Journal of Foraminiferal Research, v. 55, no. 3, p. 245–275, July 2025

SYSTEMATIC TAXONOMY OF *PULLENIATINA*

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ABSTRACT

***Pulleniatina* is a genus of non-spinose planktonic foraminifera that evolved in the late Miocene and survives in the modern ocean. It is biostratigraphically useful because its evolution tracks through a series of morphospecies that have different biochronological ranges, and for much of its history it has exhibited rapid reversals of its preferred direction of coiling. Six morphospecies are recognized: *P. finalis*, *P. obliquiloculata*, *P. praecursor*, *P. praespectabilis*, *P. primalis*, and *P. spectabilis*. Each of these is illustrated, described, and distinguished using Scanning Electron Micrographs (SEMs) of the type material and new light microscope and SEM images. Detailed synonymy lists are presented. The biostratigraphic ranges, geographic distributions, paleoecologies, and phylogenetic relationships of each morphospecies are reviewed.**

INTRODUCTION

In recent years it has become increasingly evident that a thorough taxonomic revision of Neogene and Quaternary planktonic foraminifera is a desirable community objective. The publication of the *Atlas of Oligocene Planktonic Foraminifera* (Wade et al., 2018) completed a trio of Paleogene atlases (after the Paleocene – Olsson et al., 1999, and Eocene – Pearson et al., 2006), and much recent progress has been made on Late Jurassic and Cretaceous systematics (reviewed in Petrizzo et al., 2024). This has left planktonic foraminifer workers in the paradoxical position that the older parts of the fossil record of the group are better known, or at least better systematized, than the Neogene and Quaternary, for which the last major syntheses date back to the 1980s (Saito et al., 1981; Kennett & Srinivasan, 1983; Bolli & Saunders, 1985). There has also been much recent progress in our understanding of modern planktonic foraminifera (reviewed in Brummer & Kučera, 2022) and especially their genetics (reviewed in Morard et al., 2024), which has implications for understanding past evolution. A Neogene and Quaternary Planktonic Foraminifera Working Group (NQPFWG) was established to coordinate new study under the aegis of the International Commission on Stratigraphy/International Union of Geological Sciences. The main aim of the Working Group is to establish a revised taxonomy, genus by genus, using a consistent framework and approach, eventually leading to a comprehensive review and synthesis. Because of the ambitious scale of this project, it was decided that taxonomic contributions should be published as stand-alone, peer-reviewed, and open-access papers as and when they become available. The developing taxonomy will then be communicated through online resources such as mikrotax.org (www.mikrotax.org/pforams), and the entire corpus will be revised and synthesized when the project is finally complete.

This paper is devoted primarily to the systematic taxonomy of the biostratigraphically and paleoceanographically important genus *Pulleniatina*. The approach adopted here is similar to that of previous taxonomic atlases. Our intention is to produce a workable and readily communicable taxonomic scheme based on a thorough revision of the type material and the history of previous work and opinions, combined with new observations. The basic unit of taxonomy is the Linnean ‘species’, expressed in standard binomial nomenclature and subject to revision and synonymy according to the rules of the International Code of Zoological Nomenclature (ICZN). These taxa should be distinguishable from other similar forms on the basis of their observed morphology, independent of biostratigraphic information. The taxonomy needs to be applicable to fossil and modern material, and the stratigraphic ranges of the various forms in reference sections worldwide should provide the basis of a workable biostratigraphy based on correlating local bottom (B) and top (T) occurrences.

Experience shows that the fossil record does not consist of neatly packaged and readily distinguishable species (say, consisting entirely of *Pulleniatina praecursor*) that suddenly change into others (say, *P. obliquiloculata*). Instead, shifting morphologies usually change slowly over time. A simple fixed ‘typological’ taxonomy cannot represent this ‘biological reality’. At any particular time-slice in the past, the species-level taxa delineated here may or may not correspond to groups of genetically related inter-breeding (or potentially inter-breeding) individuals that are separate from other such groups. Often it is the case that forms referable to one taxon fully intergrade with another through time. A given fossil population during such a transition may divide into forms that are closer to one holotype (e.g., *P. praecursor*) or another (e.g., *P. obliquiloculata*), and so the populations become artificially split. For this reason, we refer to the species-level taxa as ‘morphospecies’, and we use them without implying that they necessarily correspond to what a biologist would recognize as ‘biological’ species. This usage is consistent with previous taxonomic atlases such as the Eocene and Oligocene. Nevertheless, it is also possible to track evolutionary lineages as they evolve as intergrading populations through the various named stages, and the points where they diverge from one another in splitting (cladogenetic) events (e.g., Pearson & Ezard, 2014). Identifying phylogenetic divergences and true extinction events is, therefore, a separate aim from identifying the first and last occurrences of a partly arbitrary and historically contingent group of named morphospecies.

The present-day biodiversity is just another time slice in the ongoing evolution of *Pulleniatina*, but it is obviously of special interest to a wide group of marine biologists and ecologists who may not be equally concerned about fossil populations and taxa. It is also the only time slice for which we can observe the development and ecology of living organisms and determine their genetics. It so happens that biologists tend to recognize just one ‘biological species’, *P. obliquiloculata* (e.g., Brummer & Kučera, 2022), even though another of

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the widely recognized paleontological morphospecies, *P. finalis*, also extends to the modern. Despite the fact that these two morphospecies appear to fully intergrade as part of a single population, we do not subsume *P. finalis* into *P. obliquiloculata* because separating them is biostratigraphically useful, as *P. finalis* appeared much later in time than *P. obliquiloculata*. The two types of usage of species-level taxa are not contradictory provided one is clear about what sort of taxon is being discussed – a 'biological species' or a typological morphospecies, and we use *P. finalis* in the latter sense. Even so, appearances may be deceptive in this particular case. Recent research by Fabbrini et al. (in press), discussed below, indicates that the *P. finalis* morphospecies may have some biological reality, either as a closely related but genetically separate biospecies or a megalospheric asexually-produced variant. More research on modern populations is required to examine these possibilities.

Genetically, the biospecies *P. obliquiloculata* is unusually diverse in comparison with most other planktonic foraminifera, at least in terms of its ribosomal DNA (rDNA) gene. It has been suggested that it may consist of two or three 'cryptic species' that have different but overlapping environmental and geographic tolerances (Ujiié et al., 2012; André et al., 2014) as well as scores of distinguishable variants called 'molecular operation taxonomic units' (Morard et al., 2016, 2024). How long these entities may have existed in the past, and could persevere into the future, is currently an open question. It seems likely that evolution constantly generates cryptic diversity in the form of genetically isolated or semi-isolated strains that may variously thrive, diversify, and die out within the same broad environmental niche without causing lasting ecological speciation and long-term morphological divergence (cladogenesis). Pearson & Penny (2021) suggested that this mode of evolution may account for the periodic 'coiling reversals' that are observed in the fossil record of *Pulleniatina*, which may mark 'population sweeps' where one cryptic morphotype, which happens to have a particular coiling direction preference, replaces another. Although all modern *Pulleniatina* are dextral, some modern species have cryptic genotypes with different coiling direction preferences (for instance *Globorotalia truncatulinoides*; Ujiié et al., 2010). Cryptic diversity and population sweeps may be more characteristic of *Pulleniatina* evolution than other planktonic foraminifera, for reasons not yet understood.

Our current phase of research on *Pulleniatina* for the NQPFWG followed three separate strands, which have resulted in independent publications. The first of these was a review of the biostratigraphic occurrences of the various morphospecies using a common stratigraphic and biochronological framework. This was an involved task because the literature is quite large, and the taxonomy, biostratigraphic schemes, and timescales have evolved greatly over the last ~70 years. The results were published by Pearson et al. (2023) and are summarized below and discussed on a species-by-species basis in the Systematic Taxonomy.

The second strand of research involved a detailed reassessment of *Pulleniatina* test morphology using, in particular, micro-computed x-ray tomography (micro-CT) of selected representative specimens of all morphospecies and high-resolution study of broken tests using SEM. This investigation of internal morphology is important for understanding test construction and particularly how the adult morphology is generated from irregular 'streptospiral' coiling in some morphospecies. This work (Fabbrini et al., in press) feeds into the formal species descriptions presented below.

The third strand, reported here, was to conduct a thorough taxonomic review of the genus by studying and categorizing previous research and published images, as well as making new observations of our own. The taxonomy consists of six separate morphospecies, treated in alphabetical order below as *P. finalis*, *P. obliquiloculata*, *P. praecursor*, *P. praespectabilis*, *P. primalis*, and *P. spectabilis*. The new figured material is from seven sites including specimens from all oceans and a variety of stratigraphic levels (Table 1). Note that Neogene and Quaternary subseries (e.g., middle Miocene) are regarded in this work as informal units equivalent to the formal units recently ratified by the International Subcommission on Neogene Stratigraphy so as to avoid the confusing situation of having to switch between informal and formal units at the Paleogene/Neogene boundary.

