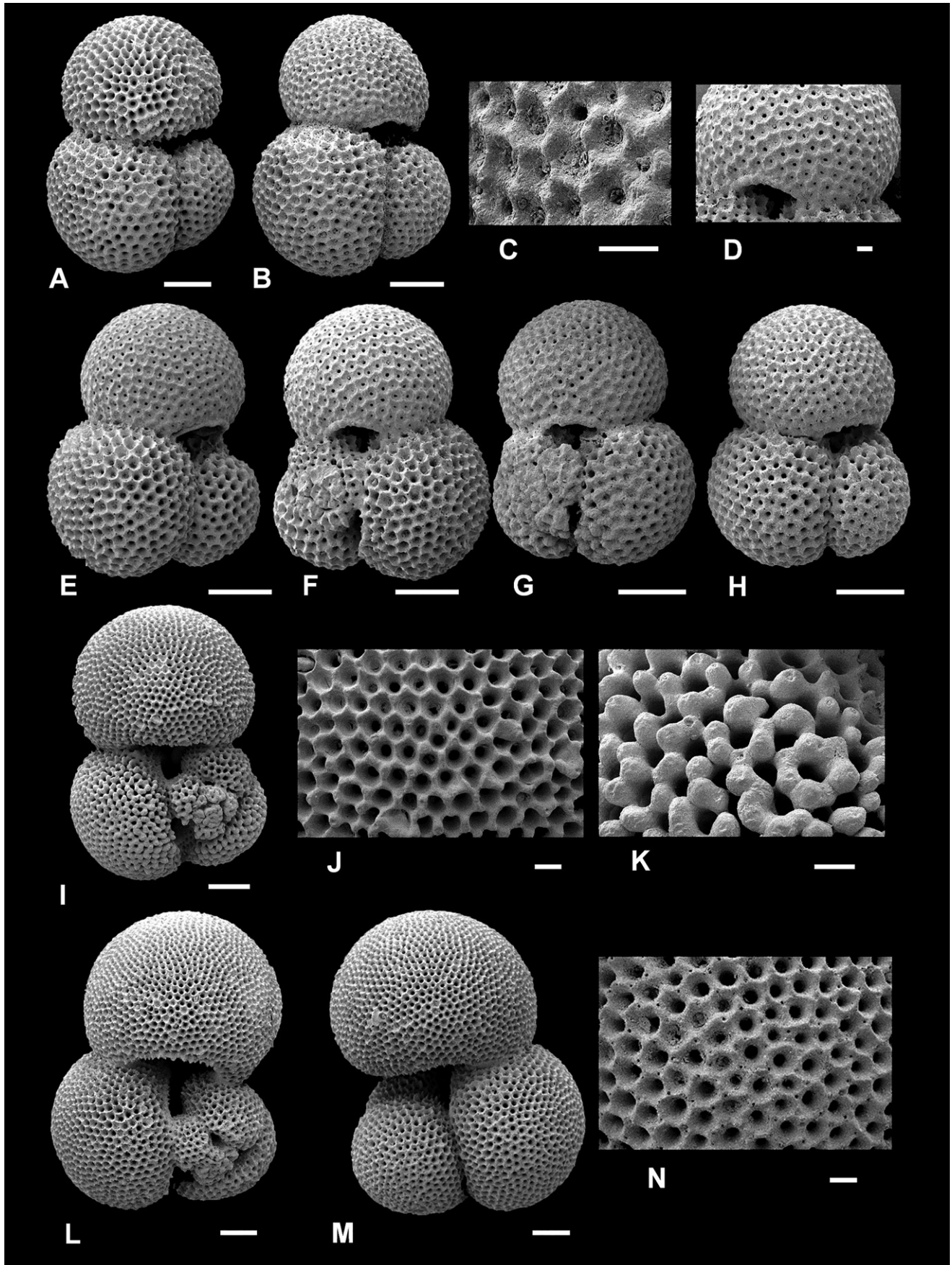
works that accurately demonstrate the morphospecies concept employed herein in their illustrations, and the nomenclatural differences in past literature. Conversely, the occurrence of *G. fistulosa* is a rarer assemblage component, with a much more restricted stratigraphical range (mid-Pliocene to early Pleistocene), and has therefore been documented and illustrated on fewer occasions. For this morphospecies, a comprehensive synonymy list is provided, referencing each illustrated specimen here considered to accurately represent our *G. fistulosa* morphospecies concept. Each synonymy list serves as a reference to what are considered here to be morphospecies exemplars, as much misidentification and nomenclatural complexity exists in the wealth of past literature.

Systematic palaeontology

<p style="text-align:center">Order Foraminiferida d'Orbigny, 1826
Superfamily Globigerinacea Carpenter, Parker & Jones, 1862
Family Globigerinidae Carpenter, Parker & Jones, 1862
Subfamily Globigerininae Carpenter, Parker & Jones, 1862
Genus <i>Trilobatus</i> Spezzaferri, Kucera, Pearson, Wade, Rappo, Poole, Morard, & Stalder, 2015</p>

Type species. *Globigerina triloba* Reuss, 1850.

Diagnosis. Type of wall: normal perforate, spinose, coarsely cancellate 'sacculifer-type' wall texture, though commonly obscured by a heterogeneous secondary, 'gametogenic' calcite. Test morphology: test low trochospiral, three to four usually globose, near-spherical chambers in the final whorl, generally high chamber expansion rate; sutures distinct, depressed, slightly straight to curved on both sides; umbilicus typically narrow; primary aperture usually extraumbilical-umbilical, generally a low arch, numerous apertures on spiral side, one per chamber, placed at the sutures of the preceding chamber and third-previous chamber (see Spezzaferri *et al.* 2015 for further detail).

Remarks. *Trilobatus* is discerned from its ancestor *Globoturborotalita* Hofker, 1976 by possessing one or more supplementary apertures on the spiral side. *Globigerinoides* Cushman, 1927 also possesses supplementary apertures but differs from *Trilobatus* as the latter possesses a strictly *sacculifer*-type wall texture, whereas the former exhibits a *ruber*- or *ruber/sacculifer*-type wall texture (see Hemleben & Olsson 2006 for wall texture classification). Morphospecies of *Globigerinoides* also show a tendency towards higher arched primary apertures, whilst those of *Trilobatus* generally have low-arched, often slit-like primary apertures. *Globigerinoidesella* differs in having digitate protuberances on the final chamber(s) and usually exhibits a larger test size compared to *Trilobatus*. See also Spezzaferri *et al.* (2015, table 2) for comparison of morphological characters.

Trilobatus was erected to encompass the 'sacculifer lineage' (*sensu* Spezzaferri *et al.* 2015), and distinguish it from the 'ruber lineage', which were both formerly part of *Globigerinoides* Cushman, 1927. Spezzaferri *et al.* (2015) demonstrated that the two lineages developed independently and thus placed the two groups in separate genera to avoid polyphyly (see Introduction for further detail).

Range. Latest Oligocene to Recent.

<p style="text-align:center"><i>Trilobatus trilobus</i> (Reuss, 1850)
(Figs 6A–O, 16E, 17A, E)</p>

1850 *Globigerina triloba* Reuss: 374, pl. 47, fig. 11a–e.
1957 *Globigerinoides triloba triloba* (Reuss); Bolli: 112, pl. 25, fig. 2a–c.
1960 *Globigerinoides triloba triloba* (Reuss); Jenkins: 353, pl. 2, fig. 5a–c.
1966 *Globigerinoides trilobus trilobus* (Reuss); Jenkins: 9, pl. 2, fig. 8a–c.
1967 *Globigerinoides quadrilobatus trilobus* (Reuss) Closs: 340, pl. 1, fig. 22.
1975 *Globigerinoides quadrilobatus trilobus* (Reuss) Srinivasan: 139, pl. 2, fig. 7.
1983 *Globigerinoides triloba* (Reuss) Kennett & Srinivasan: 62, pl. 13, figs 1–3.
1994 *Globigerinoides trilobus* (Reuss) Loeblich & Tappan: 107, pl. 206, figs 1–6.
2012 *Globigerinoides trilobus* (Reuss) Rögl: 181, pl. 1, figs 1–7.

Figure 7. Typical *Trilobatus immaturus* and intergradation with *Trilobatus quadrilobatus*. **A–K,** *Trilobatus immaturus* (LeRoy, 1939); **L–N,** *Trilobatus quadrilobatus* (d'Orbigny, 1846). **A–C, I–K,** ODP Site 926, Ceara Rise, western tropical Atlantic, 11H/04/50–52 cm (**A, B,** umbilical view; **C,** detail wall texture and infilled pores; **I,** spiral view; **J,** detail of final chamber wall texture; compare with **K,** detail of penultimate chamber where primary wall texture is obscured by thick gametogenic calcite); **D–H,** GLOW-3, south-west Indian Ocean (**D,** detail of wall texture and imperforate lip on first supplementary aperture; **E, H,** umbilical view; **F, G,** spiral view). **L–N,** GLOW-3, south-west Indian Ocean (**L,** spiral view; **M,** umbilical view; **N,** detail of wall texture including clear spine holes). Scale bars = 100 μm, except for close-up images **C, D, J, K, N,** where scale bars = 20 μm.
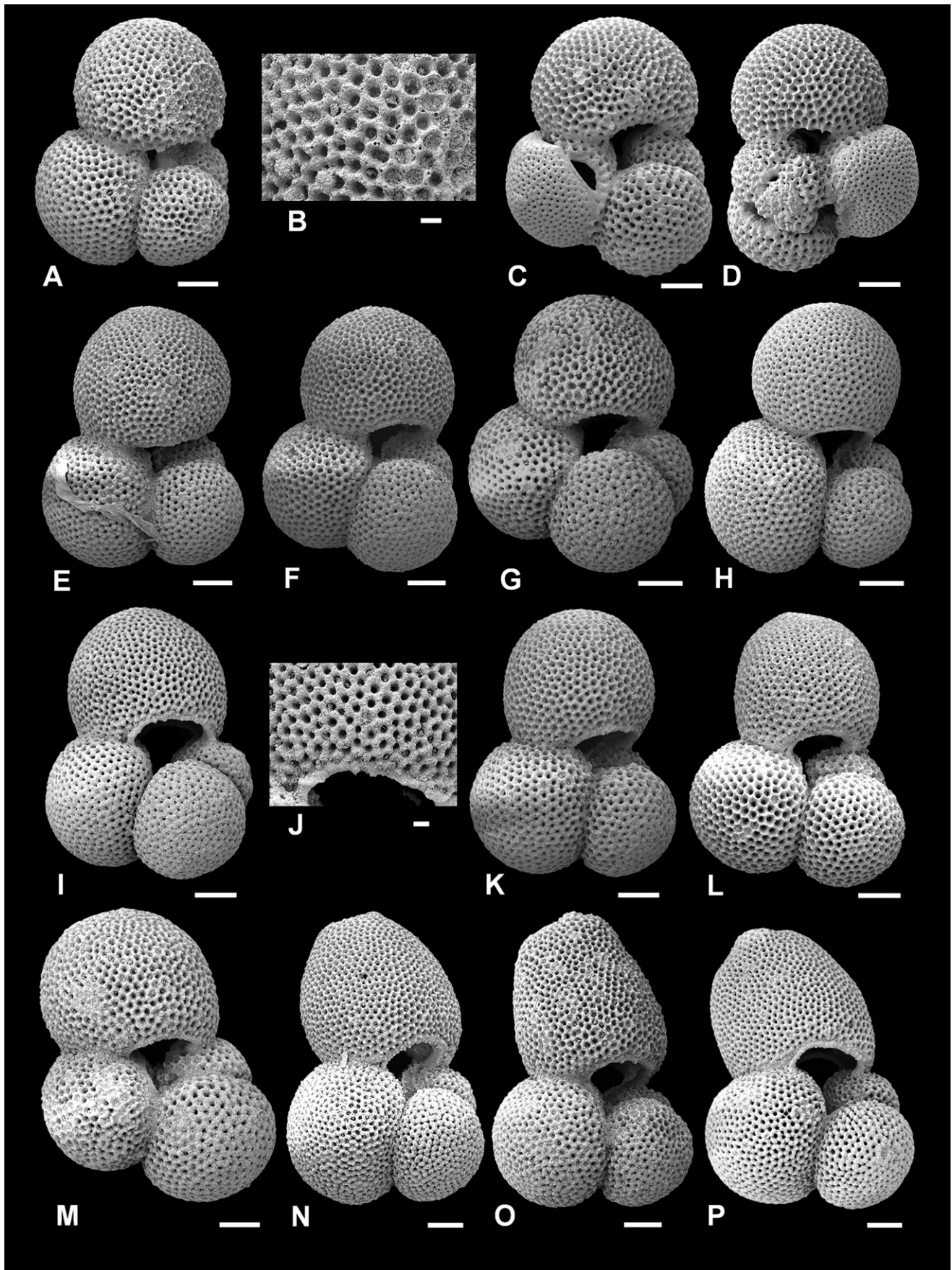
2018 *Trilobatus trilobus* (Reuss) Spezzaferri, Olsson, & Hemleben: 300–302, pl. 9.14, figs 1–21.

Description. Type of wall: spinose, coarsely cancellate (often termed polygonal or honeycomb) 'sacculifer-type' wall texture. Test morphology: low trochospire, initially involute, later more evolute coiling, coiling direction random, three globose, near-spherical chambers in the final whorl, increasing rapidly in size as added, final chamber larger than all other chambers combined; sutures distinct, depressed, straight to slightly curved on both sides; umbilicus narrow; primary aperture interiomarginal-umbilical, a low arch, slit-like, no bordering rim; supplementary apertures small, placed at the sutures of the preceding chamber and third-previous chamber, often only one visible due to infilling or secondary calcification.

Note: description is based on the original description and species concept of Reuss (1850, p. 374), and also Kennett & Srinivasan (1983, p. 62) and Rögl (2012, p. 182), but is here emended and extended.

Remarks. *Trilobatus trilobus* is distinguished from *T. immaturus* and *T. quadrilobatus* by having more rapidly enlarging chambers in the final whorl, resulting in a final chamber that is larger than all other chambers combined. The last chamber is more embracing of the earlier chambers owing to tighter coiling, whereas *T. immaturus* and *T. quadrilobatus* are more loosely coiled with generally more than three chambers in the final whorl (3.5 to 4). *Trilobatus trilobus* differs from *T. sacculifer* which possesses a sac-like final chamber and from *G. fistulosa* which has protuberances. *Globigerinoides altiaperturus* Bolli, 1957 differs primarily in possessing a high-arched, semi-circular primary aperture, whereas in *T. trilobus* it is low and slit-like.

Type locality. Reuss (1850, p. 374) first described *Globigerina triloba*, documenting its occurrence in five separate localities from four countries (Romania, Poland, Austria [two localities] and Italy; see also Rögl 2012, p. 181 for details). Rögl (2012) illustrated numerous specimens from these localities and designated a neotype (here reproduced in Fig. 17) from the Polish locality material of Reuss (1867). Therefore, the type locality is the salt mine Wieliczka, near Krakow, Poland.

Taxonomic history. Reuss (1850, p. 374) described the new species *Globigerina triloba* and illustrated a specimen that clearly exhibits multiple apertures (pl. 47, fig. 11a–e). Reuss (1850) also highlighted how the last chamber is larger than the preceding chambers. The sutures are deeply incised, giving this morphospecies a distinct 'three-lobed' appearance, which explains the derivation of the name *trilobus*. After the introduction of *Globigerinoides* Cushman, 1927, *T. trilobus* was accordingly assigned to this genus by later workers (see synonymy list).