(PALEO)ECOLOGY SYNTHESIS

Modern *Pulleniatina obliquiloculata* is an abundant tropical species (Kučera et al., 2005) that occurs in all the ocean basins, with peak concentrations in the West Pacific warm pool (WPWP). It is also seasonally abundant in warm western boundary currents, such as the Kuroshio Current and Gulf Stream, typically with an autumn peak outside its core area (Jonkers & Kučera, 2015). Sediment trap (e.g., Anand et al., 2003; Xu et al., 2005) and plankton net (e.g., Ravelo & Fairbanks, 1992; Watkins et al., 1996; Rippert et al., 2016; Rebotim et al., 2017; Yu et al., 2024) data indicate that it calcifies in a subsurface thermocline habitat that varies in depth regionally and with water column conditions. Its principal food source appears to be chrysophyte algae and diatoms (Anderson et al., 1979; Spindler et al., 1984). In this it differs from its closest living relative, *Neogloboquadrina dutertrei* (see discussion below), which occupies similar depth habitats but is thought to be omnivorous (Toue et al., 2022). Many areas of the oligotrophic oceans below 40° latitude host a permanent Deep Chlorophyll Maximum (DCM) between ~40 m and ~180 m depth (Cornec et al., 2021). This habitat seems to provide the food supply for *Pulleniatina* and matches well with its geographic and depth distribution. *Pulleniatina* does not have an obligate symbiotic relationship with photosynthetic algae in the way that many mixed-layer dwelling spinose species maintain large numbers of dinoflagellate symbionts around the cell (Takagi et al., 2019).

The subsurface habitat of modern *Pulleniatina* is reflected in its stable isotope ratios and trace element concentrations (e.g., Shackleton & Vincent, 1978; Ravelo & Fairbanks, 1992; Xu et al., 2008; Nathan & Leckie, 2009; Sadekov et al., 2009; Wejnert et al., 2010; Rippert et al., 2016; Dang et al., 2018; Stainbank et al., 2019). A number of studies have also reported data from fossil *Pulleniatina*. Keller (1985) found *Pulleniatina primalis* to have slightly less negative $\delta^{18}O$ values than *Trilobatus sacculifer* and suggested it lived in the shallow subsurface. Whitman & Berger (1992) measured *Pulleniatina* throughout its stratigraphic range at DSDP Site 526 in the

TABLE 1. Samples reviewed as part of this study with list of newly figured specimens.

Site	Sample	Estimated age (Ma)	Species	Figure
ODP Hole 873B, Wodejebato Guyot, tropical western Pacific Ocean, 11°53.796′N, 16°55.188′E	873B-3H-3, 10-12 cm	Pliocene Zone N19-N20/21, 4.40 Ma	*Pulleniatina spectabilis*	12.2, 12.7, 12.9a–b
	873B-3H-5, 110-112 cm	Pliocene Zone N19, 4.60 Ma	*Pulleniatina praespectabilis*	10.6, 10.7, 10.9a–b, 10.10, 10.11, 10.12, 10.13
			Pulleniatina primalis	11.8, 11.9a-b
	873B-3H-7, 30-32 cm	Pliocene Zone N18, 4.95 Ma	*Pulleniatina primalis*	11.4, 11.7
ODP Hole 925A, Ceara Rise, equatorial Atlantic Ocean, 4°12.249′N, 43°29.334′E	925A-1H-CC	Pleistocene Zone PT1b, 0.245 Ma	*Pulleniatina obliquiloculata*	8.9
IODP Hole U1482A, northwest Australian margin, tropical eastern Indian Ocean, 15°05.2382′S, 120°26.1049′E	U1482A-15H-CC	Pliocene Zone PL4, 3.36 Ma	*Pulleniatina praecursor*	9.4, 9.5a–c, 9.11, 9.12
	U1482A-22H-CC	Pliocene Zone PL1, 5.03 Ma	*Pulleniatina primalis*	11.10, 11.11a–b
	U1482A-23H-CC	Pliocene Zone PL1, 5.26 Ma	*Pulleniatina praespectabilis*	10.4
IODP Hole U1483A, northwest Australian margin, tropical eastern Indian Ocean, 13°03.3227′S, 121°48.2424′E	U1483A-1H-4, 75-77 cm	Pleistocene Zone PT1b, 0.054 Ma	*Pulleniatina finalis*	7.7a–b
			Pulleniatina obliquiloculata	8.4, 8.7a–b, 8.10a–c
	U1483A-11H-2, 50-52 cm	Pleistocene Zone PT1a, 0.99 Ma	*Pulleniatina obliquiloculata*	8.2, 8.5a–c, 8.8
	U1483A-15H-6, 49-51 cm	Pleistocene Zone PT1a, 1.46 Ma	*Pulleniatina obliquiloculata*	8.6, 8.11
	U1483A-20H-2, 50-52 cm	Pleistocene Zone PT1a, 1.91 Ma	*Pulleniatina finalis*	7.3, 7.6a–c
	U1483A-23H-CC	Pleistocene Zone PL6, 2.30 Ma	*Pulleniatina praecursor*	9.10
IODP Hole U1488A, Eauripik Rise, equatorial western Pacific Ocean, 2°02.5891′N, 141°45.2864′E	U1488A-1H-2, 80-82 cm	Pleistocene Zone PT1b, 0.095 Ma	*Pulleniatina finalis*	7.2a–c
			Pulleniatina obliquiloculata	8.3a–c
	U1488A-9H-4, 60-62 cm	Pliocene Zone PL5, 3.14 Ma	*Pulleniatina praecursor*	9.7
	U1488A-9H-CC	Pliocene Zone PL5, 3.28 Ma	*Pulleniatina praecursor*	9.2, 9.3a–c
	U1488A-10H-4, 50-52 cm	Pliocene Zone PL4, 3.42 Ma	*Pulleniatina praecursor*	9.6
	U1488A-12H-CC	Pliocene Zone PL2, 4.33 Ma	*Pulleniatina primalis*	11.2, 11.3a–c, 11.7
			Pulleniatina spectabilis	12.3a–b, 12.4a–c, 12.5a–f, 12.6a–c, 12.8a–b
	U1488A-16H-4, 80-82 cm	Pliocene Zone PL1, 5.28 Ma	*Pulleniatina praespectabilis*	10.3a–c, 10.5a–c
	U1488A-20H-4, 71-83 cm	Pliocene Zone PL1, 6.09 Ma	*Pulleniatina primalis*	11.5a–b, 11.6
	U1488A-21H-6, 9-11 cm	Miocene Zone M13, 6.59 Ma	*Pulleniatina primalis*	11.12a–e
RV *Pelagia* Station GLOW10 (Seagap High, Tanzanian margin, tropical western Indian Ocean, 9°14′24″ S, 40°21′0″E)	GLOW10-BX, 0-1 cm	Holocene Zone PT2b, 0.0 Ma	*Pulleniatina finalis*	7.4a–d, 5
RV *Pelagia* Station GLOW22 (Kitunda Block, Tanzanian margin, tropical western Indian Ocean, 9°50′53″ S, 40°34′44″E)	GLOW22BX-20-21 cm	Pliocene upper Zone PL1, ∼ 4.4 Ma	*Pulleniatina praecursor*	9.8a–d, 9.9
			Pulleniatina praespectabilis	10.8a–c

western equatorial Pacific, finding *Pulleniatina* to be offset in δ^{18}O from co-occurring *T. sacculifer* by about +0.5% around the time of the origin of *P. primalis*, with the degree of offset increasing through the Pleistocene to ~ +1.0%, albeit with considerable inter-sample variability which they attributed to varying equatorial upwelling at the site. Their record remains important because the long time series covers almost the entire evolutionary history of the genus. Van Eijden (1995) reported multispecies oxygen and carbon stable isotopic data from a sample from around the Miocene/Pliocene boundary at DSDP Site 757 in the Indian Ocean, finding *P. primalis* to inhabit the shallow subsurface. Pearson & Shackleton (1995) reported *Pulleniatina* oxygen and carbon isotope data (variously *P. primalis*, *P. praecursor*, and *P. obliquiloculata*) alongside various other species from multiple stratigraphic levels in ODP Site 871 (Limalok Guyot, Marshall Islands area, western tropical Pacific Ocean), all data being consistent with a similar habitat to that reported by van Eijden (1995). Palmer et al. (1998) reported boron isotope ratios of both *P. obliquiloculata* and *P. praecursor* at Site 871 indicative of a relatively acidic subsurface depth habitat (reconstructed at 50–150 m), which is consistent with the oxygen and carbon isotope evidence.

Pearson & Penny (2021) measured single-specimen isotope analyses from various fossil assemblages containing both right and left coiling forms of *P. obliquiloculata*. They found a large inter-specimen range of ~1‰ in both δ^{18}O and δ^{13}C. In some cases, the sinistral and dextral populations were statistically indistinguishable, but in others there was a significant difference in the mean values of both isotopes, which they interpreted as indicating subtly different habitat preferences (such as depth or seasonality). These differences are not persistent over time and were interpreted as representing the existence of transient varieties.

Multi-species planktonic foraminifer isotope data from a variety of sites and sample levels were reported in Boscolo-Galazzo et al. (2021). A representative selection of one Indian Ocean (Site U1482) and two Pacific (Sites U1490 and 872) sites is plotted in Figure 1 along with the earlier data of van Eijden (1995). These data agree with Whitman & Berger (1992) by indicating that *Pulleniatina* has consistently occupied a similar subsurface ecological niche throughout its history, always lacking the carbon isotope enrichment seen in shallow-dwelling photosymbiotic species. Also evident in Figure 1 is an apparent deepening trend in which oxygen isotope differentials between *Pulleniatina* and mixed-layer species increased through time. This is part of a general pattern of niche expansion in planktonic foraminiferal assemblages, which Boscolo-Galazzo et al. (2021, 2022) have linked to global cooling since the middle Miocene. Those authors suggested that as subsurface waters cooled and bacterial respiration rates slowed, deeper habitats became gradually less acidic and developed improved food supply as particulate organic matter penetrated deeper into the water column. The average depth of the nutricline may have increased with more oligotrophic conditions in the surface mixed layer and greater light penetration, deepening the DCM, and therefore the preferred depth habitat.

Dang et al. (2024) produced a high-resolution record of *P. obliquiloculata* δ^{18}O and δ^{13}C paired with mixed layer *Globigerinoides ruber* for the last 4 million years at IODP Site U1489. They also found a long-term divergence of values between the two species (similar to Whitman & Berger, 1992), which they interpreted as a signal of thermocline cooling.