Bolli (1957, p. 113) named *Globigerinoides triloba altiapertura* (= *Globigerinoides altiaperturus*) as a subspecies for forms similar to *T. trilobus* and *T. immaturus* morphotypes, but possessing a higher arched, semi-circular primary aperture (see also Bolli & Saunders 1985, p. 192). However, *G. altiaperturus* is probably not closely related to *T. trilobus* (see Kennett & Srinivasan 1983, text-fig. 9; and Spezzaferri *et al*. 2015, fig. 5). Whilst *G. altiaperturus* is included in the above distinguishing features section, these morphospecies should not be confused morphologically due to their contrasting primary aperture morphology and wall texture.

Trilobatus trilobus has the most conservative morphology of the morphospecies in this study, as exemplified in Figure 6. This is mostly attributable to our strict concept of *T. trilobus* regarding the dominance of the final chamber; it must be larger than all of the preceding chambers combined (*sensu* Bolli 1957) (see Morphometrics and biometrics). *Trilobatus trilobus* intergrades with *T. immaturus*, so using the relative size of the last chamber as the primary delimiting character is arbitrary. However, it can be estimated without using scanning electron microscopy and is easily quantified using morphometrics, thus making it an excellent discerning feature. In the morphometric results, a *T. trilobus* final chamber dominance ratio (FCDR) must be greater than or equal to 1, whereas in *T. immaturus* the FCDR value must be less than 1 (Fig. 19). The ratio compares chamber area (μm^2) from a two-dimensional image (see Methods). In *T. trilobus*, the final chamber volume should also be larger than the rest of the test volume. As the final chambers always have a regular, globose morphology (i.e. no flattening or extension as in *T. sacculifer*), specimens with ratios of more than 1

Figure 8. Typical *Trilobatus quadrilobatus* and intergradation with *Trilobatus sacculifer*. **A–K,** *Trilobatus quadrilobatus* (d'Orbigny, 1846); **L–P,** *Trilobatus sacculifer* (Brady, 1877). **A, B, E, F, G–K,** ODP Site 871, Limalok Guyot, Marshall Islands, equatorial Pacific 3H/03/60–62 cm (**A, E–I, K,** umbilical view; **B,** detail of wall texture, including spine holes, infilled pores, broadened interpore ridges; **J,** detail of wall texture and imperforate lip developed on primary aperture); **C, D,** GLOW-3, south-west Indian Ocean (**C,** umbilical view; **D,** spiral view). **L–P,** ODP Site 871, Limalok Guyot, Marshall Islands, equatorial Pacific 3H/03/60–62 cm (**L–P,** umbilical view; for **L** note slight chamber flattening compared with **I–K**). Scale bars = 100 μm, except for close-up images **B** and **J**, where scale bars = 20 μm.
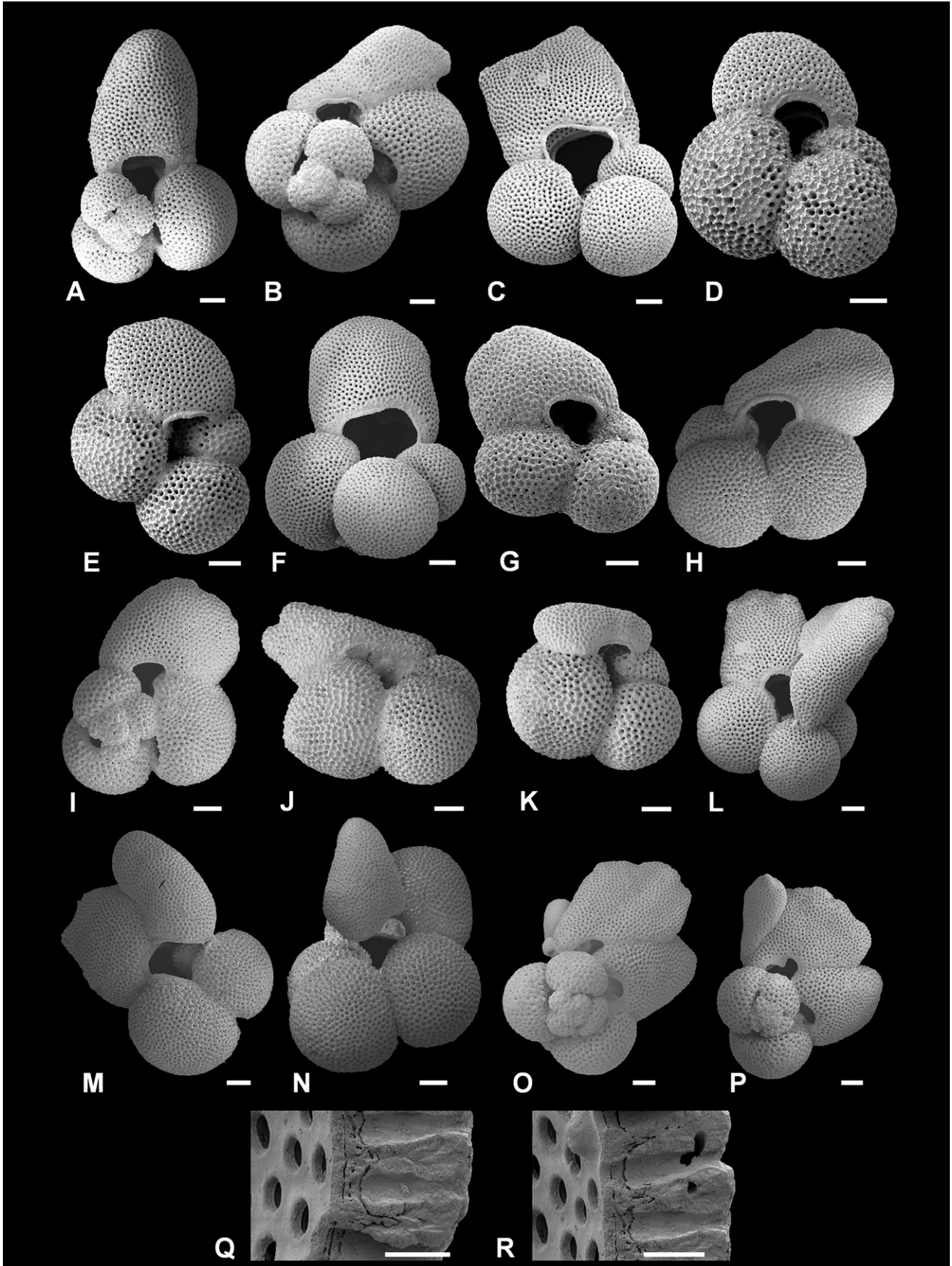
can also be used to equate to a larger chamber volume (μm^3) ratio. Typically, the maximum diameter of the final chamber is also greater than the maximum diameter of the rest of the test. However, occasionally the first two chambers of the final whorl appear marginally wider than the last chamber (e.g. Fig. 6D), yet this is still considered a *T. trilobus* because of the dominant last chamber (i.e. an FCDR value of > 1).

Conversely, if the final chamber is not larger than all preceding chambers, then the specimen cannot be *T. trilobus*. Essentially, this means that *T. trilobus* cannot possess a kummerform final chamber (*sensu* Berger 1969; see also Olsson 1973). This consequently results in many specimens with kummerform final chambers being assigned to *T. immaturus* (e.g. Fig. 7A–D; see *T. immaturus*, Remarks).

Trilobatus trilobus has a *sacculifer*-type wall texture (Fig. 6C), although this is commonly obscured by secondary, 'gametogenic' calcite. In particular, the initial chambers of the final whorl are more heavily calcified and the *sacculifer*-type wall texture is less evident (e.g. Fig. 6C). Secondary calcification also affects the preceding whorl on the spiral side, and the small chambers are often indistinct. If the preceding whorl cannot be clearly observed to identify the spiral side, it is distinguished by the position of the largest aperture. The umbilical side possesses an extraumbilical-umbilical aperture, whereas the spiral side has a central supplementary aperture placed at the base of the final chamber at the sutures of the preceding and third-preceding chambers.

Trilobatus immaturus (LeRoy, 1939)
(Figs 6P, 7A–K, 17B, F)

1939 *Globigerinoides sacculifera* var. *immatura* LeRoy: 263, pl. 3, figs 19–21.
1957 *Globigerinoides triloba immatura* LeRoy; Bolli: 113, pl. 25, figs 3a–4c.
1964 *Globigerinoides triloba immatura* LeRoy; LeRoy: F42, pl. 14, fig. 16.
1967 *Globigerinoides quadrilobatus immaturus* LeRoy; Closs: 340, pl. 1, fig. 15.
1969 *Globigerinoides triloba immatura* LeRoy; Mohan: 36, pl. 4, figs 3, 4.

1975 *Globigerinoides quadrilobatus immaturus* LeRoy; Srinivasan: 138, pl. 2, fig. 4.
1981 *Globigerinoides quadrilobatus immaturus* LeRoy; Chaproniere: 112, fig. 5D, a–d.
1983 *Globigerinoides immaturus* LeRoy; Kennett & Srinivasan: 64, pl. 13, figs 7–9.
2018 *Trilobatus immaturus* LeRoy; Spezzaferri, Olsson, & Hemleben: 289–292, pl. 9.9, figs 1–21.

Description. Type of wall: spinose, coarsely cancellate (often termed polygonal or honeycomb) '*sacculifer*-type' wall texture. Test morphology: low trochospire, 3 to 3.5 globose, spherical chambers in the final whorl increasing moderately in size as added; sutures distinct, depressed, straight to slightly curved on both sides; umbilicus narrow; primary aperture extraumbilical-umbilical, generally a low arch, typically no bordering rim; small supplementary apertures on spiral side, one per chamber, placed at the sutures of the preceding chamber and third-previous chamber, sometimes the only one visible due to infilling or secondary calcification.

Note: description is based on the original species concept of LeRoy (1939, p. 263) and also Bolli (1957, pp. 112–113) and Kennett & Srinivasan (1983, p. 64), but is here emended and extended.

Remarks. *Trilobatus immaturus* is distinguished from *T. trilobus* by having looser coiling and a lower rate of chamber expansion in the final whorl, resulting in a final chamber that is not larger than the other chambers combined. *Trilobatus quadrilobatus* differs in typically possessing four chambers in the final whorl, and having a lower rate of chamber expansion, resulting in almost equal-sized chambers. The last chamber is more embracing of the earlier chambers owing to tighter coiling, whereas *T. quadrilobatus* is more loosely coiled. Thus, *T. immaturus* can be seen as intermediate in morphology between *T. trilobus* and *T. quadrilobatus*. *Trilobatus immaturus* differs from *T. sacculifer* which possesses a sac-like final chamber and *G. fistulosa* which has protuberances.

Type locality. Telisa Shales, Tapoeng Kiri area, Rokan-Tapanoeli, central Sumatra, Indonesia.

Taxonomic history. *Trilobatus immaturus* was named by LeRoy (1939, pp. 263–264) as *Globigerinoides*

Figure 9. Morphological variation in the final sac-like chamber(s) of *Trilobatus sacculifer* (Brady, 1877). **A–G, I,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (**A, B, I,** spiral view, in **A** note elongated sac-like chamber; **C–G,** umbilical view, in **D** note kummerform sac-like chamber, in **F** note large, asymmetrical aperture with surrounding imperforate area); **H, J–P,** ODP Site 871, Limalok Guyot, Marshall Islands, equatorial Pacific 3H/03/60–62 cm (**H, J–N** umbilical view, in **J** note lobate sac-like chamber, in **K** note kummerform sac-like chamber, in **L–N** note two sac-like chambers; **O, P,** spiral view; note three sac-like chambers); **Q, R,** GLOW-3, south-west Indian Ocean (cross sectional view of wall, showing relict spines embedded within wall and chamber layers). Scale bars: **A–P** $= 100\,\mu m$; **Q, R** $= 20\,\mu m$.
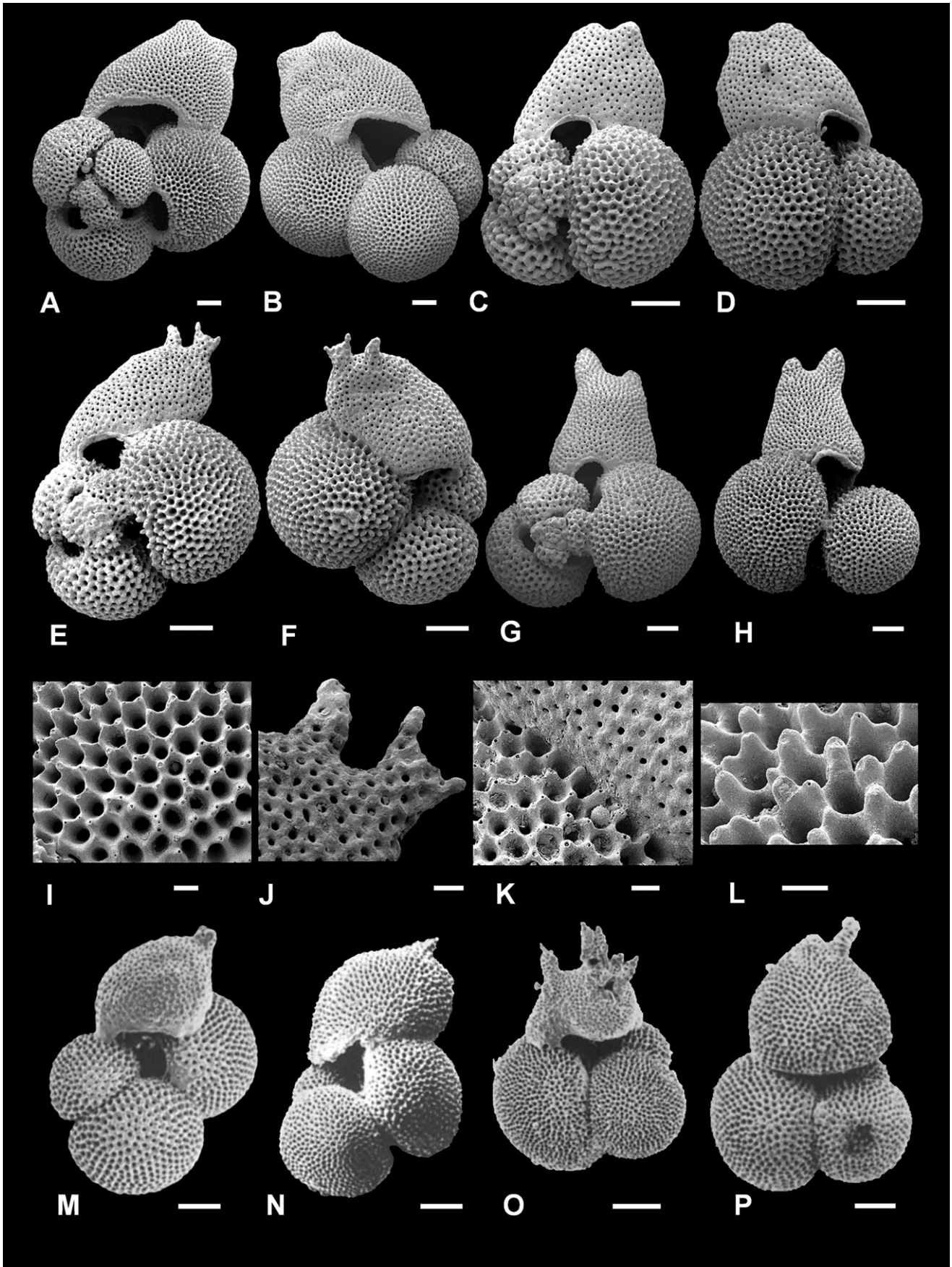
sacculiferus var. *immatura*. LeRoy (1939) originally considered *Globigerinoides sacculiferus* var. *immatura* a varietal form of *T. sacculifer* and thus did not provide a formal description. He noted the close morphological similarity with *T. sacculifer* but considered it "either an early or immature form" (LeRoy 1939, p. 263) because of the absence of the characteristic sac-like final chamber, and this explicates the derivation of the name. The *immaturus* variety was assigned to *Globigerinoides* Cushman, 1927, based on the presence of multiple apertures which LeRoy (1939) clearly illustrated in the holotype images. These illustrations depict a morphotype broadly similar to that of the original images for *T. trilobus* by Reuss (1850), but it has slightly more than three chambers (approximately 3.5) and a slightly lower chamber expansion rate in the final whorl (see Fig. 17). Bolli & Saunders (1985) suggested that the differences were minimal; however, Bolli's (1957) concept is well suited to delimit the morphospecies.

Bolli (1957, p. 112) clarified the differences between *T. trilobus* and *T. immaturus*, stating that "*G. triloba triloba* differs from *G. triloba immatura* in having a final chamber that is larger than all the earlier chambers combined" (see also Jenkins [1960, p. 354] and Kennett & Srinivasan [1983, p. 64] for their comparable distinctions). These differences were also well illustrated by Bolli (1957, i.e. compare text-fig. 21.1 and pl. 25, fig. 2a–c [*T. trilobus*] with text-fig. 21.2 and pl. 25, figs 3a–4c [*T. immaturus*]). Although originally naming *immaturus* as a varietal form of *sacculifer*, LeRoy (1964) subsequently followed Bolli's (1957) designation of *immaturus* as a subspecies of *trilobus*. In contrast, other workers (e.g. Closs 1967; Srinivasan 1975; Chaproniere 1981) considered *T. immaturus* to be a subspecies of *quadrilobatus* (see synonymy list), following Blow & Banner's (1960, 1965) assertion regarding the aforementioned senior priority of *quadrilobatus* and it being a 'central form'. *Trilobatus immaturus* also has an intermediate morphology between *T. trilobus* and *T. quadrilobatus*, and intergrades with both (Figs 6–8), and thus is often reported as a subspecies of *T. trilobus* and *T. quadrilobatus*.

Kennett & Srinivasan (1983) avoided a trinomial nomenclature for this group, giving *T. immaturus* species status (as *Globigerinoides immaturus*), as binomial nomenclature is now standard taxonomic practice for planktonic foraminifera (e.g. Olsson *et al.* 1999; Pearson et al. 2006; Pearson & Wade 2015; Wade *et al.* 2018a). Since the taxonomic revision of Spezzaferri *et al.* (2015), *immaturus* has been assigned to the newly erected genus *Trilobatus*, and we adhere to this designation.

In some respects, *T. immaturus* can be considered a 'wastebasket' taxon (e.g. Longoria & Gamper 1995, p. 332; Aze *et al.* 2011, p. 921; Pearson & Wade 2015, p. 12), although note the slightly different meaning envisaged herein. Firstly, owing to the strict morphological concept of *T. trilobus*, that morphospecies cannot possess a kummerform final chamber (see *T. trilobus* Taxonomic history, above). This means that *T. immaturus* has a high proportion of forms with a kummerform final chamber (see Fig. 7A, B), because it is augmented by the inclusion of forms which cannot be referred to as *T. trilobus*. This may also explain why the maximum size of *T. immaturus* is often similar to that of *T. trilobus* (Fig. 18), rather than being more of an intermediate size between *T. quadrilobatus* and *T. trilobus*. Secondly, whilst 'typical' *T. trilobus* and *T. quadrilobatus* have distinctive morphology, the name *T. immaturus* has come to represent any intermediate morphology which does not fit with the *T. trilobus* and *T. quadrilobatus* morphospecies concepts. Nevertheless, André *et al.* (2013, fig. 8) highlighted that the morphospecies name *immaturus* has seen the rarest usage of the *T. sacculifer* plexus names in the fossil record to Recent, in comparison with the three-chambered *T. trilobus* and the three and a half- to four-chambered *T. quadrilobatus*.

The wall texture is *sacculifer*-type (exemplified in Fig. 7C, D), although as with all *T. sacculifer* plexus members, secondary calcification commonly obscures the original wall texture and especially the spine holes (Fig. 7J, K). The secondary calcification does not affect all chambers equally; the close-up images in Figure 7J and K are from the final and penultimate chambers, respectively. The penultimate chamber has probably

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Figure 10. Incipient protuberance development in Pleistocene to modern *Trilobatus sacculifer*. **A–L,** GLOW-3, south-west Indian Ocean (**A, D, F, J,** spiral view; **B, E, G, K,** umbilical view), in **B** note lobate sac-like chamber, in **E** note thin final sac-like chamber with different wall texture appearance relative to rest of test; **C;** detail of wall texture including spine holes; **H,** detail of two incipient protuberances; **I,** contrasting wall texture appearance in thinner final sac-like chamber with smooth topography, and penultimate chamber with well-developed *sacculifer*-like texture and spine holes; **L,** detail of wall texture showing raised spine bases); **M,** Barbados, Caribbean Sea, specimen cultured after plankton net collection (umbilical view; reproduced from Brummer *et al.* 1987, pl. 1, fig. 14); **N,** Barbados, Caribbean Sea, specimen cultured after SCUBA dive collection (umbilical view; reproduced from Bé *et al.* 1982, fig. 12); **O, P,** Barbados, Caribbean Sea, specimens cultured after SCUBA dive collection (umbilical view; note multiple incipient protuberances; reproduced from of Hemleben *et al.* 1987, pl. 2, figs 11, 12). Scale bars = 100 μm, except close-up images (**I–L**) where scale bars = 20 μm.
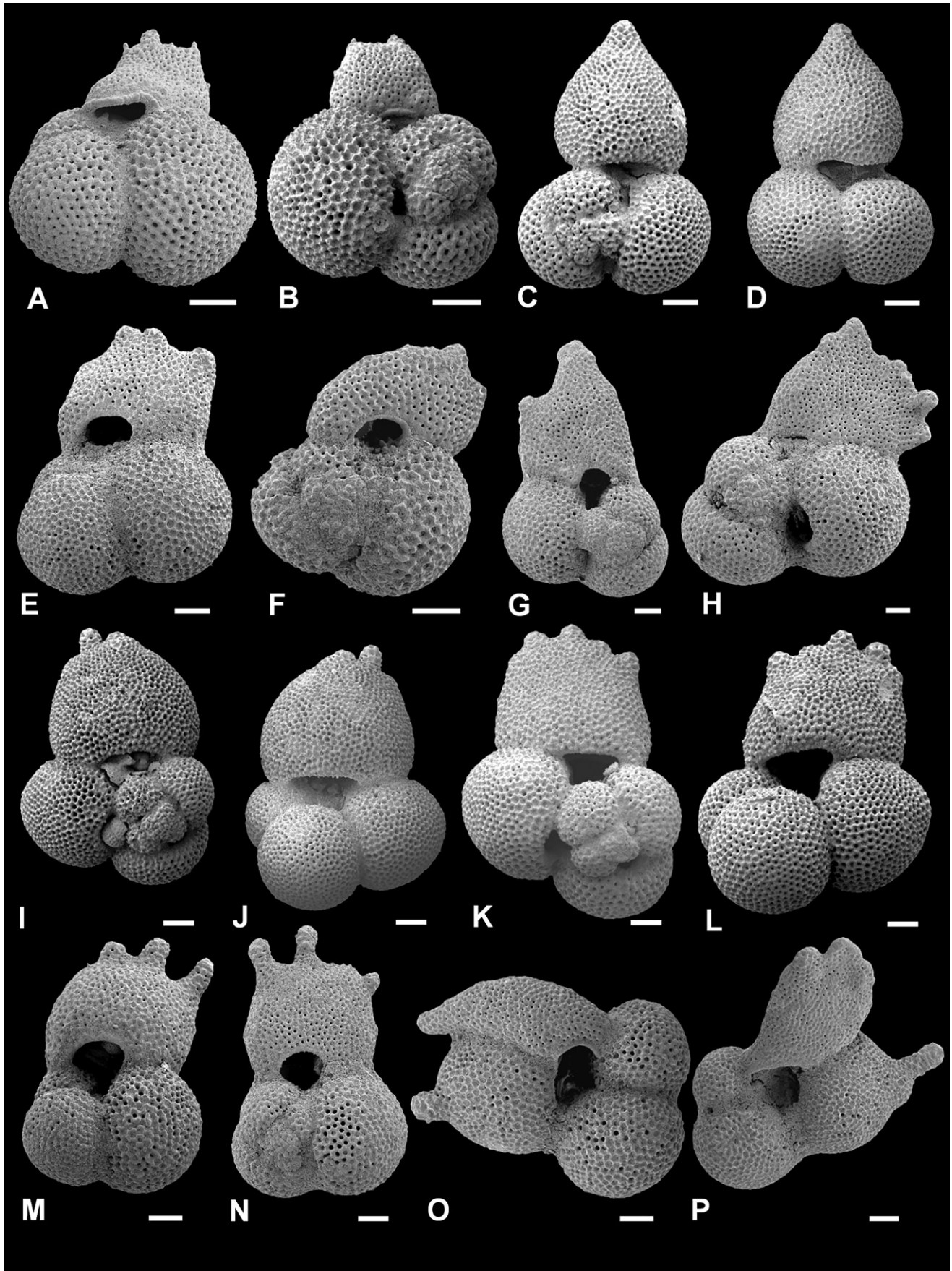
been affected more severely by secondary calcification, and also previous chambers often add more calcite during precipitation of succeeding chambers.

Trilobatus sacculifer is generally considered to have arisen from *T. quadrilobatus* (e.g. Kennett & Srinivasan 1983). However, we also observe intergradation between *T. immaturus* and *T. sacculifer* (Fig. 7B–H), despite *T. immaturus* usually being intermediate in morphology between *T. trilobus* and *T. quadrilobatus*. These specimens show clear evidence of imperforate lips on the primary and first supplementary apertures, and the final chambers are slightly more flattened than 'typical' *T. immaturus* specimens. Though the *T. immaturus*-*T. sacculifer* intermediate morphotypes (Fig. 7B–H) occur less frequently than *T. quadrilobatus*-*T. sacculifer* intermediate morphotypes (Fig. 8H–N), a sac-like chamber may also develop on forms which would otherwise be referred to *T. trilobus*, highlighting how the morphospecies are closely related. The fossil evidence presented here corresponds with the evidence from Recent forms which suggests that the morphospecies of the *T. sacculifer* plexus represent one (biological) species, as the sac-like chamber may develop from *T. trilobus*, *T. immaturus* or *T. quadrilobatus*.

Trilobatus quadrilobatus (d'Orbigny, 1846)
(Figs 7L–N, 8A–K, 15A, 17C, G)

1846 *Globigerina quadrilobata* d'Orbigny: 164, pl. 9, figs 7–10.
1960 *Globigerinoides quadrilobatus* (d'Orbigny); Banner & Blow: 17, pl. 4, fig. 3a, b.
1983 *Globigerinoides quadrilobatus* (d'Orbigny); Kennett & Srinivasan: 66, pl. 14, figs 1–3.
2003 *Globigerinoides quadrilobatus* (d'Orbigny); Li, McGowran, & Brunner: 20, pl. P6, figs 16, 17.
2012 *Globigerinoides quadrilobatus* (d'Orbigny); Rögl: 188, pl. 2, figs 3, 4.
2013 *Globigerinoides quadrilobatus* (d'Orbigny); Fox & Wade: 400, fig. 11.4.
2018 *Trilobatus quadrilobatus* (d'Orbigny); Spezzaferri, Olsson, & Hemleben: 296–298, pl. 9.12, figs 1–20.

Description. Type of wall: spinose, coarsely cancellate *sacculifer*-type wall texture.

Test morphology: low trochospire, 3.5 to typically 4 globose, near-spherical chambers in the final whorl increasing slowly-moderately in size as added; sutures distinct, depressed, straight to slightly curved on both sides; umbilicus narrow; primary aperture extraumbilical-umbilical or umbilical, generally a low arch, often broad, typically no bordering rim; prominent supplementary apertures on spiral side, one per chamber, placed at the sutures of the preceding chamber and third-previous chamber, occasionally only one visible due to infilling or secondary calcification.
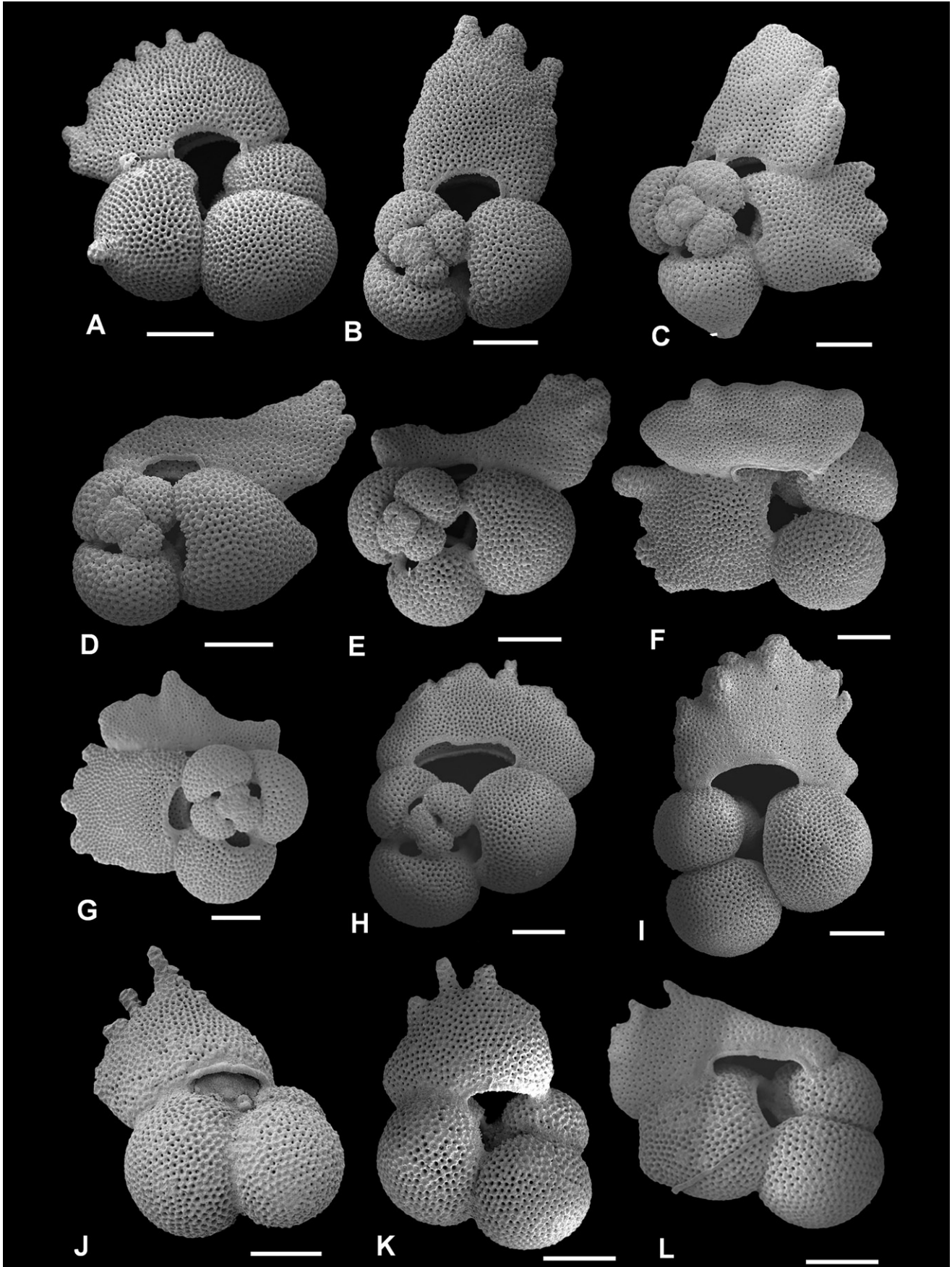
Note: description is based on the original description and species concept of d'Orbigny (1846, p. 164), and that of Banner & Blow (1960, pp. 17–19) and Kennett & Srinivasan (1983, p. 66), but is here emended.