In general, the combined isotopic data indicate that all *Pulleniatina* species have occupied similar subsurface niches since their origin, although likely deepening and cooling with time. The carbon isotope data suggest that the genus has always been asymbiotic. We note that when multiple *Pulleniatina* species from the same samples have been analyzed, the measurements are generally within analytical error. Perhaps surprisingly, this includes the morphologically divergent *P. primalis* – *P. spectabilis* lineage for which no evidence of habitat differentiation has yet emerged (Fig. 1G). Thus, the data do not support the intriguing hypothesis of Srinivasan & Sinha (1998, 2000) that the restricted geographic range of *P. spectabilis* might be explained because it occupied a particularly deep niche that prevented migration through the shallow seaways of the Indonesian Throughflow.

BIOGEOGRAPHY SYNTHESIS

The synonymy lists developed as part of this study (see below) are all supported by illustrated specimens that are approved herein according to a unified taxonomy and therefore constitute a 'gold standard' for defining the biogeographic patterns. There are, however, many other recorded occurrences of *Pulleniatina* taxa, published in taxonomic lists, tables, and range-charts, that are not supported by illustrations or taxonomic discussion. These have been brought together in the 'Triton' database (Fenton et al., 2021). This resource has been subject to taxonomic standardization at the generic level (Fenton et al., 2021) but not at the species level and may include differing species concepts. For instance, as discussed in detail below, some authors do not recognize taxa such as *Pulleniatina praecursor* and *Pulleniatina finalis* and would include such specimens under other names. The paleogeographic map tool developed by Dr. Jeremy Young for mikrotax.org (https://www.mikrotax.org/system/ranges-tritonbiogeog.php; see Pearson et al., 2023) provides a useful interactive way of plotting the Triton data and viewing the relative frequency of species records compared to other taxa. The user is able to select taxa and restrict time intervals that can help investigate dispersal and contraction events. In this section, we combine the two approaches—Triton database and formal synonymy lists—to summarize the biogeographic history of *Pulleniatina*.

The likely ancestor of *Pulleniatina* (discussed further below) was *Neogloboquadrina acostaensis*, a cosmopolitan species that was abundant from the tropics to the high latitudes, although absent from the polar seas and (possibly) the North Pacific gyre (Fig. 2C). In the early part of its range, *P. primalis* was restricted to the tropical Indo-Pacific (Fig. 2B). This is presumably where it evolved, in an instance of 'parapatric' speciation, around 6.55 Ma (Pearson et al., 2023). It invaded the Atlantic Ocean around 5.33±0.25 Ma (the date has yet to be determined accurately), around which time it also expanded its range into mid-latitudes of all three major ocean basins (Fig. 2A).

The evolution of the *P. praespectabilis*–*spectabilis* lineage was accompanied by further restriction of the biogeographic ranges (Fig. 3). The lineage is unknown from the Atlantic,

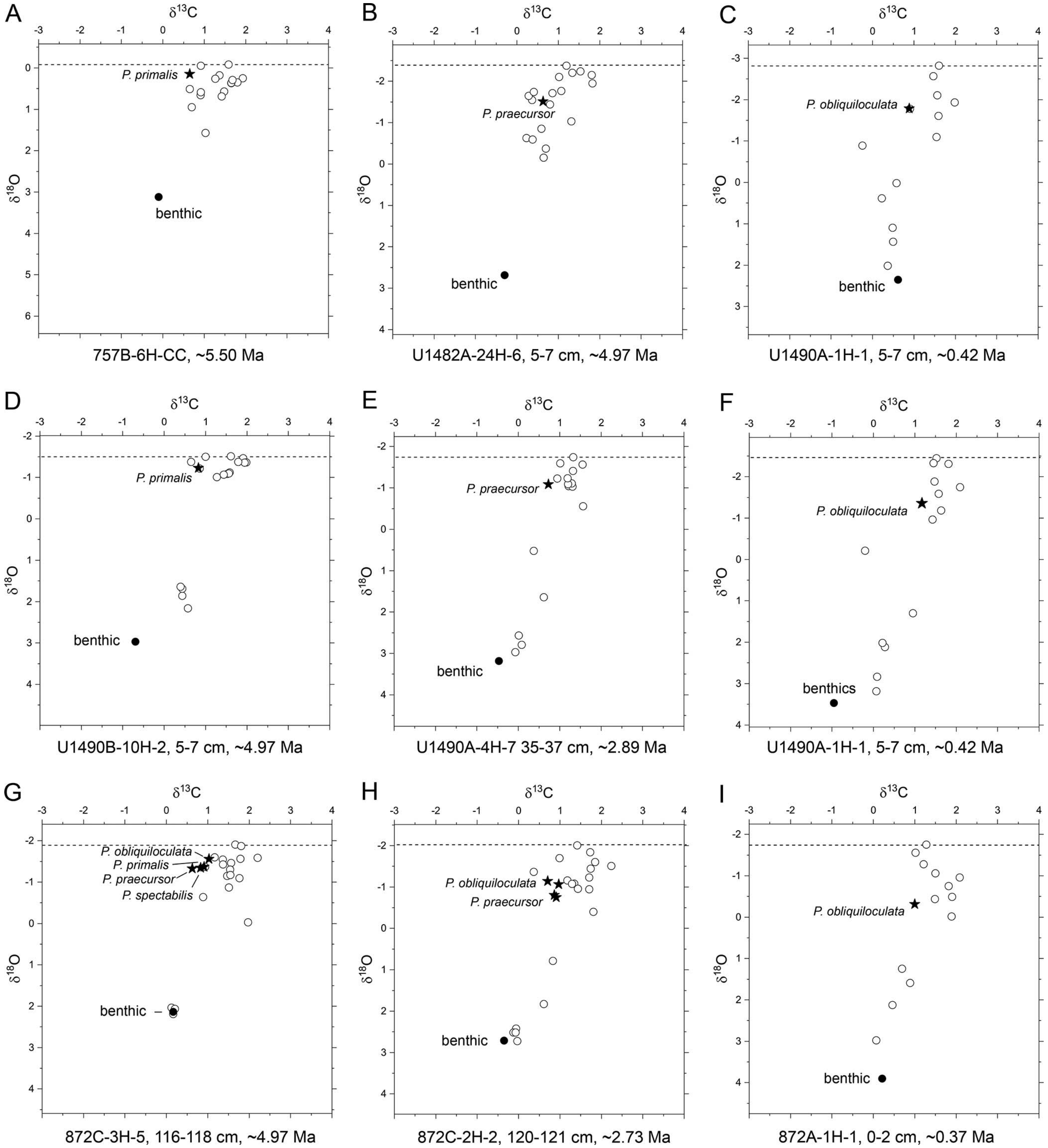
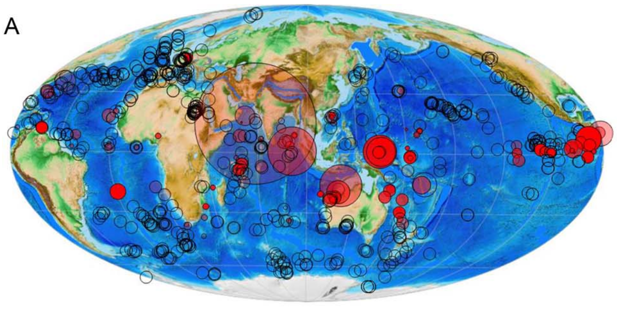
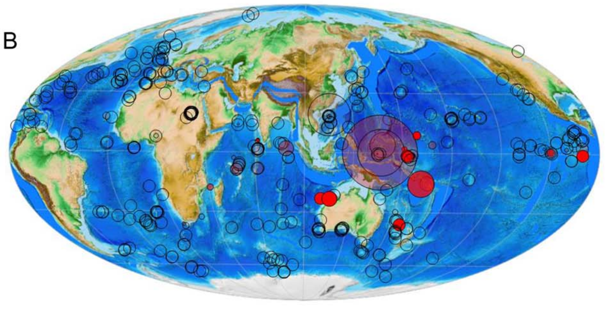


FIGURE 1. Oxygen and carbon stable isotope cross-plots of foraminiferal assemblages arranged by location and time. Data are plotted to a common scale with the vertical axis aligned with the most negative $\delta^{18}O$ value in each assemblage (dashed lines). Black stars = *Pulleniatina* species, as labeled. White circles = other planktonic foraminifera from the same assemblage. Black circles = benthic foraminifera. Sample level and estimated ages are as per the panel captions. A, ODP Site 757, Ninetyeast Ridge, tropical Indian Ocean. B–C, IODP Site U1482, northwest Australia margin, eastern tropical Indian Ocean. D–F, IODP Site U1490, Eauripik Rise, western equatorial Pacific Ocean. G–I, ODP Site 872, Lo-En Guyot, Marshall Islands, western tropical Pacific Ocean. Data from Van Eijden (1995) (panel A) and Boscolo-Galazzo et al. (2021) (panels B–I).