Remarks. *Trilobatus quadrilobatus* is distinguished from *T. sacculifer* in possessing a globular, near-spherical final chamber as opposed to a sac-like final chamber. *Trilobatus sacculifer* also possesses a distinct lip bordering the primary aperture, whilst *T. quadrilobatus* has no lip (though gradation between the two morphospecies occurs). *Trilobatus quadrilobatus* also shows morphological gradation with *T. immaturus*, but differs in having a lower chamber expansion rate and a more open umbilicus and typically having four spherical chambers in the final whorl. *Trilobatus quadrilobatus* has a broad resemblance to the short-ranging Oligo–Miocene morphospecies *Trilobatus primordius* (Blow & Banner 1962), but *T. primordius* only possesses one supplementary aperture on the spiral side and may not have a strictly *sacculifer*-type wall texture (the original description of *T. primordius* by Blow & Banner [1962, p. 115] states it has a "markedly cancellate and punctate" surface).

Type locality. Nussdorf (= Nuβdorf), Rara, Vienna Basin, Austria.

Taxonomic history. d'Orbigny (1846) described *Globigerina quadrilobata* from the Vienna Basin, Austria. He noted that the final four chambers were of almost equal size, increasing only marginally in size as added (d'Orbigny 1846, p. 164). The original illustrations (d'Orbigny 1846, pl. 9, figs 7–10; also reproduced numerous times, e.g. in Papp & Schmid 1985, pl. 54, fig. 7 and Bolli & Saunders 1985, p. 193, fig. 20.18) clearly show this low chamber expansion rate in the final whorl. No supplementary apertures are visible in

Figure 11. *Trilobatus sacculifer* with incipient protuberances and intergradation with *Globigerinoidesella fistulosa*. **A–J,** *Trilobatus sacculifer* (Brady, 1877); **K–P,** *Globigerinoidesella fistulosa* (Schubert, 1910). **A–J,** ODP Site 1115, Woodlark Basin, western Pacific; 10H/04/127–129 cm (**A, D, J,** umbilical view, in **A** note kummerform final sac-like chamber; **B, C, H, I,** spiral view, in **B** note kummerform final sac-like chamber); **E–G,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (**E,** umbilical view; **F, G,** spiral view). **K, L, O, P,** ODP Site 1115, Woodlark Basin, western Pacific; 10H/04/127–129 cm (**K,** spiral view; **L,** umbilical view; note multiple small protuberances and broad flattened final chamber; **O, P,** umbilical view); **M, N,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (umbilical view). Scale bars = 100 μm.

the illustrations or are recorded in the original description, although, as also discussed by Banner & Blow (1965), this omission does not preclude the possibility of supplementary apertures having been present on the specimen. Unfortunately, the original vial labelled '*G. quadrilobata*', examined by Banner & Blow (1960) and later Papp & Schmid (1985), did not contain d'Orbigny's (1846) figured specimen, but it was found to contain a suite of 11 specimens of at least three different morphospecies. According to Banner & Blow (1960), only five specimens were of the quadrilobate form. Despite multiple morphospecies being present, Banner & Blow (1960) reasoned that the contents of the vial were a suite of syntypic specimens for *quadrilobata* and designated a lectotype from one of the five quadrilobate forms. They assigned *quadrilobata* to *Globigerinoides* Cushman, 1927.

Banner & Blow's (1960) record of the *quadrilobata* morphotype was almost its first reported occurrence in more than a century. Cushman (1946, p. 19) had found only one record of *quadrilobata* in the literature, noting that even this reported occurrence was probably not conspecific with d'Orbigny's (1846) concept, and suggested that the name be "allowed to lapse". The designation of a lectotype by Banner & Blow (1960) was described as a 'resurrection' by Todd (1961) and Jenkins (1966). Moreover, numerous authors disputed the validity of the presumed syntypic suite of specimens and thus the designated lectotype (e.g. Todd 1961; Bandy 1964a, b; Jenkins 1966, 1971; Bolli & Saunders 1985). The main arguments were threefold: (1) the contents of the vial, regardless of its label of '*G. quadrilobata*', undoubtedly contained multiple morphospecies and should not have been considered syntypic despite containing 'quadrilobate' specimens; (2) the designated lectotype was not wholly consistent with d'Orbigny's original (and sparse) concept (nor indeed were any of the 11 specimens). Bandy (1964a, b) referred *quadrilobata* back to the genus *Globigerina* primarily because d'Orbigny's concept did not specify any supplementary apertures; and (3) numerous specimens apparently consistent with d'Orbigny's original concept (i.e. not the concept of Banner & Blow) were apparently found in samples from the type locality (e.g. Bandy 1964b).

In two subsequent publications, Banner & Blow (1962, 1965) endeavoured to vindicate their lectotype selection, and considered their *quadrilobata* morphotype

to be an evolutionarily 'central form', giving rise to both *T. trilobus* and *T. sacculifer*. This is of importance because most authors, contrarily, consider *T. trilobus* to be the more 'primitive' form, giving rise to *T. quadrilobatus* (e.g. Kennett & Srinivasan 1983). Other workers (e.g. Fleisher 1974, p. 1023) noted that the lectotype was probably not conspecific with the original concept, but argued it should be retained because of the wide prior usage. Chaproniere (1981, p. 110) also argued in favour of *quadrilobatus* and Banner & Blow's (1960, 1965) concept, and distinguished between *trilobus*, *immaturus* and *quadrilobatus* as separate subspecies of *Globigerinoides quadrilobatus* (i.e. a trinomial nomenclature with *quadrilobatus* as the central species). He also considered numerous other morphospecies to be subspecies of *G. quadrilobatus* that are here not in accordance with our definition of the plexus (Chaproniere 1981).

To add further complication, Banner & Blow's (1960) lectotype was apparently lost and is therefore not available for examination. Papp & Schmid (1985) designated a replacement lectotype from the remaining material of the original vial, choosing a broadly similar specimen to the first lectotype. The validity of this lectotype might be disputed for the same aforementioned reasons. Despite the questionable lectotype selection(s), and rejection by other workers, the Banner & Blow (1960, 1965) concept of *quadrilobatus* has been used consistently since its inception.

Ultimately, the proliferation of the name *quadrilobatus* can be attributed to the taxonomic authority of Banner and Blow, and that Kennett & Srinivasan (1983) considered *quadrilobatus* a distinct morphospecies to *trilobus*, *immaturus* and *sacculifer* in their taxonomic atlas of Neogene planktonic foraminifera. Their influential work has been extensively used as the foremost taxonomic authority for Neogene planktonic foraminifera for more than 30 years. They posited a lineage of *trilobus-immaturus-quadrilobatus-sacculifer*. Many populations (fossil and Recent) contain a 3.5–4-chambered form that is not consistent with the species concepts of *trilobus*, *immaturus* or *sacculifer*; such a morphotype is often called *quadrilobatus*.

Spezzaferri *et al.* (2015) recently reinvigorated this debate in their investigation into the polyphyletic genus *Globigerinoides*. As the lectotype of Papp & Schmid (1985) possesses a relatively high-arched aperture and a

Figure 12. A–C, F–L, *Globigerinoidesella fistulosa* (Schubert, 1910); **D, E,** *Trilobatus sacculifer* (Brady, 1877). **A–C,** ODP Site 926, Ceara Rise, western tropical Atlantic; 7H/05/27–29 cm (**A,** umbilical view; **B, C,** spiral view); **F–I, K,** ODP Site 926, Ceara Rise, western tropical Atlantic; 8H/02/52–54 cm (**F, I, K,** umbilical view; **G, H,** spiral view); **J, L,** ODP Site 926, Ceara Rise, western tropical Atlantic; 7H/05/27–29 cm (umbilical view). **D, E,** ODP Site 926, Ceara Rise, western tropical Atlantic; 7H/05/27–29 cm (spiral view). Scale bars = 200 μm.

C. R. Poole and B. S. Wade
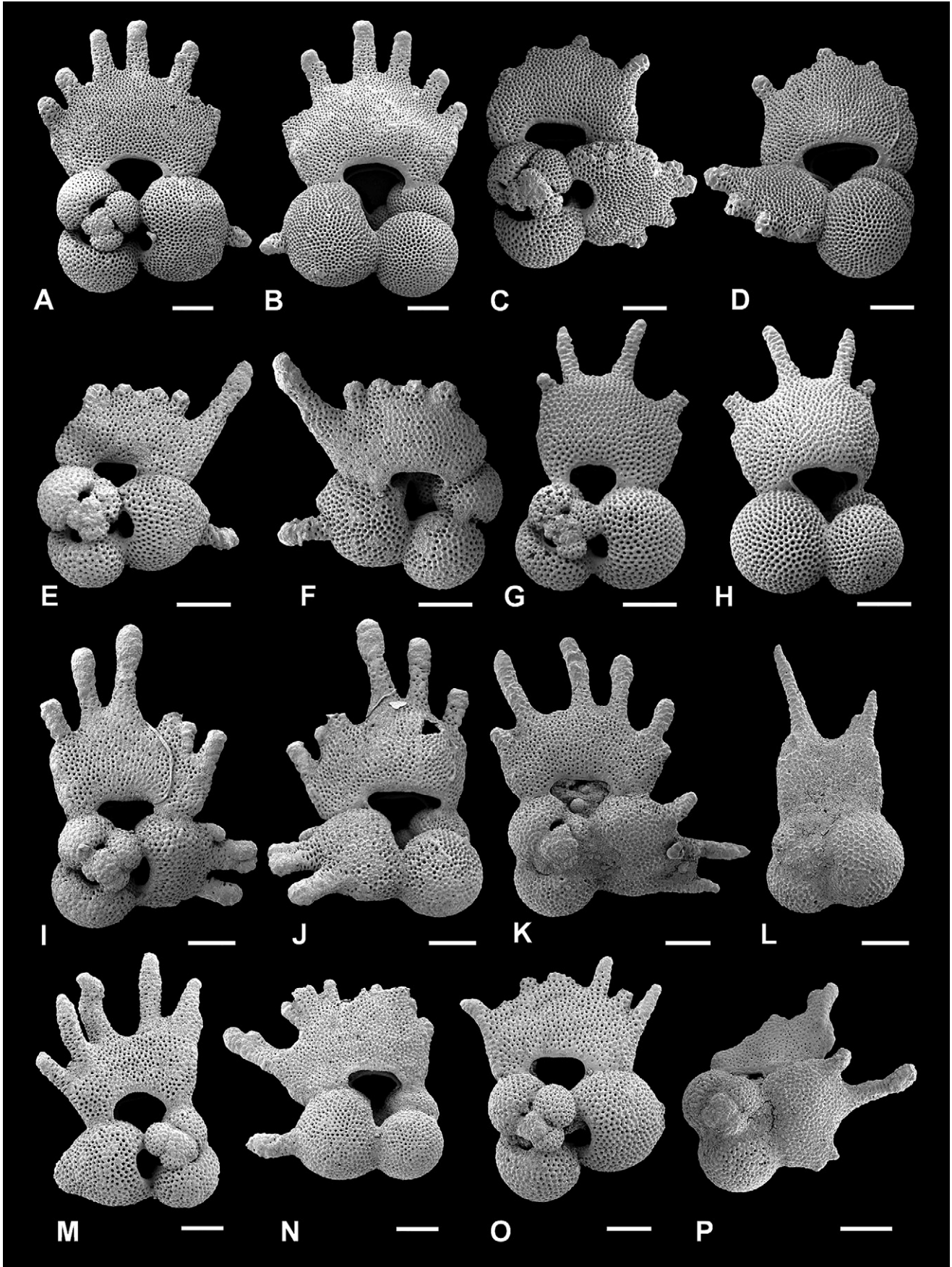
difficult-to-ascertain wall texture, Spezzaferri *et al.* (2015) placed it in the 'ruber group' (i.e. in *Globigerinoides*), rather than in new genus *Trilobatus*, where the rest of the *sacculifer* plexus (*T. trilobus*, *T. immaturus* and *T. sacculifer*) morphospecies were re-assigned. Placing the *quadrilobatus* lectotype in *Globigerinoides* rather than *Trilobatus* effected a radical change to the species concept because *quadrilobatus* had been consistently associated with the *T. sacculifer* plexus in most works since Banner & Blow (1960). A key problem is that the lectotype specimen of Papp & Schmid (1985) does not adequately exemplify the morphospecies concept of *quadrilobatus* used by most authors (i.e. the concept of Banner and Blow [1960, 1965] and Kennett & Srinivasan [1983]). Spezzaferri *et al.* (2015) stated that the lectotype does not have a *sacculifer*-type wall texture, yet this is considered one of the diagnostic characters for the whole *T. sacculifer* plexus (e.g. Banner & Blow 1960, 1965; Kennett & Srinivasan 1983). The illustrated lectotype in Papp & Schmid (1985) is not exceptionally preserved and the wall texture is somewhat ambiguous. It appears from the SEM reproduction in Figure 17 to have variable wall texture, and in a re-examination of the specimen, evidence of a *sacculifer*-type texture has been identified in *quadrilobatus* (Spezzaferri *et al.* 2018), thus re-aligning *quadrilobatus* with the *T. sacculifer* plexus. It is of note that other specimens with a *quadrilobatus* morphology clearly show a markedly cancellate, *sacculifer*-type texture (e.g. Stewart *et al.* 2004, pl. 1, fig. E [exceptionally preserved Tanzanian specimen]; Rögl 2012, pl. 3, fig. 6).

An additional minor factor to consider is that the generally larger size of *T. sacculifer* and *T. quadrilobatus* compared to *T. immaturus* and *T. trilobus* means that the *T. quadrilobatus* and *T. sacculifer* wall textures may appear less coarsely cancellate than those of *T. immaturus* and *T. trilobus*. We provide further evidence for a cancellate, *sacculifer*-type wall texture for *T. quadrilobatus* (Figs 7N, 8B), confirming its place within *Trilobatus*.

It appears that the lectotype specimen selected by Papp & Schmid (1985) may not have been a 'typical' *quadrilobatus* morphotype based on the widely used concept from Kennett & Srinivasan (1983). We agree with previous authors (Todd 1961; Bandy 1964a, b; Jenkins 1966; Fleisher 1974; Bolli & Saunders 1985) that the lectotype of Banner & Blow (1960) and

replacement lectotype of Papp & Schmid (1985) for *quadrilobatus* may not have been conspecific with d'Orbigny's (1846) original (and sparse) concept. However, it is also evident from our observations and those of other workers (e.g. Stewart *et al.* 2004; Rögl 2012) that a 3.5–4-chambered morphotype with a *sacculifer*-type wall texture exists. This morphotype is not consistent with the *T. trilobus*, *T. immaturus* or *T. sacculifer* descriptions and concepts, yet clearly intergrades with these other plexus members and is closely related. We consider this morphotype to be *T. quadrilobatus* (Figs 7L–N, 8A–K). We therefore follow Spezzaferri *et al.* (2018) and refer the *quadrilobatus* morphospecies (i.e. the concept of Kennett & Srinivasan [1983], and that of this study) to the new genus *Trilobatus*.

The SEM illustrations highlight the intergradation between both *T. immaturus*-*T. quadrilobatus* and *T. quadrilobatus*-*T. sacculifer*. For example, the *T. quadrilobatus* specimen in Figure 7L–N is intermediate between *T. immaturus* and *T. quadrilobatus sensu stricto*, as it has a relatively high chamber expansion rate in the final whorl compared to *T. quadrilobatus sensu stricto* (Fig. 8A–G). However, the prominence of the fourth chamber as well as the larger size is used to distinguish it from *T. immaturus*. As the forms intergrade, this delimitation is arbitrary, but through using a combination of chamber expansion rate, prominence of fourth chamber, size, and similarity to our suggested morphospecies exemplars (see Fig. 17) it is possible to delimit *T. immaturus* and *T. quadrilobatus*.

The transition between *T. quadrilobatus* and *T. sacculifer* is illustrated in Figure 8. The forms in Figure 8A–G are considered the morphospecies exemplars for *T. quadrilobatus*, whilst Figure 8H–P show progressive flattening and extension of the final chamber. The specimens in Figure 8H–K do not show significant flattening of the final chamber and are regarded as *T. quadrilobatus*, whereas Figure 8L–P are considered to have final chamber flattened enough to be *T. sacculifer* (and Fig. 8P is considered *T. sacculifer sensu stricto*). There is also a tendency towards higher arched primary apertures and the development of a bordering imperforate lip. Although some *T. quadrilobatus* specimens also possess an imperforate lip (e.g. Fig. 8F), it is infrequent. In contrast, almost all *T. sacculifer* specimens possess a prominent lip (it is a defining character), and even regularly possess a lip on the

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Figure 13. *Globigerinoidesella fistulosa* (Schubert, 1910). **A–O,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (**A, C, E, G, I, K, M–O,** spiral view, in **K** note infilled apertures; **B, D, F, H, J,** umbilical view); **L,** ODP Site 1115, Woodlark Basin, western Pacific; 10H/03/104–106 cm (spiral view; infilled apertures); **P,** ODP Site 1115, Woodlark Basin, western Pacific; 10H/04/127–129 cm (spiral view; infilled apertures). Scale bars = 200 μm.
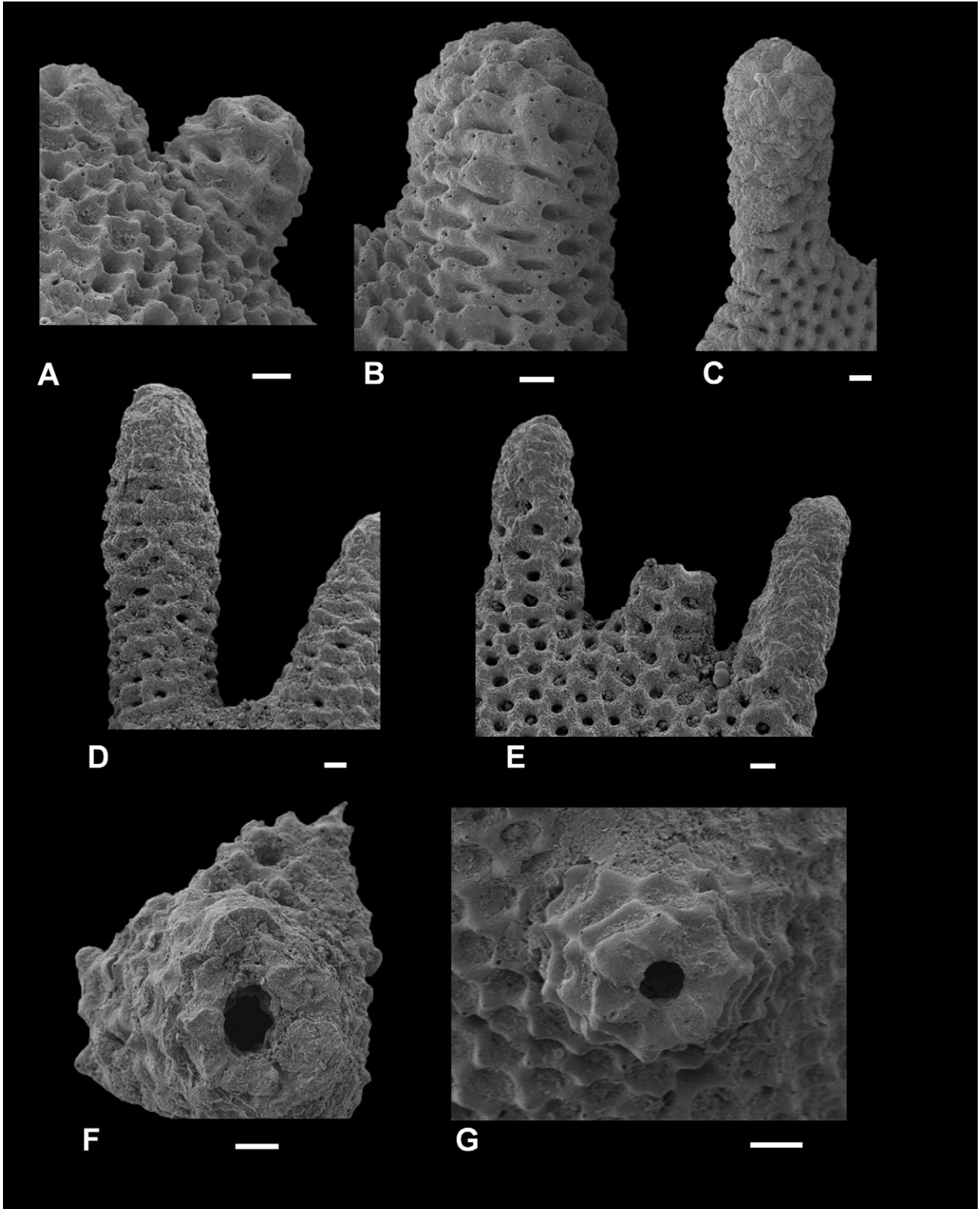
first supplementary aperture on the spiral side as well (Figs 9B, 10C, 11B, F).

Trilobatus sacculifer (Brady, 1877)
(Figs 8L–P, 9, 10, 11A–J, 12D, E, 14A, 16A–D, 17D, H)

1862 *Globigerina helicina* d'Orbigny; Carpenter, Parker & Jones: pl. 12, fig. 11 [note: not valid species name as 'Globigerina helicina' was used by d'Orbigny for a different species concept; see remarks].

1877 *Globigerina sacculifera* Brady: 535 [original description but not illustrated].

1884 *Globigerina sacculifera* Brady: 604, pl. 80, figs 11–17 and pl. 82, fig. 4 [numerous samples from the *Challenger* Expedition; illustrations reproduced in Jones (1994)].

1940 *Globigerinoides sacculifera* (Brady); Coryell & Rivero: 340, pl. 42, figs 24, 25, 32.

1954 *Globigerinoides sacculifera* (Brady); Cushman, Todd & Post: 369, pl. 91, fig. 7.

1957 *Globigerinoides triloba sacculifer* (Brady); Bolli: 113, pl. 25, figs 5a–6.

1959 *Globigerinoides triloba sacculifera* (Brady); Blow: 188, pl. 11, fig. 63a, b.

1964 *Globigerinoides triloba sacculifera* (Brady); LeRoy: F42, pl. 14, fig. 18.

1967 *Globigerinoides quadrilobatus sacculifer* (Brady); Closs: 340, pl. 1, fig. 21.

1970 *Globigerinoides trilobus sacculifer* (Brady); Bolli: 626, pl. 1, fig. 5.

1983 *Globigerinoides sacculifer* (Brady); Pujol & Duprat: 612, pl. 4, figs 4, 5.

1983 *Globigerinoides sacculifer* (Brady); Kennett & Srinivasan: 66, pl. 14, figs 4–6.

1994 *Globigerinoides sacculiferus* (Brady); Loeblich & Tappan: 107, pl. 205, figs 1–3, 7–9.

2006 *Globigerinoides sacculifer* (Brady); Williams, Schmidt, Wilkinson, Miller & Taylor: 154, pl. 1, figs 1–11.

Description. Type of wall: spinose, normal perforate, coarsely cancellate (often termed polygonal or honeycomb) 'sacculifer-type' wall texture. Test morphology: low trochospire, initially involute, later more evolute
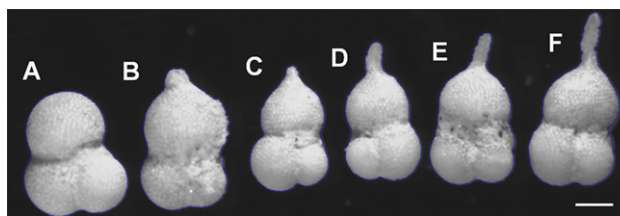

Figure 15. Protuberance development from *immaturus* and *quadrilobatus* morphotypes resulting in *fistulosa* morphotypes (light microscope images). **A,** *Trilobatus quadrilobatus* (d'Orbigny, 1846); **B, C,** *Trilobatus immaturus* (LeRoy, 1939); **D–F,** *Globigerinoidesella fistulosa* (Schubert, 1910). **A,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (umbilical view). **B, C,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (umbilical view). **D–F,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (umbilical view). Scale bar = 100 μm.

coiling, coiling direction random, three to four chambers in the final whorl, rapidly enlarging, adult chambers typically globose, near-spherical, until the last chamber, which is a flattened, sac-like shape exhibiting extreme variation in size and shape; sutures distinct, depressed, straight to slightly curved on both sides; umbilicus narrow to moderate; primary aperture umbilical, sometimes umbilical-extraumbilical, a low–medium arch, often broad and/or asymmetrical, with bordering imperforate lip; numerous supplementary apertures on spiral side, one per chamber, placed at the sutures of the preceding chamber and third-previous chamber.

Note: description is based on the original description and species concept of Brady (1877, p. 535), and also those of Brady (1884, p. 604), Banner & Blow (1960, p. 22) and Kennett & Srinivasan (1983, p. 65), but is here emended and extended.

Remarks. *Trilobatus sacculifer* is distinguished from *T. trilobus*, *T. immaturus* and *T. quadrilobatus* by the presence of a distinctive flattened, sac-like chamber which is often elongate or lobate; the other three morphospecies possess only globose, (near-)spherical chambers throughout all adult chambers. It also differs from these morphotypes by the presence of a distinct lip bordering the primary aperture. *Trilobatus sacculifer* differs from *G. fistulosa* by the lack of clear protuberances on any of

Figure 14. *Trilobatus sacculifer* and *Globigerinoidesella fistulosa* protuberance ultrastructure. **A,** *Trilobatus sacculifer* (Brady, 1877); **B–G,** *Globigerinoidesella fistulosa* (Schubert, 1910). **A,** ODP Site 1115, Woodlark Basin, western Pacific; 10H/04/127–129 cm (incipient protuberance with surface texture continuous from chamber). **B, C, F, G,** ODP Site 1115, Woodlark Basin, western Pacific; 10H/04/127–129 cm (**A,** numerous spine holes present, many pores obscured/distorted; **B,** surface texture change towards protuberance ends with blocky thick calcite obscuring pores; **F,** cross-sectional view of broken protuberance, showing hollow interior; **G,** cross-sectional view of broken protuberance, showing hollow interior); **D, E,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (**D,** surface texture change towards protuberance ends; blocky thick calcite obscuring pores; **E,** left protuberance marked by change in wall texture at protuberance end, right protuberance has all original surface texture obscured). Scale bars = 20 μm.

the final chambers, although the final chamber may be lobate.

Type locality. The type material for *T. sacculifer* is from a loose 'chalk' block, from New Ireland, Papua New Guinea (Brady 1877). The 'chalk' block was in fact a fragment of a carved figure, made by local inhabitants of the island and obtained by missionary Reverend G. Brown (Brown 1877; pp. 140–141; see also Liversidge 1877; Parker 1967). Rather than being

sourced from the mainland itself, the 'chalk' block was actually derived from seafloor deposits, where it had been extruded, apparently by earthquakes (Brown 1877) and/or volcanic activity (Brady 1884), onto the shore and then used by local inhabitants for a carved figure. The surrounding seafloor deposits off New Ireland indeed contain such 'chalk' material (e.g. Exon *et al.* 1986), and are likely the source of the type material for *T. sacculifer*.
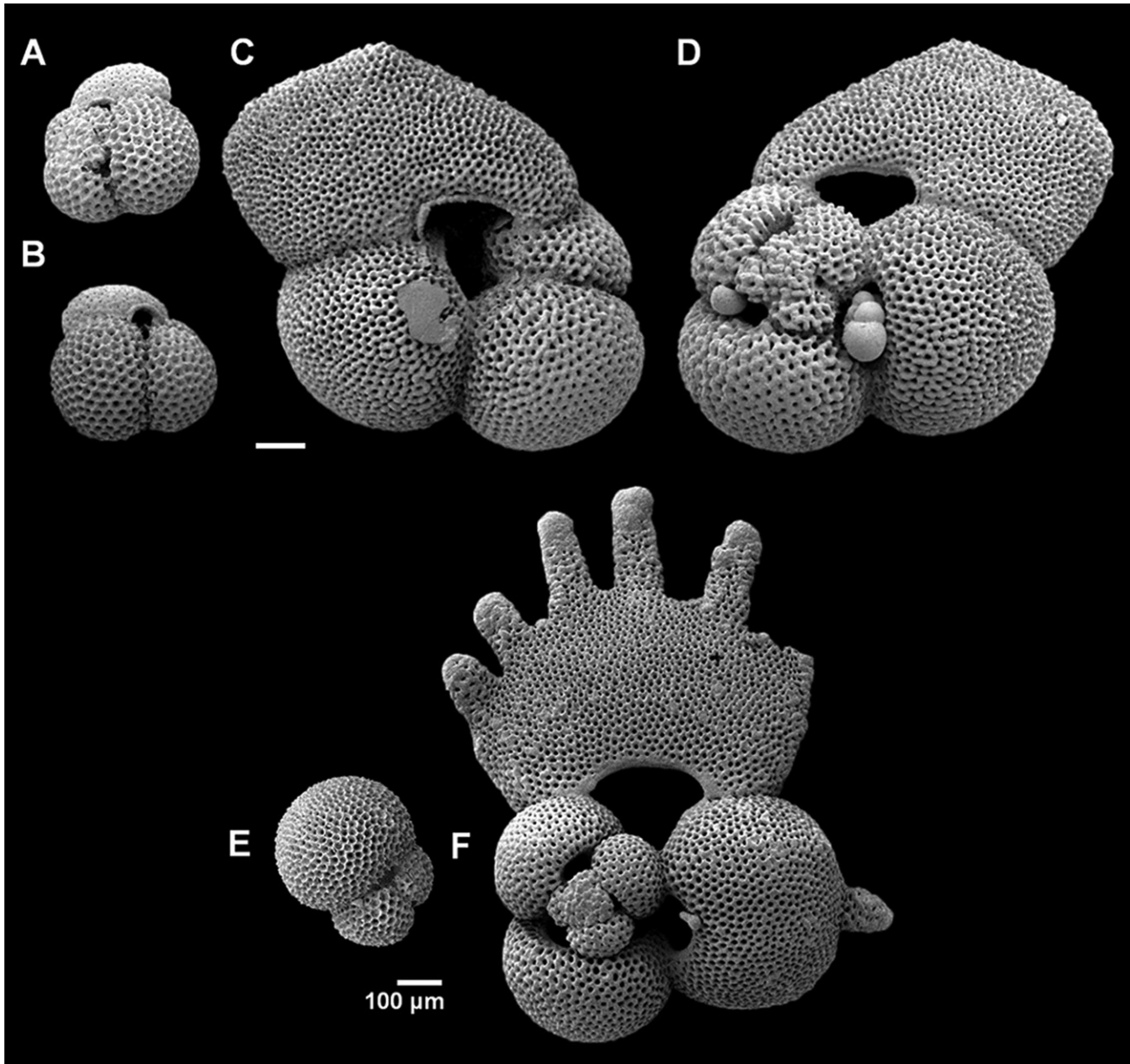
Figure 16. Size and ontogeny contrasts in the *Trilobatus sacculifer* plexus. **A–D,** *Trilobatus sacculifer* (Brady, 1877); **E,** *Trilobatus trilobus* (Reuss, 1850); **F,** *Globigerinoidesella fistulosa* (Schubert, 1910). **A–D,** GLOW-3, south-west Indian Ocean (**A, D,** spiral view; **B, C,** umbilical view, **B** is similar to *subsacculifer* morphospecies, see text). **E,** GLOW-3, south-west Indian Ocean (spiral view; earlier whorls obscured). **F,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (spiral view). Scale bars = 100 μm.