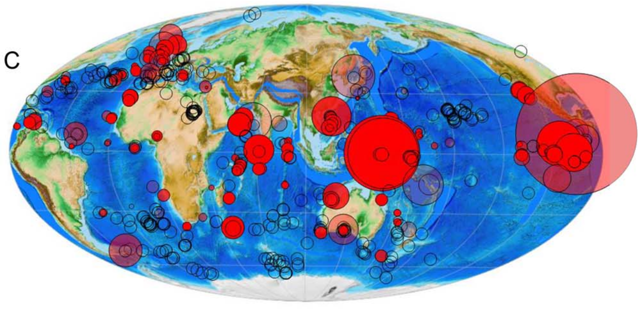
despite the existence of *P. primalis* there. Rare occurrences of *P. praespectabilis* in the Indian Ocean include a single record from the Arabian Sea (Fleisher, 1974) and specimens from the Tanzanian and northwest Australian margins that are illustrated herein for the first time (see Systematic Taxonomy section, below). *Pulleniatina spectabilis* is only known from the tropical Pacific except for a single documented occurrence from the Indian Ocean (Podder et al., 2021), which we have not been



Pulleniatina primalis, 3–5.5 Ma



Pulleniatina primalis, 5.5–9 Ma

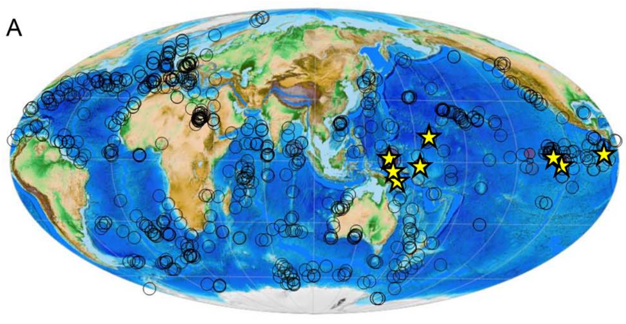


Neogloboquadrina acostaensis, 5.5–9.0 Ma

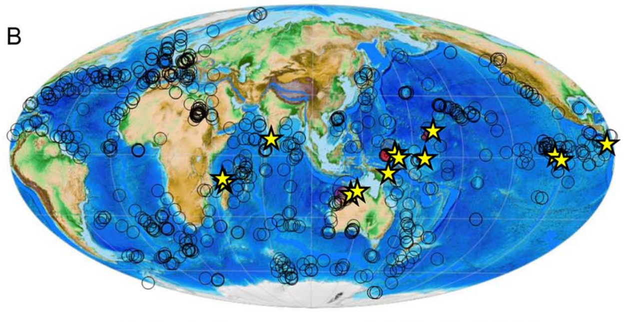
FIGURE 2. Geographic ranges of *Neogloboquadrina acostaensis* and *Pulleniatina primalis* in the Triton database (Fenton et al., 2021). A, *P. primalis* in the time window 3.0–5.5 Ma. B, *P. primalis* in the time window 5.5–9.0 Ma. C, *N. acostaensis* in the time window 5.5–9.0 Ma. All sites with samples in the time interval are plotted as circles. The opacity of the red fill is proportional to percentage of samples within the time window that contain the taxon. Circle size is proportional to the average abundance of species occurrences relative to other species. Basemaps are from GPlates2.1 (Müller et al., 2018). Flat blue areas are subducted crust. Interactive versions of the maps with dynamic links to the data are available at https://www.mikrotax.org/system/ranges-tritonbiogeog.php (last accessed 10.10.2024).

able to confirm with images. The ancestry of *P. spectabilis* appears to be a case of progressive specialization: first with the evolution of the tropical *P. primalis* from the cosmopolitan *N. acostaensis*, and then with the increasingly restricted biogeographic ranges of *P. praespectabilis* and *P. spectabilis*.

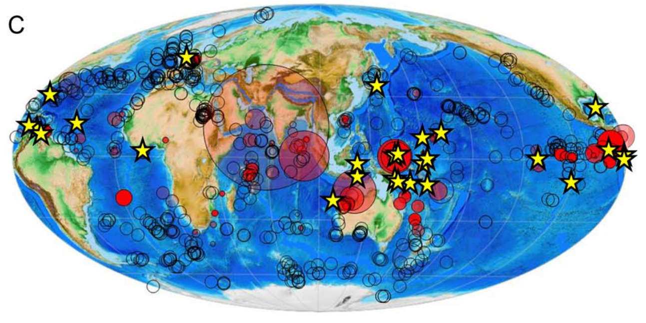
The *Pulleniatina primalis–praecursor–obliquiloculata* lineage occurs across the Indo-Pacific and Atlantic sectors, except that the lineage is absent from the Atlantic in the time window 3.41–2.26 Ma. A notable exception in the Triton database is the apparent absence of *P. praecursor* from the western Indian Ocean. This is probably a taxonomic and sampling artefact because not all specialists have chosen to recognize *P. praecursor* as a separate entity. We examined a sample from offshore Tanzania (Sample GLOW22-BX-20-21 cm; see Table 1 for details) and found very abundant *P. praecursor*, from which two specimens are illustrated in the Systematic Taxonomy.



Pulleniatina spectabilis, 3–5.5 Ma



Pulleniatina praespectabilis, 3–5.5 Ma

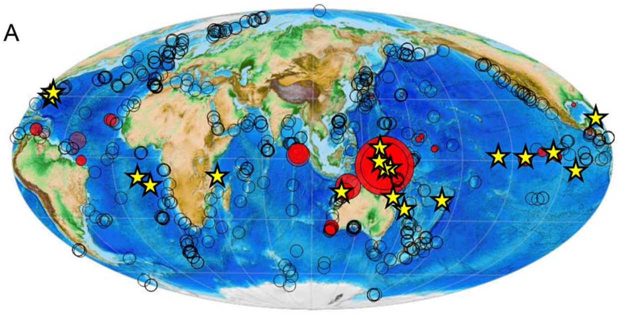


Pulleniatina primalis, 3–5.5 Ma

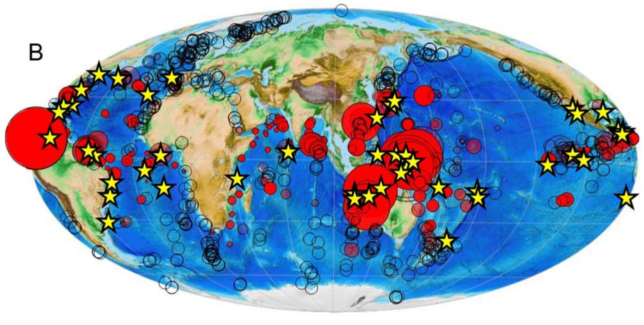
FIGURE 3. Geographic ranges of *Pulleniatina spectabilis*, *P. praespectabilis*, and *P. primalis* for the time window 3.0–5.5 Ma. Symbols from the Triton database (Fenton et al., 2021) as for Figure 2, except overlaid gold stars for confirmed occurrences in the synonymy lists presented below. Basemaps are from GPlates2.1 (Müller et al., 2018). Interactive versions of the maps with dynamic links to the Triton data are available at https://www.mikrotax.org/system/ranges-tritonbiogeog.php (last accessed 10.10.2024).

The *P. finalis* morphospecies appears to have a similar geographic range to the more widely recognized *P. obliquiloculata*, although it may be more confined to warmer waters (Fig. 4). It is currently difficult to judge whether its apparently more restricted range is real or a taxonomic artefact of some workers not recognizing it. For instance, like *P. praecursor*, there are no published occurrences of *P. finalis* from the western Indian Ocean, but we found abundant specimens offshore Tanzania (Sample GLOW10-BX, 0-1 cm; see Systematic Taxonomy below), alongside *P. obliquiloculata*.

Pulleniatina seems to have been absent from the Mediterranean Sea and Red Sea throughout its history (Thunell, 1979)



Pulleniatina finalis, 0.1-2.0 Ma



Pulleniatina obliquiloculata, 0.1-2.0 Ma

FIGURE 4. Geographic ranges of *Pulleniatina finalis* and *P. obliquiloculata* for the time window 0.1–2.0 Ma. Symbols from the Triton database (Fenton et al., 2021) as for Figure 2, except overlaid gold stars for *P. finalis* represent confirmed occurrences in the synonymy lists presented below. Basemaps are from GPlates2.1 (Müller et al., 2018). Interactive versions of the maps with dynamic links to the Triton data are available at https://www.mikrotax.org/system/ranges-tritonbiogeog.php (last accessed 10.10.2024).

except for one reported invasive occurrence (Zenetos et al., 2008) and two instances in Mediterranean sediments that are unconfirmed by images (Serrano et al., 2007; Casalbore et al., 2010; see Pearson et al., 2023, for further discussion). The absence of *Pulleniatina* and some other species from these restricted seas is probably a function of the seas' anomalous stratification and nutrient profiles (Azibeiro et al., 2023).

BIOSTRATIGRAPHY SYNTHESIS

Pearson et al. (2023) recalibrated 183 previously published local biostratigraphic horizons on a common timescale using the same unified taxonomy presented here. These biohorizons are distributed among 16 *Pulleniatina* bioevents, which are variously top and bottom occurrences, coiling changes, and geographic expansions or contractions. Of these, nine are regarded as of particular use in biostratigraphic schemes; the others are too gradational for high-resolution biostratigraphy although they also provide biostratigraphic control over longer timescales (Table 2). A summary range-chart with suggested evolutionary relationships and lineages is presented in Figure 5.

SYSTEMATIC TAXONOMY

Order FORAMINIFERIDA d'Orbigny, 1826
Superfamily GLOBIGERINOIDEA Carpenter, Parker & Jones, 1862

Family PULLENIATINIDAE Cushman, 1927a; revised herein

Type genus: *Pulleniatina* Cushman, 1927a

Pulleniatininae Cushman, 1927a, p. 89.
Pulleniatinidae Loeblich & Tappan, 1984, p. 41.
Neogloboquadrinidae Darling et al., 2004, p. 7659.