The *Trilobatus sacculifer* plexus – type specimens and generalized morphological intergradation sequence

T. trilobus
Neotype
Rögl (2012)

T. immaturus
Holotype
LeRoy (1939)

T. quadrilobatus
Lectotype
Papp and Schmid
(1985)

T. sacculifer
Lectotype
Banner and
Blow (1960)

A   B   C   D
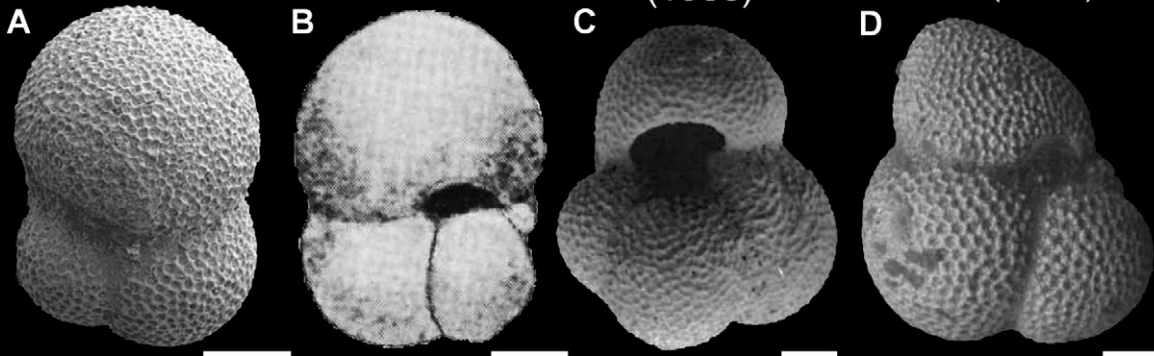
Decreasing chamber expansion rate and final chamber dominance →

Increase in size range and maximum size →

Development of sac-like chamber →

Development of imperforate apertural rim →

Looser chamber coiling (chambers less embracing) →

Extraumbilical-umbilical aperture   Umbilical aperture →

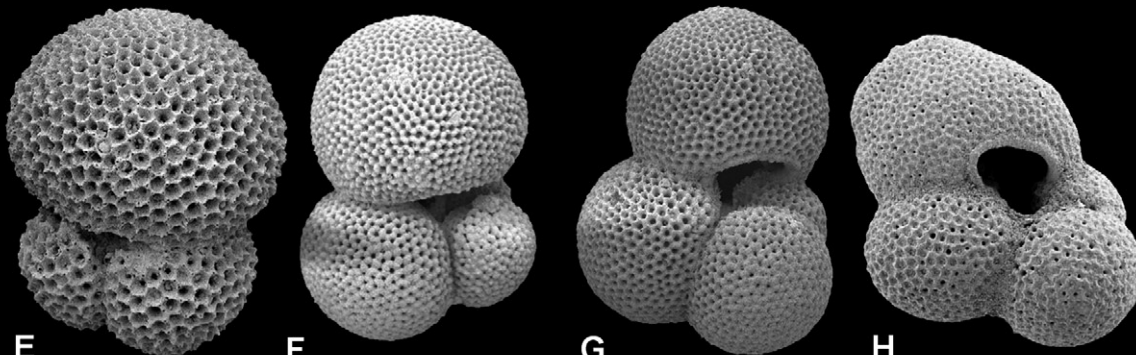Slit-like aperture   Low arched aperture   Moderate arched aperture
(increased variability) →

Morphospecies exemplars (selected in this study)

E   F   G   H

T. trilobus   *T. immaturus*   *T. quadrilobatus*   *T. sacculifer*

Taxonomic history. Brady (1877) observed that despite a specimen with a sac-like final chamber having been previously illustrated by Carpenter *et al.* (1862, pl. 12, fig. 11) under the name *Globigerina helicina* d'Orbigny, the *helicina* form had actually been described to represent a very different morphology (typically viewed as a morphological variant of *Globigerinoides ruber*). Hence, Brady (1877) erected the new species, *Globigerina sacculifera*, and provided a brief description. Though not illustrated by Brady (1877), a more detailed description and accompanying illustrations of ideotypic specimens were provided subsequently in Brady (1884, pl. 80, figs 11–17 and pl. 82. fig. 4; see also corresponding figures in Jones 1994). The subsequent illustrations were from North Pacific 'Challenger Expedition' material, rather than from the original type material of New Ireland, Papua New Guinea. However, the syntypic suite of specimens of Brady (1877) were subsequently examined by Banner & Blow (1960), including description and designation of a lectotype. Interestingly, the line drawings (pl. 4, fig. 1a, b) of their selected lectotype showed no lip or rim bordering the primary aperture, and their description specifically states its absence (Banner & Blow 1960, p. 22), despite this being a diagnostic character of the morphospecies (e.g. Kennett & Srinivasan 1983; this study). Williams *et al.* (2006) presented the first SEM images of Banner & Blow's lectotype (reproduced here in Fig. 17). Their SEM images of the lectotype and paralectotypes clearly resolve the matter, as each possesses a lip.

After Cushman (1927) erected *Globigerinoides*, *sacculifer* was accordingly placed in this genus by subsequent authors because it exhibits multiple supplementary apertures, although see various nomenclatural combinations in the synonymy list. Following Spezzaferri *et al.* (2015), *sacculifer* has been transferred to the new genus, *Trilobatus*, and we adhere to this designation.

The large morphological variation in the sac-like final chamber of *T. sacculifer* has been widely acknowledged, including kummerform (similar to the *T. subsacculifer* Cita, Premoli Silva & Rossi morphospecies), lobate, tapering and pointed morphologies. Todd (1964, p. 1073) recognized not only the biostratigraphical

potential of *G. fistulosa*, but also the lack of biostratigraphical value in forms with simply lobate chambers (i.e. 'incipient protuberances'). Sac-like chambers that are lobate and/or have incipient protuberances have little biostratigraphical value as they have approximately the same stratigraphical range as *T. sacculifer sensu stricto*, which extends from the lower Miocene to Recent (see also Belford 1988). However, we observe that forms with incipient protuberances do increase in abundance during the stratigraphical range of *G. fistulosa* (mid-Pliocene to early Pleistocene). Irregular final chambers and aberrant morphologies are common to all morphospecies of planktonic foraminifera (Mancin & Darling 2015), but are generally not treated any differently to 'normal' specimens in terms of taxonomy. For example, incipient protuberances also occur in unrelated morphospecies such as *Globigerina bulloides* (Mancin & Darling 2015, pl. 3, fig. 3) and *Globigerinoides ruber* (Hanagata & Nobuhara 2015, fig. 20.9), but are not considered distinct morphospecies.

Although there is morphological gradation between *T. quadrilobatus* and *T. sacculifer* (i.e. forms with final chambers of intermediate morphology between spherical and flattened sac-like chambers), all *T. sacculifer sensu stricto* possess a distinct lip on the primary aperture (see description) even if it is a kummerform specimen.

Wall cross-sections: although the spine holes and primary wall texture are often obscured by gametogenic calcite, cross-sectional views of the wall of *T. sacculifer* show relict spines present. The specimens in this study are relatively large planktonic foraminifera, particularly some *T. sacculifer* specimens and virtually all *Globigerinoidesella fistulosa*, which are regularly more than 1 mm in size. These large specimens produce walls which can be at least 40 μm thick (Fig. 9Q, R), even those with thin or no gametogenic calcite.

Notes on the 'subsacculifer' morphospecies. *Globigerinoides sacculifer subsacculifera* Cita, Premoli Silva & Rossi, 1965 was erected for specimens of similar gross morphology to *T. sacculifer*, but possessing a smaller test and less-developed sac-like final chamber. The last chamber is elongated, but not as pointed and

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Figure 17. *Trilobatus sacculifer* plexus, showing type specimens (**A–D**), morphological intergradation sequence and morphospecies exemplars (**E–H**). **A, E,** *Trilobatus trilobus* (Reuss, 1850); **B, F,** *Trilobatus immaturus* (LeRoy, 1939); **C, G,** *Trilobatus quadrilobatus* (d'Orbigny, 1846); **D, H,** *Trilobatus sacculifer* (Brady, 1877). **A,** salt mine Wieliczka, near Krakow, Poland (umbilical view; neotype image reproduced from Rögl 2012, pl. 1, fig. 1). **B,** Telisa Shales, Tapoeng Kiri area, Rokan-Tapanoeli, Central Sumatra, Indonesia (umbilical view; holotype image reproduced from LeRoy 1939, pl. 3, fig. 19). **C,** Nussdorf (= Nuβdorf), Rara, Vienna Basin, Austria (umbilical view; lectotype image reproduced from Papp & Schmid 1985, pl. 3, fig. 19). **D,** New Ireland, Papua New Guinea (umbilical view; lectotype of Banner & Blow 1960, image reproduced from Williams *et al.* 2006, pl. 1, fig. 1). **E,** GLOW-3, south-west Indian Ocean (umbilical view). **F,** ODP Site 871, Limalok Guyot, Marshall Islands, equatorial Pacific 3H/03/60–62 cm (umbilical view). **G,** ODP Site 871, Limalok Guyot, Marshall Islands, equatorial Pacific 3H/03/60–62 cm (umbilical view). **H,** ODP Site 1115, Woodlark Basin, western Pacific; 11H/04/25–27 cm (umbilical view). Scale bars = 100 μm.
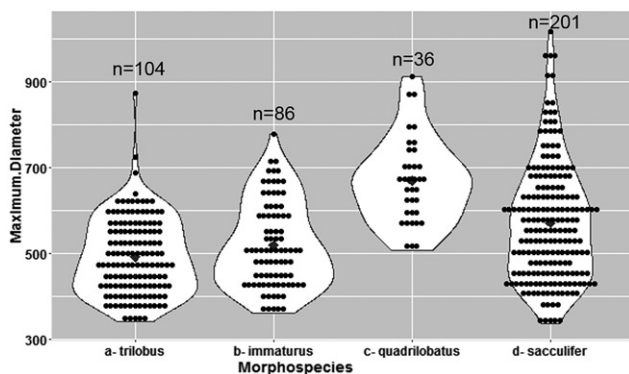
Figure 18. Distribution plot of test diameters (μm) in the *Trilobatus sacculifer* plexus from sample GLOW-3. Black dots each represent an individual specimen, grouped at a bin width of 20 μm per stacked row. Black diamond = mean size. White filled 'violin distributions' show variation in values.
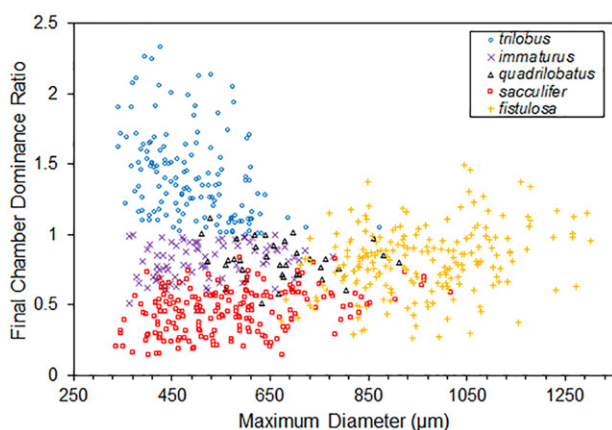

Figure 19. Surface area of the final chamber compared to the remaining test is expressed in the final chamber dominance ratio, which is plotted against maximum test diameter for *Trilobatus sacculifer* plexus morphospecies and *Globigerinoidesella fistulosa*. *Trilobatus trilobus* values are inherently ≥ 1 as this forms part of its morphospecies concept (see text).

protruding as in *T. sacculifer* (Cita *et al.* 1965). Spezzaferri *et al.* (2015) transferred *subsacculifer* to the new genus *Trilobatus*.

However, subsequent to the original description, *T. subsacculifer* has only been rarely recorded despite its apparent biostratigraphical utility, as the stratigraphical range was reported as early Miocene to early–middle Miocene by Spezzaferri (1994). Few succeeding observations of *T. subsacculifer* exist, but reported occurrences include Bizon & Bizon (1972, p. 242, figs 1–4), Rögl (1975), Poignant & Pujol (1978, p. 673, pl. 12, figs 11, 12), Fordham (1986), Spezzaferri (1994, pl. 13, fig. 3a–c), Coccioni *et al.* (1997), Odin *et al.* (1997), Spezzaferri *et al.* (2002) and Gennari *et al.* (2013).

Spezzaferri *et al.* (2002, p. 245) listed *T. subsacculifer* as a warm-water planktonic indicator. Their supposition receives support from the stable isotope analyses of *T. subsacculifer* by Bicchi *et al.* (2003), which show that *T. subsacculifer* probably had a similar depth ecology to modern *T. sacculifer*. Cita *et al.* (1965) suggested *T. subsacculifer* may represent the ancestral stock for *T. sacculifer*.

Here, we report examples similar in morphology to *T. subsacculifer*, but from the Pliocene–Pleistocene (i.e. considerably later than the highest occurrence reported by Spezzaferri 1994). Although *T. sacculifer* is far more common in the same samples, smaller forms akin to the *T. subsacculifer* morphology are present in each site investigated (ODP Sites 871, 926, 1115, and GLOW samples). The final chamber is generally diminutive (regularly kummerform), with a less-developed sac-like shape, and the specimens are smaller than typical *T. sacculifer*. We regard these specimens simply as phenotypic variants of *T. sacculifer*, forming an end member of the large intraspecific variability in this morphospecies. Even the small sac-like chambers have an imperforate lip that borders the aperture, which is a characteristic property of *T. sacculifer*. Thus *T. subsacculifer* may be a junior synonym of *T. sacculifer*, but further work from Miocene samples is required.

Genus ***Globigerinoidesella*** El-Naggar, 1971

Type species. *Globigerina fistulosa* Schubert, 1910.

Diagnosis. Type of wall: normal perforate, spinose, cancellate '*sacculifer*-type' wall texture, though the '*sacculifer*-type' wall texture is commonly obscured by secondary, 'gametogenic' calcite, heterogeneously distributed around the test, and particularly concentrated on the distal ends of protuberances. Test morphology: trochospiral, typically four chambers in the final whorl. Adult chambers increasing rapidly in size in the final whorl, initially globular and inflated, with final chambers becoming broad and flattened, possessing one or multiple digitate protuberances on individual chambers; sutures distinct, depressed, straight to slightly curved on both sides; open umbilicus, moderate to large; primary aperture typically umbilical, a broad, low to moderate arch with bordering lip or imperforate band; multiple supplementary apertures on spiral side, four to five visible, one per chamber, situated centrally at the sutures of the previous and third-previous chambers.

Note: diagnosis derives from the original genus concept of El-Naggar (1971), and also that of Banner (1982), Loeblich & Tappan (1987) and Spezzaferri *et al.* (2015, table 2).

Remarks. *Globigerinoidesella* El-Naggar, 1971 is distinguished from its ancestral genus *Trilobatus* Spezzaferri *et al.*, 2015 and also *Globigerinoides* Cushman, 1927 by the development of one to numerous elongate ('finger-like') protuberances on the final one to five chambers. The test size is also generally greater than in *Trilobatus* or *Globigerinoides*. Other digitate genera differ in generally possessing only one extension per chamber or simply displaying whole-chamber elongation (without distinct protuberances).

Taxonomic history. El-Naggar (1971) proposed a revised classification for the superfamily Globigerinacea, in which radially elongated tests and/or chambers (i.e. 'digitate' forms) were considered a generic-level distinguishing character. Whilst other unrelated genera have been proposed and defined by being digitate, and thus contain exclusively digitate morphospecies, the genus *Globigerinoides* Cushman, 1927 traditionally encompassed both non-digitate morphospecies and the digitate *Globigerinoides fistulosus* (Schubert, 1910). Therefore, El-Naggar (1971) proposed the new genus *Globigerinoidesella* to separate *fistulosus* from the rest of the non-digitate *Globigerinoides* morphospecies. El-Naggar (1971) considered the new genus to be monospecific, containing solely *G. fistulosa* (Schubert, 1910).

Loeblich & Tappan (1994) recognized two further species of *Globigerinoidesella*. They transferred Belford's (1962) *Globigerinoides quadrilobatus hystricosus* to *Globigerinoidesella* (i.e. *Globigerinoidesella hystricosa*) as a "phylogenetically primitive" form of the more developed *G. fistulosa*. Their *G. hystricosa* is intermediate in morphology between *G. fistulosa sensu stricto* and *T. sacculifer*. They also named a new species, *Globigerinoidesella bollii* Loeblich & Tappan, 1994, based on the *G. trilobus* 'A' specimens of Bolli (1970) and an additional specimen from Tappan & Loeblich (1982). Their *G. bollii* form differed from *G. hystricosa* and *G. fistulosa* in possessing protuberances that projected in more than one plane (i.e. protruding in different directions). It was also an unfortunate species name selection, as a separate morphospecies had already been described as *Globigerinoides bollii* by Blow (1959).

Despite these three forms being proposed as species of *Globigerinoidesella*, El-Naggar's (1971) genus concept was not adhered to or accepted by many workers, though notable exceptions include Loeblich & Tappan (1987, 1994) and Hanagata & Nobuhara (2015). Essentially, subsequent publications did not accept *Globigerinoidesella*, continuing to refer to *fistulosa* as a species of *Globigerinoides* (i.e. *Globigerinoides fistulosus*). Most workers have also not accepted *G. bollii* and *G. hystricosa* as valid morphospecies either; specimens

of equivalent morphology to Loeblich & Tappan's *hystricosa* and *bollii* concepts have generally been referred to as *Globigerinoides fistulosus*.

Spezzaferri *et al.* (2015) recently re-introduced *Globigerinoidesella* following El-Naggar's (1971) original concept and considered *G. fistulosa* the sole species. In this study, *Globigerinoidesella* is also recognized as a distinct genus following El-Naggar (1971) and Spezzaferri *et al.* (2015). It is here regarded as monospecific, as *Globigerinoidesella bollii* and *Globigerinoidesella hystricosa* are considered synonymous with *G. fistulosa*. Therefore, *G. fistulosa* is the type and only species.

Stratigraphical range. Middle Pliocene to early Pleistocene (Zone PL3 [Atlantic]/PL5 [Pacific] to Zone PT1) (Wade *et al.* 2011).

Globigerinoidesella fistulosa (Schubert, 1910)
(Figs 11K–P, 12A–C, F–L, 13, 14B–G, 15D–F, 16F)

1910 *Globigerina fistulosa* Schubert: 324, text-fig. 2.
1911 *Globigerina fistulosa* Schubert; Schubert: 100, text-fig. 13a–c.
1933 *Globigerinoides sacculifera* var. *fistulosa* (Schubert, 1910); Cushman: [pages not numbered], pl. 34, fig. 6a–c [locality not given].
1954 *Globigerinoides sacculifera* var. *fistulosa* (Schubert, 1910); Cushman, Todd & Post: 369, pl. 91, fig. 13.
1954 *Globigerinoides sacculifera* var. *fistulosa* (Schubert, 1910); Hamilton & Rex: 792, pl. 254, fig. 14.
1962 *Globigerinoides quadrilobatus fistulosus* (Schubert, 1910); Belford: 16, pl. 4, figs 7–10.
1962 *Globigerinoides quadrilobatus hystricosus* Belford: 17, pl. 4, figs 11–14.
1964 *Globigerinoides sacculifer fistulosa* (Schubert, 1910); Todd: 1084, pl. 290, fig. 6.
1965 *Globigerinoides sacculifer fistulosa* (Schubert, 1910); Todd: 64, pl. 26, fig. 3a–c.
1966 *Globigerinoides quadrilobatus fistulosus* (Schubert, 1910); McTavish: 35, pl. 7, figs 14, 17, 18.
1967 *Globigerinoides fistulosus* (Schubert, 1910); Parker: 154, pl. 21, figs 3, 5, 6, text-fig. 4a–d.
1970 *Globigerinoides trilobus fistulosus* (Schubert, 1910); Bolli: 579, pl. 1, figs 8–11.
1970 *Globigerinoides trilobus* 'A' (Reuss, 1850); Bolli: 579, pl. 1, figs 12–17.
1972 *Globigerinoides fistulosus* (Schubert, 1910); Jenkins & Orr (part): 1092, pl. 13, figs 1–4 [not pl. 13, figs 5–9 = *T. sacculifer*].
1972 *Globigerinoides fistulosus* (Schubert, 1910); Lamb & Beard (part): 48, pl. 31, figs 4, 7 [not pl. 31, fig. 8 = *T. sacculifer*].

1973 *Globigerinoides fistulosus* (Schubert, 1910); Krasheninnikov & Hoskins: 130, pl. 13, figs 10–12.

1974 *Globigerinoides fistulosus* (Schubert, 1910); Boltovskoy: 704, pl. 5, fig. 16.

1978 *Globigerinoides fistulosus* (Schubert, 1910); Krasheninnikov & Pflaumann: 625, pl. 4, figs 7–9.

1979 *Globigerinoides fistulosus* (Schubert, 1910); Takayanagi, Takayama, Sakai, Oda, & Kato: 78, pl. 1, figs 1, 2.

1981 *Globigerinoides fistulosus* (Schubert, 1910); Saito, Thompson, & Breger: 68–69, pl. 18, figs 1–3.

1983 *Globigerinoides fistulosus* (Schubert, 1910); Kennett & Srinivasan: 67–68, pl. 14, figs 7–9.

1983 *Globigerinoides quadrilobatus fistulosus* (Schubert, 1910); Moullade: 526, pl. 1, figs 12, 13.

1985 *Globigerinoides trilobus fistulosus* (Schubert, 1910); Bolli & Saunders: 197, text-figs 5–11.

1985 *Globigerinoides trilobus* 'A' (Reuss, 1850); Bolli & Saunders: 197, text-figs 22.1–22.3 [note: figures are reproductions of pl. 1, figs 12–14 from Bolli 1970 (see above)].

1985 *Globigerinoides fistulosus* (Schubert, 1910); Ujiié: 110, pl. 5, fig. 1.

1986 *Orbulina quadrilobata* (d'Orbigny, 1846); Fordham: 102, pl. 11, fig. 19.

1987 *Globigerinoidesella fistulosa* (Schubert, 1910); Loeblich & Tappan: 490, pl. 536, figs 7, 8 [note: figures are reproductions from Jenkins & Orr (1972); pl. 13, figs 2, 3].

1990 *Globigerinoides fistulosus* (Schubert, 1910); Vincent & Tourmarkine (part): 800, pl. 2, figs 1, 2 [note: not pl. 2, fig. 3 = *T. sacculifer*].

1991 *Globigerinoides quadrilobatus fistulosus* (Schubert, 1910): Chaproniere: 212, pl. 3, figs 1–3.

1993 *Globigerinoides fistulosus* (Schubert, 1910); Chaisson & Leckie: 158, pl. 2, fig. 4.

1994 *Globigerinoides quadrilobatus fistulosus* (Schubert, 1910); Chaproniere & Nishi: 224, pl. 4, figs 25–27.

1994 *Globigerinoidesella bollii* Loeblich & Tappan: 107, pl. 207, figs 4–6.

1994 *Globigerinoides fistulosus* (Schubert, 1910); Perembo (part): pl. 4, fig. 6 [note: not pl. 4, fig. 5 = *T. sacculifer*].

1995 *Globigerinoides fistulosus* (Schubert, 1910); Pearson: 59, pl. 5, fig. 7.

2007 *Globigerinoides fistulosus* (Schubert, 1910); Dowsett & Robinson: 118, pl. 2, fig. 3.

2013 *Globigerinoides fistulosus* (Schubert, 1910); Hayashi, Idemitsu, Wade, Idehara, Kimoto, Nishi, & Matsui: 98, fig. 6.4a–6.4b.

Description. Type of wall: normal perforate, spinose, cancellate 'sacculifer-type' wall texture. However, note the 'sacculifer-type' wall texture is commonly obscured by a heterogeneous secondary, 'gametogenic' calcite, particularly on the distal ends of protuberances. Test morphology: test size large (typically > 0.5 mm), medium trochospire, becoming more highly trochospire in larger specimens, initially involute but coiling later becomes evolute and expansive to accommodate large final chambers; typically four chambers in the final whorl (may be three and a half or rarely four and a half); early chambers globular, inflated, but last chamber or multiple chambers in the final whorl usually become broad and flattened, extended radially and/or tangentially, with one to numerous elongate protuberances of variable size extending outward from test, generally in one plane, forming an extremely lobulate profile; sutures distinct, depressed, straight to slightly curved on both sides; open umbilicus, moderate to large; primary aperture umbilical, may be umbilical-extraumbilical, a broad, low to moderate arch, arch shape often flattened and asymmetrical, with bordering lip or imperforate band; numerous supplementary apertures on spiral side, usually four or five visible, one per chamber, placed at the sutures of the previous chamber and third-previous chamber, the largest of which may also exhibit a lip or imperforate band, smallest supplementary apertures often obscured by infilling and/or secondary calcification.

Note: description derives from the original description and species concept of Schubert (1910, p. 324) and also from Schubert (1911, pp. 100–101), Saito *et al*. (1981, p. 68) and Kennett & Srinivasan (1983, p. 68), but is here emended.

Remarks. *Globigerinoidesella fistulosa* is distinguished from the ancestral *Trilobatus sacculifer* plexus (*T. sacculifer*, *T. quadrilobatus*, *T. immaturus* and *T. trilobus*) by the presence of one or more elongate protuberances on the final chamber or chambers and its generally larger test size. It is differentiated from other digitate species by its strictly *sacculifer*-type wall texture and by usually possessing numerous protuberances on individual chambers, rather than just one protuberance per chamber or an elongated chamber.

Type locality. First described from a *Globigerina* 'Marl' located at Siminis on Djaul Island, just off New Ireland, Papua New Guinea.

Taxonomic history. Schubert (1910, p. 324) named *Globigerina fistulosa*, commenting on the elongate protuberances as the characteristic feature. Indeed, the derivation of the species name *fistulosa* is from the Latin 'fistula' denoting a hollow tube or pipe, where 'fistulosa' is to bear numerous *fistula*. The new species was named within a text section devoted to *Globigerina sacculifera* Brady, 1877 (= *Trilobatus sacculifer*), and Schubert (1910) probably thought the two morphotypes

to be closely related. He illustrated (Schubert 1910, text-fig. 2) the spiral side of a single *G. fistulosa* specimen, which exhibits distinct protuberances on the final two chambers. In a subsequent publication, Schubert (1911, pp. 100–101, fig. 13) provided further description and illustrations of three other *G. fistulosa* specimens, also from the New Ireland area of Papua New Guinea. Though it appears no holotype or suite of type specimens was ever designated or deposited for the new species.

After Cushman (1927, p. 87) erected the genus, *Globigerinoides*, to encompass forms with supplementary apertures on the spiral side, subsequent workers accordingly placed *fistulosa* into *Globigerinoides*, often as a subspecies of *sacculifer*, *trilobus* or *quadrilobatus* (see synonymy list). El-Naggar (1971) considered the digitate protuberances to be a genus-level character, thus erecting *Globigerinoidesella* as a new genus, distinct from *Globigerinoides* (see above for discussion of *Globigerinoidesella*).

Belford (1962, pl. 4, figs 7–10) documented *Globigerinoides quadrilobatus fistulosus* from Papua New Guinea, but also named a new subspecies, *Globigerinoides quadrilobatus hystricosus* (pl. 4, figs 11–14), which also exhibits protuberances. Most authors place *hystricosus* in synonymy with *fistulosa*, as is the case in the present work, but several authors have erroneously used the name 'hystricosus' to represent intermediate forms with incipient protuberances (i.e. a transitional morphotype with intermediate morphology between *sacculifer* and *fistulosa*; e.g. Saito *et al.* 1981; Hemleben *et al.* 1987; Loeblich & Tappan 1994). However, Belford's (1962) original type figures clearly exhibit large protuberances, rather than a transitional specimen. In fact, Belford (1962) named *hystricosus* as a new subspecies to account for specimens where the protuberances develop from globular, inflated chambers, rather than from the flattened, sac-like chambers of *T. sacculifer*. This observation led Belford (1962) to infer two distinct lineages, whereby protuberances developed from *T. sacculifer* and *T. immaturus* independently. A sac-like chamber is clearly not a prerequisite for protuberance development; illustrative examples exist in Bolli & Saunders (1985, text-figs 22.5–22.7), Perembo (1994, pl. 4, fig. 6) and this study (Fig. 15A–E). However, these specimens are generally smaller than *G. fistulosa sensu stricto*; it is likely that the protuberances simply developed earlier in ontogeny and no sac-like chamber was ever developed. Even in *G. fistulosa sensu stricto* specimens, protuberances develop from both globular chambers and sac-like chambers (see Fig. 13). No evidence is found in this work for two independent lineages. Rather, the observation that protuberance

development occurs in more than one member of the *T. sacculifer* plexus, not just *T. sacculifer sensu stricto*, is possibly the first substantial fossil evidence to support that they are the same biological species. This corroborates with the culturing (e.g. Hemleben *et al.* 1987) and molecular genetic (André *et al.* 2013) evidence which suggests that all members of the *T. sacculifer* plexus are the same (biological) species.

Loeblich & Tappan (1994) named a new species, *Globigerinoidesella bollii*, for morphotypes which form protuberances extending in more than one plane, based on specimens of *Globigerinoides trilobus* 'A' from Bolli (1970) and Bolli & Saunders (1985). *Globigerinoidesella bollii* is also here considered synonymous with *G. fistulosa*, and has not been documented in publications after Loeblich & Tappan (1994). Although *G. fistulosa* does exhibit wide morphological variability, there is little stratigraphical value in delimiting *G. fistulosa* into multiple morphospecies. *Globigerinoidesella* is therefore regarded as monospecific, in accordance with El-Naggar (1971) and Spezzaferri *et al.* (2015).

Protuberance development. *Globigerinoidesella fistulosa sensu stricto* is a very distinctive taxon, possessing broad, flattened final chambers and finger-like protuberances. These features generally make identification of this species straightforward. However, intermediate forms are present throughout the entire range of *G. fistulosa* (mid-Pliocene to Pleistocene). In fact, intermediate forms with incipient protuberances occur in cultured specimens and are regularly present in Pleistocene to Recent assemblages (see Fig. 10), although they are much rarer than during the stratigraphical range of *G. fistulosa*. This observation forms the basis of the delimitation between *G. fistulosa* and *T. sacculifer* in this work. Samples from the GLOW Expedition (Kroon & Scientific Participants 2010) are used to determine the maximum protuberance development in Recent *T. sacculifer* plexus populations as a tool for delimiting the threshold between morphospecies. Since the last occurrence of *G. fistulosa* is in the early Pleistocene (Zone PT1), protuberance development should not occur in Recent specimens. Figure 10 highlights examples of protuberance development in specimens from the GLOW-3 sample and also from previous culturing studies (Bé et al. 1982; Brummer *et al.* 1987; Hemleben *et al.* 1987). These specimens are not considered *G. fistulosa*, but rather extreme phenotypes of *T. sacculifer*. Therefore, analogous specimens from the Pliocene–Pleistocene should not be considered *G. fistulosa* or else the stratigraphical range would effectively be extended to Recent and the biostratigraphical utility lost.