DESCRIPTION.—Family that unites the genera *Pulleniatina* and *Neogloboquadrina* and their common ancestor, possessing a normal perforate, weakly cancellate, non-spinose (in the adult), pustulose wall with a tendency to form a thick granular crust (*Neogloboquadrina*) or smooth reflective cortex (*Pulleniatina*) in the final ontogenetic stage. Test trochospiral (*Neogloboquadrina* and some *Pulleniatina*) or streptospiral (some *Pulleniatina*).

DISCUSSION.—Subfamily Pulleniatininae was established by Cushman (1927a, p. 89) to unite two genera with reflective cortexes (*Pulleniatina* and *Sphaeroidinella*), but these are not now regarded as closely related. The taxon was elevated to Family status by Loeblich & Tappan (1984, p. 41), but the Family remains attributed to Cushman by the 'Principle of Coordination' (Article 36.1 of the ICZN). Loeblich & Tappan (1987, p. 479) used Family Pulleniatinidae to encompass *Pulleniatina* and the enigmatic *Globigerinopsis* Bolli, 1962 (type species *Globigerinopsis aguasayensis* Bolli, 1962; see also Popescu & Crihan, 2011). However, in our opinion *Globigerinopsis* bears little resemblance to *Pulleniatina* and is from older (middle Miocene) strata; it has been suggested to be a spinose form similar to *Globigerinella* (Srinivasan, 1975) although requiring further study. Our own preliminary investigations of new images of the type series of *Globigerinopsis* taken for us by Dr. Monika Doubrawa at the Natural History Museum, Basel, appear to confirm this, so that genus is herein excluded from the Pulleniatinidae.

Morphological and stratigraphic data have long indicated a close relationship between *Pulleniatina* and *Neogloboquadrina* (Banner & Blow, 1967, and subsequent studies; reviewed and augmented in Fabbrini et al., in press). Genetic data (Darling et al., 2004; Aurahs et al., 2009; Ujiié et al., 2012; André et al., 2014; Ujiié & Ishitani, 2016; Morard et al., 2024) also indicate that *Pulleniatina* is closely related to *Neogloboquadrina*, for which the type species is *Globigerina dutertrei* d'Orbigny 1839 = *N. dutertrei* in our taxonomy. Here, Family Pulleniatinidae is emended to be used in a third sense to encompass *Pulleniatina* and *Neogloboquadrina* and their common ancestor. Note that Family Neogloboquadrinidae has been used by several authors in much the same sense (Darling et al., 2004, 2006; Aurahs et al., 2009; Schiebel & Hemleben, 2017), but Pulleniatinidae is the correct name because it has date priority.

The available genetic evidence (Morard et al., 2024) indicates that *Pulleniatina* nests within *Neogloboquadrina*, and that modern *Pulleniatina obliquiloculata* is a sister taxon to *N. dutertrei* with the two other extant species of *Neogloboquadrina*, *N. incompta* and *N. pachyderma*, being more distantly related. This is in accordance with the fossil record, in which the ancestor of *P. obliquiloculata*, *P. primalis*, is thought to have evolved from pre-existing *Neogloboquadrina acostaensis*, itself the direct ancestor of modern *N. dutertrei* (e.g., Banner & Blow, 1967). The ultimate bounds of Family Pulleniatinidae depend on unravelling the early phylogenetic history of *Neogloboquadrina*,

TABLE 2. The most useful biochronological marker events for *Pulleniatina*. For discussion and references to the full literature see Pearson et al. (2023).

Bioevent (* = primary event)	Mechanism	Age (Ma)	Error ± (Ma)	Main reference(s)
* 'L1' coiling shift	Population sweep	0.86	0.01	Saito (1976) Pearson & Penny (2021)
Top 'L5' coiling shift	Population sweep	1.78	0.01	Chuang et al. (2018) Pearson & Penny (2021)
LAD *P. praecursor*	Pseudoextinction	1.90	0.15	Brönnimann & Resig (1971) Pearson et al. (2023)
FAD *P. finalis*	Pseudospeciation	1.97	0.17	Chaisson & Pearson (1997) Pearson et al. (2023)
*Bottom 'L5' coiling shift	Population sweep	2.02	0.01	Chaproniere & Nishi (1994) Pearson & Penny (2021)
*Atlantic Ocean reappearance	Dispersal	2.24	0.02	Chaisson & Pearson (1997) Maniscalco & Brunner (1998) Fraass et al. (2017)
*Atlantic Ocean disappearance	Contraction	3.37	0.005	Chaisson & Pearson (1997) Fraass et al. (2017)
LAD *P. primalis*	Pseudoextinction	4.00	0.60	Chaproniere & Nishi (1994) Pearson (1995) Pearson et al. (2023)
*'L9' coiling shift, Pacific Ocean	Population sweep	4.06	0.02	Chaisson & Pearson (1997) Groeneveld et al. (2021) Expedition 320/321 Scientists (2010a, b) Pearson et al. (2023)
*LAD *P. spectabilis*	Extinction	4.27	0.05	Hays et al. (1969) Chaisson & Leckie (1993) Expedition 320/321 Scientists (2010b) Kaushik et al. (2020) Pearson et al. (2023)
FAD *P. obliquiloculata*	Pseudospeciation	4.22	0.12	Weaver & Raymo (1986) Kaushik et al. (2020) Pearson et al. (2023)
FAD *P. praecursor*	Pseudospeciation	4.52	0.10	Brönnimann & Resig (1971) Saito (1985) Pearson et al. (2023)
FAD *P. spectabilis*	Pseudospeciation	5.14	0.10	Expedition 320/321 Scientists (2010b)
*FAD *P. primalis* (Atlantic Ocean)	Dispersal	5.33	0.25	Chaisson & Pearson (1997)
FAD *P. praespectabilis*	Pseudospeciation	5.98	0.05	Brönnimann & Resig (1971) Pearson et al. (2023)
*FAD *P. primalis* (tropical Indo-Pacific)	Speciation	6.50	0.10	Jenkins (1978) Keigwin (1982) Chaisson & Leckie (1993) Expedition 320/321 Scientists (2010a) Lam et al. (2022) Pearson et al. (2023)

which currently requires more study. Particularly uncertain at the time of writing are the relationships between the tropical *N. acostaensis – N. humerosa – N. dutertrei* lineage and three high latitude groups consisting of 1) modern *N. pachyderma* and *N. incompta* and their ancestors; 2) an extinct lineage leading to *N. atlantica*, which as the name suggests is most common in the Atlantic; and 3) another extinct group that may include *N. kagaensis* and is most common in the Pacific. It seems likely that the common ancestor of all these forms (and, by extension, *Pulleniatina*) was a long-ranging morphospecies that first appeared in the late Oligocene, originally described as *Globorotalia opima* subsp. *continuosa* by Blow (1959). Spezzaferri (1994) and Leckie et al. (2018) included this in the extinct (and moderately diverse) genus *Paragloborotalia* as '*P. continuosa*'. In contrast, other authors (e.g., Kennett & Srinivasan, 1983; Chaisson & Leckie, 1993) included it in *Neogloboquadrina* as '*N. continuosa*'. Part of the problem is that a clear morphological distinction between the genera *Paragloborotalia* and *Neogloboquadrina* has yet to be firmly established. There may ultimately be a case for extending Family Pulleniatinidae to encompass some or even all fossil *Paragloborotalia* species, but an even more fundamental problem that needs to be resolved is the spinose versus non-spinose nature of the wall of the various fossil morphospecies. This is because all modern *Pulleniatina* and *Neogloboquadrina* are non-spinose, at least in their adult morphology (notwithstanding claims of spines or spine bases in the juvenile discussed further below; Lipps, 1966; Burt & Scott, 1975), but *Paragloborotalia* was originally described as spinose (Cifelli, 1982), and there is good evidence that at least some species were indeed sparsely spinose as adults (reviewed in Leckie et al., 2018). Were spines lost in the evolution of this group, or are there separate clades of spinose and non-spinose forms possessing similar generalized morphologies that have been confused in the genera *Paragloborotalia* and *Neogloboquadrina*? Resolving this question will also help better define the limits of the non-spinose genus *Neogloboquadrina* and Family Pulleniatinidae.

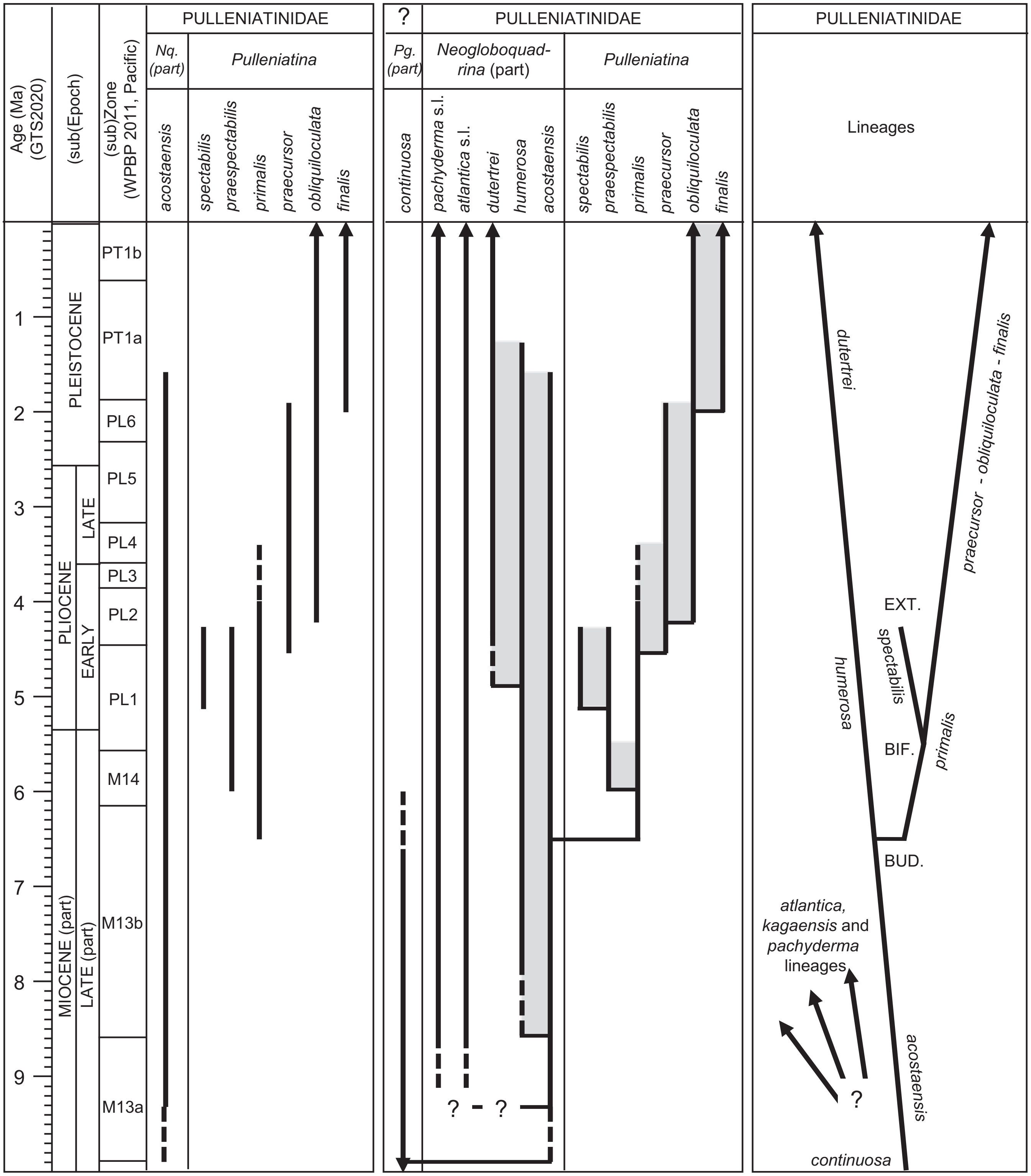


FIGURE 5. Stratigraphic ranges and inferred phylogenetic relationships of *Pulleniatina* and related forms. Vertical bars represent stratigraphic presence. Dashed bars and '?' represent uncertainty. Grey shaded fields represent intergradation between morphospecies without clear morphological separation. GTS2020 = Geological Timescale 2020 (Gradstein et al., 2020). WPBP 2011 = Wade et al. (2011). Nq. = *Neogloboquadrina*. Pg. = *Paragloborotalia*. s. l. = sensu lato. EXT. = extinction. BIF. = bifurcating cladogenesis. BUD. = budding cladogenesis.

Another issue to be considered is that the globorotaliiform genus *Globoconella* is genetically similar to *Neogloboquadrina* (Aurahs et al., 2009; Morard et al., 2024). It may also be descended from *Paragloborotalia continuosa*, although probably in an earlier branching event than the *Neogloboquadrina*/*Pulleniatina* divide. Modern *Globoconella inflata* has a reflective cortex like *Pulleniatina*, but the fossil record suggests that this is probably a convergent feature. Nevertheless, there may be a case for expanding Family Pulleniatinidae to accommodate *Globoconella*, for which more research on lower and middle Miocene globorotaliiform genera is required to confirm the critical phylogenetic relationships.

STRATIGRAPHIC RANGE. —Upper (?) Miocene to Recent.

Genus *Pulleniatina* Cushman, 1927a

Type species: *Pullenia obliquiloculata* Parker & Jones, 1865

Pulleniatina Cushman, 1927a, p. 90.

DESCRIPTION.—Nonspinose planktonic foraminifera with a weakly cancellate, porous wall capped by a smooth reflective cortex in the terminal stage; initially trochospiral with a tendency for involute streptospiral coiling in some species.

DISCUSSION.—The name *Pulleniatina* is a diminutive of *Pullenia* (Parker & Jones in Carpenter et al., 1862), which in turn was named after William Pullen (1813–1887), polar navigator and Captain of HMS *North Star*. Parker & Jones (1865) included their species *obliquiloculata* in *Pullenia*, but the type species, *P. sphaeroides* (d'Orbigny in Deshayes, 1832), is now regarded as an unrelated benthic form. Parker & Jones (1865) did, however, recognize similarities with *Globigerina* and other genera that are now known to be planktonic. Cushman (1914, p. 22) stated that *obliquiloculata* was "the only one of the genus [i.e., *Pullenia*] that has been found as a pelagic form." Later, Cushman (1927a) devised a separate genus *Pulleniatina* to accommodate it, grouping it with other planktonic foraminifera in Subfamily Pulleniatininae (see above) and Family Globigerinidae.

Cushman (1927a) described *Pulleniatina* as having initially globigeriniform coiling but becoming involute and smooth, without spines. The distinctive 'streptospiral' coiling mode, described by Loeblich & Tappan (1964) and Banner & Blow (1967, p. 148–150), is most strongly expressed in *Pulleniatina finalis* (Fabbrini et al., in press). The prefix 'strepto-' is from the Greek for 'twisted' and reflects the fact that the coiling axis shifts during ontogeny making the test irregularly coiled. The species *P. obliquiloculata* and *P. finalis* are also strongly involute with quite rapidly expanding chamber size such that adult chambers frequently overlap and envelop much of the earlier portion of the test. The first species to evolve, *P. primalis*, is trochospiral, as are the members of the *spectabilis* lineage (Fabbrini et al., in press).

The main feature that unites all members of the genus and distinguishes them from *Neogloboquadrina* is the smooth reflective cortex in terminal stage (gametogenic) forms. Another difference is that adult *Neogloboquadrina* typically possess a well-defined apertural lip, which is absent in *Pulleniatina*. According to Schiebel & Hemleben (2017), the smooth cortex is formed when the individual migrates to deeper water near the end of its life cycle.

Burt & Scott (1975) suggested that *Pulleniatina* is not was spinose in its early ontogeny and illustrated a series of dissected specimens bearing what they suggested were spine bases on the early chambers (see also Cushman, 1927a; Parker, 1962; Lipps, 1966). Although this is possible, in view of its probable evolutionary origin from *Paragloborotalia*, which is thought to have been spinose (Cifelli, 1982; Olsson et al., 2006; Leckie et al., 2018), the structures illustrated by Burt & Scott (1975) are tentatively interpreted here as pustules that are somewhat dissolved in some specimens, revealing their inner layers rather than spine bases. Most modern authors simply refer to the genus as being non-spinose (e.g., Hemleben et al., 1989; Schiebel & Hemleben, 2017).

STRATIGRAPHIC RANGE.—Upper Miocene (6.50 ± 0.10 Ma; Pearson et al., 2023) to Recent.

TAXONOMIC KEY.—Several previous authors have provided taxonomic descriptions of the various morphospecies of *Pulleniatina* with suggested means of discriminating between them (Banner & Blow, 1967; Saito et al., 1981; Kennett & Srinivasan, 1983; Bolli & Saunders, 1985). As is often the case with planktonic foraminifera, species discrimination is not generally based on single unambiguous characters, but rather on suites of features that in combination make a given specimen closer morphologically to one type specimen rather than another. This lends an inevitable degree of subjectivity to the process, which can be lessened, to some extent, by describing those features that are most useful in taxonomic discrimination. Such features are often geometrically linked; for instance, the coiling mode, aperture shape, chamber shape, and overall morphology are all partly inter-dependent. Unless there is some obvious and workable dividing line between taxa, species discrimination should be based on a consideration of all available characters. The taxonomic key presented in Table 3 was developed after investigations including the internal morphology using 3D models generated from micro-CT data of selected typical specimens as described by Fabbrini et al. (in press).

SYNONYMS AND INVALID TAXA.—Five valid taxa that are herein regarded as synonyms or probable synonyms of *Pulleniatina* species are re-illustrated in Figure 6: *Globigerina antillensis* Bermúdez 1961; *Pulleniatina obliquiloculata* var. *trochospira* Hartono 1964; *Pulleniatina okinawaensis* Natori 1976; *Globigerina santamariaensis* McCulloch 1977; and *Pulleniatina alticuspis* Carreño 1985. Another name, *Pulleniatina praepulleniatina* Lloyd 1961, is a nomen nudum. These are discussed in the Systematic Taxonomy below.

EXCLUDED TAXA.—We note six species have been described as belonging to *Pulleniatina* but are herein excluded from the genus, as follows: *Pulleniatina semiinvoluta* Germeraad 1946 was made the type species of the benthic genus *Rotaliatinopsis* by Banner & Blow (1967). *Pulleniatina praepulleniatina* Brönnimann & Resig 1971 is regarded here as referable to *Neogloboquadrina*. Fordham (1986) named four taxa of which three—*Pulleniatina mayeri* subsp. *plana* Fordham (1986, pl. 18, fig. 3a–c), *Pulleniatina mayeri* subsp. *juvenis* Fordham 1986 (pl. 18, fig. 7a–c), and *Pulleniatina mayeri* subsp. *polygonia* (pl. 18, fig. 20a–c)—have relatively flat inner whorls and are considered referable to *Globorotaloides*. These need to be investigated further, but it seems *polygonia* is a likely

TABLE 3. Simplified taxonomic key to species of *Pulleniatina*.