Protuberance development is also associated with thick 'crust' development on the distal ends of protuberances, which obscures the primary wall texture (Fig. 14). In many cases the spine holes and pores are completely obscured (e.g. Fig. 14C). However, spine holes were observed on some protuberances (e.g. Fig. 14B). These are the first spine holes discovered on *G. fistulosa* protuberances, which demonstrate that protuberances were spinose during life. This would have increased the effective size and surface area of the organism and may have enabled larger or more successful prey capture.

As described in the systematic taxonomy, protuberance development can occur on morphotypes that would otherwise be assigned to *T. immaturus* or *T. quadrilobatus*. This is illustrated in Figure 15, where single protuberances have developed from spherical final chambers, rather than from sac-like final chambers. Figure 15A and B, C are considered *T. quadrilobatus* and *T. immaturus*, respectively, but once protuberance development increases (Fig. 15D–F), the specimens are regarded as *Globigerinoidesella fistulosa*. Note that these specimens are all from the same sample at Site 1115, and do not indicate an evolutionary bioseries, but rather illustrate the degree of protuberance development that can occur from spherical final chambers. Whilst most protuberance development occurs on sac-like final chambers, this is not a prerequisite, as highlighted by specimens in Figure 15.

Size, shape and ontogenetic variation

Two *T. sacculifer* specimens from the same sample are shown at the same scale to illustrate the dramatic size variability in the morphospecies (Fig. 16A–D). Both specimens were assigned to *T. sacculifer* based on a flattened sac-like chamber and the development of an imperforate apertural rim, but show a stark contrast in size. However, due to the ontogenetic growth pattern exhibited in this group, this only equates to approximately three additional chambers on the larger specimen. The ontogenetic difference is also exemplified in Figure 16, which shows a specimen of *T. trilobus* and *G. fistulosa* at the same scale. Similarly, despite the dramatic size and shape difference, *G. fistulosa* appears to have passed through the same ontogenetic stages as *T. trilobus*, and subsequently added three further chambers.

In the GLOW-3 sample, the biometric results show that each morphospecies of the *T. sacculifer* plexus has a large size range (Fig. 18). Whilst *T. sacculifer* exhibits the largest specimens, it also displays the most variation, as sac-like chamber development occurs on all tests of size $> 350\,\mu$m. *Trilobatus quadrilobatus* records the largest average size, and no *T. quadrilobatus* specimens are less than $500\,\mu$m. However, note that it is also the least common morphospecies in this sample (36 out of 467; 7.7%). *Trilobatus trilobus* is generally the smallest morphospecies, although the distribution is similar to *T. immaturus*. This may be because many *T. immaturus* forms possess kummerform chambers (see Fig. 7), which impacts the final size significantly. Conversely, by definition, *T. trilobus* cannot be kummerform, as the dominant last chamber forms part of the morphospecies concept (see Systematic palaeontology). Kummerform final chambers are also common in *T. sacculifer* too, which further explains the large number of specimens with relatively small diameters.

Whilst maximum test diameters are comparable between *T. trilobus* and *T. immaturus*, specimens were assigned to *T. trilobus* if they had an FCDR of ≥ 1 (i.e.

Specimen Number	Circularity	Curvature
1	0.44	1.75
2	0.37	2.00
3	0.58	2.47
4	0.58	2.11

Figure 20. Example of circularity and curvature values for *Globigerinoidesella fistulosa* specimens. More lobate values are those in blue, those less lobate are red. Specimens 1 and 2 are more elongate and possess the lowest circularity values, but have a low perimeter length compared to test area and thus also generate low curvature values. Conversely, specimens 3 and 4 have high curvature values due to the protuberances increasing the perimeter length, but also relatively high circularity values because of the large area compared to test diameter (see Material and methods). Scale bar = $200\,\mu$m.
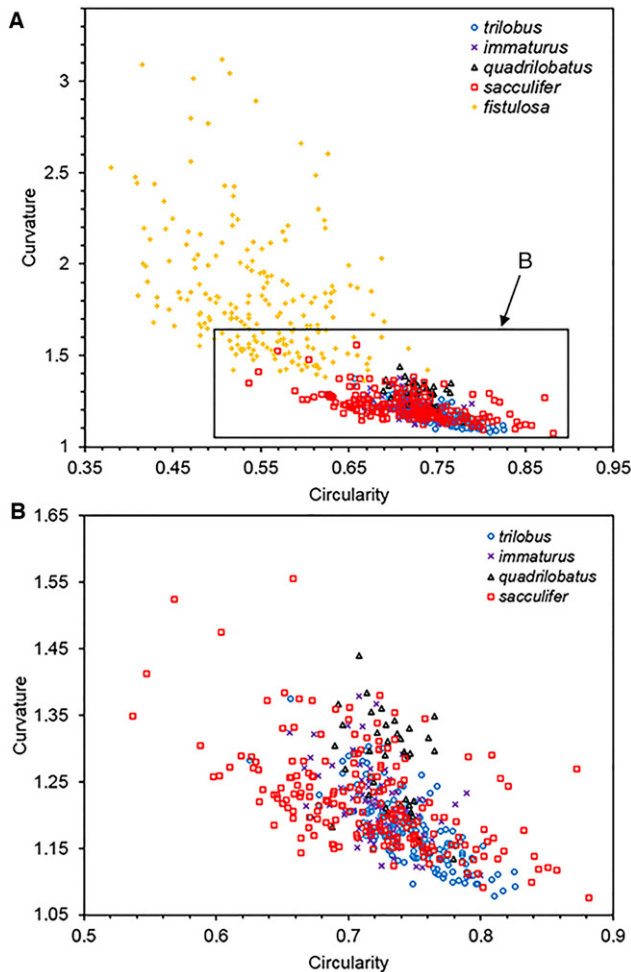
Figure 21. Lobateness of *Trilobatus sacculifer* plexus morphospecies and *Globigerinoidesella fistulosa* determined through a combination of circularity and curvature values; **A**, demonstrates the large variability, but consistently high lobateness values for *Globigerinoidesella fistulosa* compared to *T. sacculifer* plexus morphospecies (which have comparatively high circularity and low curvature). Although the *T. sacculifer* plexus morphospecies appear to form a tight cluster, the lower plot, **B**, demonstrates the variability in lobateness values (see text for discussion).

Figure 22. Exponential relationship between maximum test size and test surface area in morphospecies of the *Trilobatus sacculifer* plexus, and to a lesser extent in *Globigerinoidesella fistulosa*. The *T. sacculifer* plexus morphospecies all show comparable relationships, whereas data for *G. fistulosa* show more scatter.

if the final chamber area [μm²] was larger than the remaining test area [μm²]) (see Fig. 19). In some cases, the *T. trilobus* FCDR values are ≥ 2, indicating a final chamber that is at least double the area of the remaining chambers combined. Conversely, *T. immaturus* FDCR values are inherently less than 1 according to this morphospecies concept. *Trilobatus quadrilobatus* scores similar FCDR values to *T. immaturus*, but is distinguished by looser coiling and possessing more (3.5 to 4) chambers in the final whorl (see Systematic taxonomy). *Trilobatus quadrilobatus* is also generally larger than *T. immaturus*. Though overlap in FCDR values exists between *T. sacculifer* and other morphospecies, it
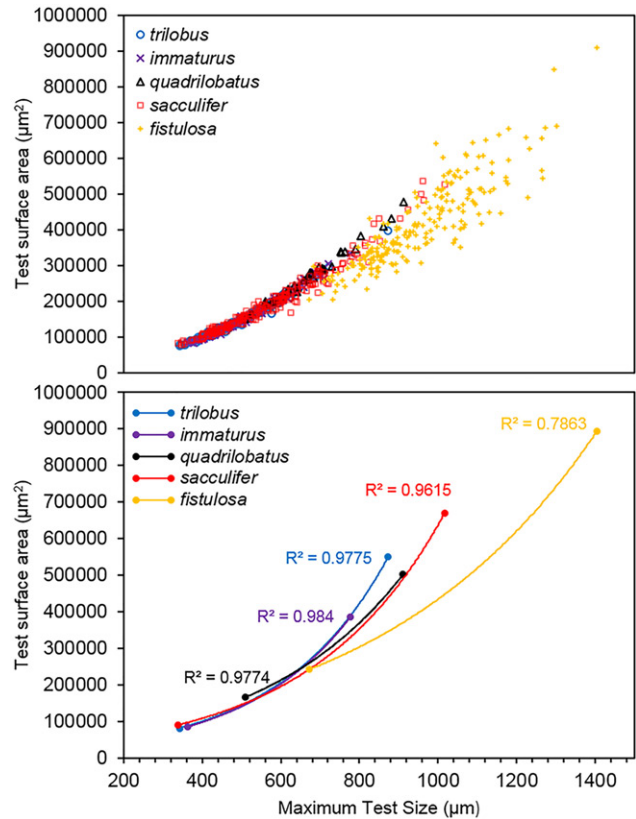
records the lowest FCDR values, independent of maximum test size. The final chamber is small relative to the rest of the test, and is often kummerform. *Globigerinoidesella fistulosa* have extremely variable FCDR values. Whilst most FCDR values are less than 1, some *G. fistulosa* specimens have dominant final chambers, and the chamber area is increased because of protuberance development.

Lobateness (circularity and curvature): final whorl chambers are most tightly embracing in *T. trilobus*, becoming more loosely coiled in *T. immaturus*, *T. quadrilobatus* and *T. sacculifer*, and thus the peripheral outlines become more lobate. The most extreme lobate outlines are those of *G. fistulosa*, because of the protuberance development on the final chambers. Two measures of lobateness were used in order to distinguish between morphospecies of the *T. sacculifer* plexus and *Globigerinoidesella fistulosa*. The primary reason for using two measures is exemplified in Figures 20 and 21, where combining circularity and curvature is shown to be good for morphospecies delimitation. Solely using

Table 1. Coiling directions of the *Trilobatus sacculifer* plexus morphospecies and *Globigerinoidesella fistulosa*. See text for site locations and age.

Coiling direction (% dextral) with 95% confidence intervals						
Morpho-species	*T. sacculifer* plexus	*trilobus*	*immaturus*	*quadrilobatus*	*sacculifer*	*fistulosa*
Average	39.0	43.8	37.2	30.6	37.8	25.7
Standard deviation	48.8	49.8	48.6	46.7	48.6	43.8
Sample size	467	144	86	36	201	222
Confidence coefficient	1.96	1.96	1.96	1.96	1.96	1.96
Margin of error	4.4	8.1	10.3	15.3	6.7	5.8
Upper bound	43.4	51.9	47.5	45.8	44.5	31.4
Lower bound	34.5	35.6	26.9	15.3	31.1	19.9

one measure is less useful: morphospecies values overlap (Fig. 20). Circularity is particularly sensitive to elongate foraminifera, whereas curvature is sensitive to foraminifera with large perimeters. Thus, the two values of lobateness were combined to account for the biases in each measure (Fig. 21). Although Figure 21 appears to show the highest lobateness variability in *Globigerinoidesella fistulosa*, these values actually have the least overlap with the other *T. sacculifer* plexus morphospecies and record the highest lobateness values. Conversely, *T. sacculifer* overlaps with all other *T. sacculifer* plexus morphospecies, in some specimens recording the highest circularity, but also having particularly high curvature in other specimens. This is due to the large variation present in the final sac-like chamber (see Figs 8–11), which affects the overall morphology because it can be thin and elongated, or less flattened and kummerform. Whilst the other morphospecies are more conservative, the sac-like final chamber is unpredictable in its morphology. *Trilobatus trilobus* is less variable and records consistently high circularity and low curvature values owing to its tightly coiled, compact test, but overlaps with *T. immaturus* and *T. sacculifer*. *Trilobatus quadrilobatus* generally records higher curvature values than *T. immaturus* and *T. immaturus*, because the looser coiling produces a higher perimeter length relative to surface area.

Maximum test diameter was also compared with test surface area (Fig. 22). In all of the *T. sacculifer* plexus morphospecies, there is a strong exponential relationship between test size and surface area in adult specimens. At smaller adult sizes, an increase in maximum test size from 300 to 500 μm only results in a marginal rise in test surface area, whereas at larger sizes, a similar 200 μm increase in maximum test size (e.g. from 600 to 800 μm) results in a more dramatic enhancement in surface area. The upper panel of Figure 22 shows the tight clustering and overlapping of each morphospecies of the *T. sacculifer* plexus. The lower panel exponential curves all exhibit extremely high R^2 values. *Globigerinoidesella fistulosa* somewhat departs from this strong exponential

trend, exhibiting considerably more variation in test area as maximum test size increases.

Coiling directions

Coiling directions were measured in 467 specimens from the *T. sacculifer* plexus and 222 specimens of *G. fistulosa* (Table 1). When grouped as a whole, the *T. sacculifer* plexus specimens show 39% dextral coiling, with a low margin of error due to the large sample size. The individual morphospecies averages are variable (note also the differing sample sizes), but all proportionately favour sinistral coiling. *Globigerinoidesella fistulosa* has only 25% dextral specimens, which is the lowest value of any of the morphospecies. However, the data for *G. fistulosa* were pooled from three closely spaced samples (in order to increase the sample size), rather than from one sample (GLOW-3) for the *sacculifer* plexus specimens. Ujiié (1968, p. 118) reported an average of 42% dextral forms for *T. sacculifer* in a modern population from the south-east Indian Ocean, which is comparable with the results presented here.

Conclusions

In this study, the original typological concepts of *T. sacculifer* plexus morphospecies, as exemplified by their respective type specimens (Fig. 17A–D), were evaluated using morphometric, biometric and SEM analyses of a population from the GLOW-3 sample (western Indian Ocean). The morphospecies intergrade with each other, best described by the morphological progression *T. trilobus*- *T. immaturus*- *T. quadrilobatus*- *T. sacculifer* (Fig. 17). This progression involves an increase in maximum size, decreasing chamber expansion rate and final chamber dominance ratio, looser chamber coiling, and changes in the position and morphology of the primary aperture. However, some *T. immaturus* also intergrade with *T. sacculifer* and sac-like chambers can also

develop from *T. trilobus*. This morphological information was used to define the morphospecies concepts in the systematic taxonomy, with relation to the original type specimens. Complementary to the type specimens, four specimens were selected to represent morphospecies exemplars for each of the four *T. sacculifer* plexus members (Fig. 17E–H).

A population-based approach was used to determine intra- and interspecific variability surrounding the type morphology in the four morphospecies of the *Trilobatus sacculifer* plexus (*T. trilobus*, *T. immaturus*, *T. quadrilobatus* and *T. sacculifer*) and in *Globigerinoidesella fistulosa*. Morphometrics, biometrics and SEM illustration of specimens from multiple ocean basins were collectively utilized to resolve taxonomic problems in these groups. Our analyses of *T. sacculifer* plexus and *G. fistulosa* populations have facilitated the basis for characterizing the morphological intergradation summarized in Figure 17, and defining the typological morphospecies concepts presented in the systematic taxonomic appraisal. Further work is ultimately required to determine the early phylogeny of this lineage, but the clear morphological intergradation between *T. sacculifer* plexus morphospecies and *G. fistulosa* demonstrates their close association.

Globigerinoidesella fistulosa sensu stricto is confined to the Pliocene–Pleistocene, but incipient protuberance development also occurs on modern specimens. We present the first evidence for spine holes in the protuberances of *G. fistulosa*, indicating an increased effective organism size. Although protuberance development typically initiates from *T. sacculifer*, leading to *G. fistulosa* through intergrading specimens, protuberances were also found to develop on specimens of *T. immaturus* and *T. quadrilobatus*. Equally, sac-like final chambers can develop from any of the *T. sacculifer* plexus morphospecies to become a *T. sacculifer*. These findings support the molecular genetic evidence indicating that morphospecies of the *T. sacculifer* plexus are the same biological species. However, we advocate using the four morphospecies concepts, here refined, to increase their palaeoecological and biostratigraphical value.

Acknowledgements

Disclosure statement

No potential conflict of interest was reported by the authors.

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Associate Editor: Stephen Stukins