Pulleniatina finalis	Large, subspherical test with 3–5 embracing chambers per whorl, a broad arched equatorial aperture and a thick wall. Strongly involute and streptospiral coiling mode. Distinguished from *P. obliquiloculata* by having an aperture that is nearly symmetrical over the periphery and a pseudo-planispiral appearance in the last whorl.
Pulleniatina obliquiloculata	Large, subspherical test with 3–4½ chambers per whorl, a broad aperture and thick wall. Moderately involute and streptospiral coiling mode with a final chamber that obscures the umbilicus. Distinguished from *P. praecursor* by having more globular chambers, less well-defined sutures, and a larger, more globular test. Not pseudo-planispiral like *P. finalis*.
Pulleniatina praecursor	Oblate subspherical test with 4–6 chambers per whorl, a broad, low aperture and a moderately thick wall. Low-spired, moderately involute and slightly streptospiral coiling mode. Distinguished from *P. primalis* by possessing an aperture that extends at least as far as the equatorial periphery and its more irregular coiling in some specimens. Smaller, thinner-walled and less distinctly streptospiral and globular than *P. obliquiloculata* with generally more chambers in the final whorl.
Pulleniatina praespectabilis	Biconvex test with acute periphery and 4–5 chambers per whorl, a broad low aperture and moderately thick wall. Medium trochospiral coiling. Distinguished from *P. primalis* by the slightly petaloid biconvex test, more triangular umbilical chamber shape, and acute periphery. Distinguished from *P. spectabilis* by the less anguloconical shape, less petaloid outline and by lacking the distinctly pinched rim.
Pulleniatina primalis	Subglobular test with 4–5 chambers per whorl, a medium arched aperture and a cortex that sometimes only partly covers the test. Medium trochospiral coiling with chambers that lean over the umbilicus. Distinguished from *Neogloboquadrina acostaensis* by the larger size, more inflated ventral side, lack of an apertural lip or flange, and the presence of a reflective cortex. Distinguished from *P. praecursor* by smaller adult size and less spherical morphology with an aperture that does not extend to the periphery. Distinguished from *P. praespectabilis* by the rounded rather than acute periphery and less triangular umbilical chambers.
Pulleniatina spectabilis	Anguloconical petaloid test with distinctly pinched periphery, 5 slightly disjunct and overlapping chambers per whorl, low arched to sub-rectangular aperture and thin wall. Distinguished from *P. praespectabilis* by its more petaloid outline and anguloconical shape and having at least one chamber with a pinched periphery.

synonym of *Globorotaloides testarugosus* (Jenkins, 1960); see Coxall & Spezzaferri (2018). *Pulleniatina mayeri* subsp. *umbilicata* Fordham 1986 (pl. 17, fig. 26 a–c) appears to be a form similar to *Paragloborotalia mayeri* but with an aberrant final chamber and aperture. One species that was previously regarded as a *Pulleniatina* synonym, *Globigerina atlantis* Bermúdez 1961 (see Saito et al., 1981), is excluded after examination of new environmental SEMs of the holotype because the wall texture and morphology are unlike the genus.

***Pulleniatina finalis* Banner & Blow, 1967**

Figs. 7.1a–7.9b

Pullenia obliquiloculata Parker & Jones, 1865.—Brady, 1884, p. 618 (partim), pl. 84, fig. 16a–b) [Recent, *Challenger* Station 224, 7°45′N, 144°20′E, North Pacific Ocean] (not pl. 84, figs. 17–20 = *Pulleniatina obliquiloculata*). (Not Parker & Jones, 1865.)

Pulleniatina obliquiloculata (Parker & Jones, 1865).—Jenkins & Orr, 1972, pl. 39, figs. 1–2 (indicated as '*P. finalis*' but included in synonymy with *P. obliquiloculata*) [Pleistocene *P. obliquiloculata* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean].—Kennett & Srinivasan, 1983, p. 202, pl. 50, figs. 6–9 [lower Pleistocene *Globorotalia truncatulinoides*/*Globorotalia tosaensis* overlap Zone, DSDP Site 208, Lord Howe Rise, southwest Pacific Ocean].—Wynn Jones, 1994, p. 132 (partim), pl. 84, fig. 16a–b (reproduced from Brady, 1884). (Not Parker & Jones, 1865.)

Pulleniatina obliquiloculata obliquiloculata (Parker & Jones).—Belford, 1988, pl. 3, fig. 5 [Dredge sample DR9, Manus Basin, western tropical Pacific Ocean], pl. 3, figs. 6–8 [Dredge sample DR5, north of Manus Island, western tropical Pacific Ocean] (all recorded as "strongly involute forms"). (Not Parker & Jones, 1865.)

Pulleniatina obliquiloculata finalis Banner & Blow, 1967, p. 140–142, pl. 2, figs. 4–10; pl. 3, fig. 5a–b; pl. 4, fig.10 [Recent, *Challenger* Station No. 344, sediment dredge at 7°54′30″S, 14°28′20″W, 420 fathoms (=768 m) depth, near Ascension Island, South Atlantic Ocean].—Belford, 1988, pl. 3, fig. 9 [Core G1, north of Manus island, western tropical Pacific Ocean].—Chaproniere & Nishi, 1994, p. 225, pl. 3, figs. 16–18 [Pleistocene *Globorotalia (Truncorotalia) crassaformis hessi* Subzone, ODP Site 836, Lau Basin, western tropical Pacific Ocean].—Lidz & McNeill, 1995, pl. 2, figs. 34–38 [Pleistocene Zone N22, CLINO borehole, Great Bahama Bank, North Atlantic Ocean].

Pulleniatina finalis Banner & Blow.—Lamb & Beard, 1972, p. 57–58, pl. 29, figs. 5–7; pl. 30, fig. 1a–f [Pleistocene *Pulleniatina finalis* subzone, Gulf of Mexico slope, North Atlantic Ocean].—Saito, 1976, p. 305, fig. 1 (lower pair) [*Vema* Core V24–58, central equatorial Pacific Ocean].—Saito et al., 1981, p. 98, pl. 31, figs. 1a–2 [core top, *Vema* Core V22-170, eastern tropical South Atlantic Ocean].—Moullade, 1983, pl. 9, figs. 11–12 [upper Pleistocene Zone N22/N23, DSDP Site 533, Blake Outer Ridge, North Atlantic Ocean].—Bolli & Saunders, 1985, p. 248–250, fig. 40.3 [holotype, reproduced from Banner & Blow, 1967], figs. 41.3–8 [Pleistocene *Globorotalia truncatulinoides* Zone, DSDP Site 73, central Pacific Ocean].—Chaproniere, 1991, pl. 3, figs. 22–24 [Pleistocene, *Sonne* piston core 76PC06-730, Queensland Plateau, offshore Queensland, Australia].—Chaproniere & Nishi, 1994, p. 225, pl. 3, figs. 16–18 [Pleistocene *Globorotalia (Truncorotalia) crassaformis hessi* Subzone, ODP Site 836, Lau Basin, western tropical Pacific Ocean].—Hayashi et al., 2013, fig. 7.13 [Pleistocene Subzone PT1b, IODP Site U1338, eastern equatorial Pacific Ocean].—Fabbrini et al., in press, figs. 2aq–av, 3h, 3p, 10a–c [Pleistocene, Subzone PT1b, IODP U1488A-1H-2, 80–82 cm, Eauripik Rise, western equatorial Pacific Ocean].

Pulleniatina obliqueloculata [sic] phenon *finalis* (Banner & Blow).—Fordham, 1986, pl. 20, figs. 24a–27b [Pliocene *P. obliqueloculata* Zone, DSDP Site 77A, eastern equatorial Pacific Ocean].

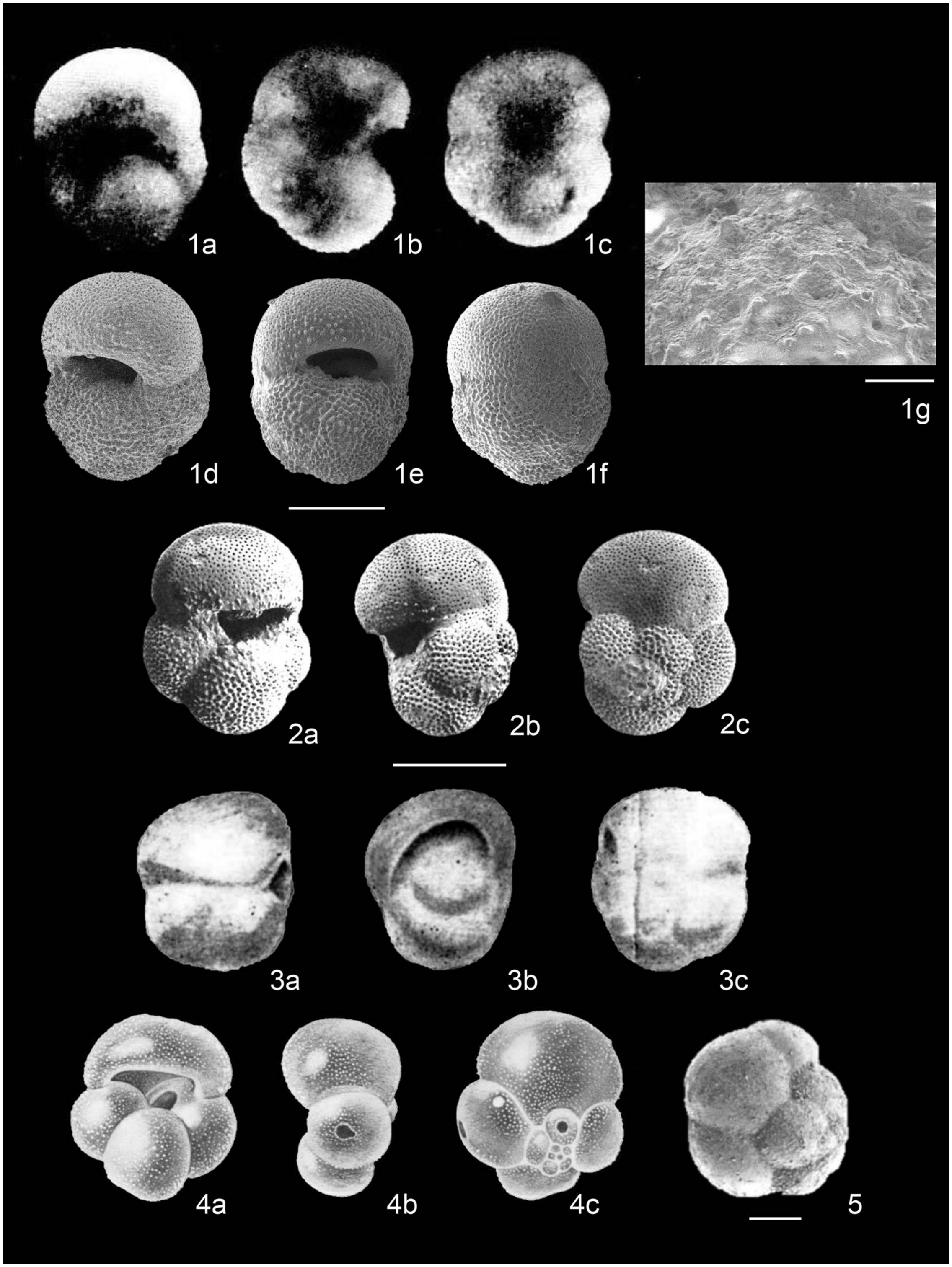


FIGURE 6. Taxa that are regarded herein as junior synonyms or possible synonyms of other *Pulleniatina taxa*, as discussed further in the Systematic Taxonomy section below. **1a–g** *Globigerina antillensis* Bermúdez 1961, holotype, Recent, *Atlantis* Station 2988, Nicholas Channel, Caribbean Sea; **1a** original illustration reproduced from Bermúdez (1961, pl. 1, fig. 1a–c), no scale available; **1d–g** new environmental SEMs of the holotype in three views with wall texture. **2a–c** *Pulleniatina okinawaensis* Natori 1976, holotype, Pleistocene *Globorotalia* (*G.*) *truncatulinoides* Zone, Chinen Fm., Okinawa Island, Ryuku Islands, Japan (reproduced from Natori, 1976, pl. 5, figs. 5a–6c). **3a–c** *Pulleniatina obliquiloculata* var. *trochospira* Hartono 1964, upper Miocene – Pliocene, Bali, Indonesia, no scale available (reproduced from Hartono, 1964, p. 10, pl. 8, figs. a–c). **4a–c** *Globigerina santamariaensis* McCulloch 1977, holotype, Bahia Santa Maria, Baja California, eastern Pacific Ocean, no scale available (reproduced from McCulloch, 1977, p. 416, pl. 172, fig. 7). **5** *Pulleniatina alticuspis* Carreño 1985, holotype, lower to middle Pliocene, Arroyo-Hondo section, Isla Maria Madre, eastern Pacific Ocean offshore Mexico (reproduced from Carreño 1985, p. 154–156, pl. 2, figs. 18–20, text-fig. 7a–c). Scale bars = 200 µm, except 1g = 20 µm.

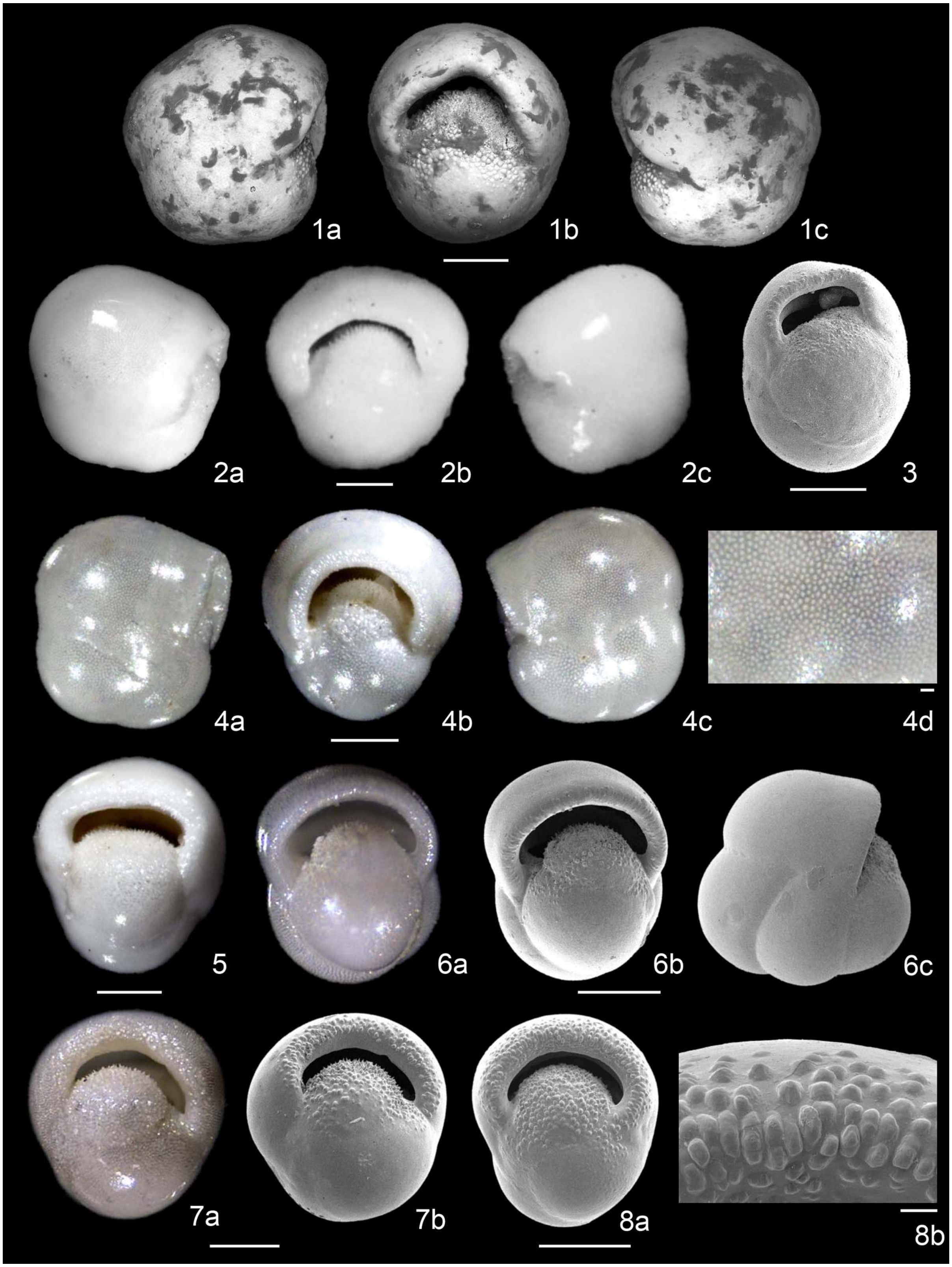


FIGURE 7. *Pulleniatina finalis* Banner & Blow, 1967. **1a–c** holotype (1966.2.3.1), environmental SEM, note wall surface is affected by scattered surface deposits (?glue), *Challenger* Station No. 344, near Ascension Island, South Atlantic Ocean. **2a–c** z-stacked LM, IODP Site U1488, equatorial Pacific Ocean, 0.095 Ma (Fabbrini et al., in press, fig. 2aq–as). **3** SEM, IODP Site U1488, equatorial Pacific Ocean, 0.095 Ma (Fabbrini et al., in press, fig. 10a). **4a–d** z-stacked LMs, RV *Pelagia* Station GLOW 10, western Indian Ocean, Holocene. Note fresh translucent wall surface with pore channels visible beneath the cortex. **5** z-stacked LMs RV *Pelagia* Station GLOW 10, western Indian Ocean, Holocene. **6a–c** z-stacked LMs and SEMs, IODP Site U1483, tropical Indian Ocean, 1.91 Ma. **7a–b, 8a–b** z-stacked LM and SEM, IODP Site U1483, tropical Indian Ocean, 0.054 Ma. Scale bars 200 µm, except 5d, 9b = 20 µm. For full sample details see Table 1.

Not *Pulleniatina obliquiloculata finalis* Banner & Blow, 1967.—Brönnimann & Resig, 1971, pl. 19, figs. 1–3 (= *P. obliquiloculata*).

DESCRIPTION.—Nonspinose, porous and weakly cancellate wall, pustulose on the chamber shoulders around and within the aperture. Wall very thick. In the terminal stage, test covered in a translucent non-porous cortex with a smooth reflective surface that can be degraded by diagenesis to a dull glossy sheen. Large, inflated test, subspherical; strongly involute coiling, initially trochospiral, then streptospiral, becoming almost planispiral in last few chambers. Umbilicus indistinct. Three to five chambers in final whorl, increasing rapidly in size except for the final few chambers which may be flattened and reduced in size and internal volume; chambers appressed and embracing, sutures gently curving, weakly depressed to indistinct beneath the cortex. Aperture a broad arch extending across the equatorial periphery, often irregular with a crimped appearance; no lip but may have a thickened rim or hooded flange, fringed by irregular pustules. Coiling exclusively dextral in Recent but variable down-core with *P. obliquiloculata*. Large, 500–800 µm.

DISTINGUISHING FEATURES.—*Pulleniatina finalis* is distinguished from *P. obliquiloculata* by having an aperture that is nearly symmetrical over the periphery and a pseudoplanispiral appearance in the last whorl.

DISCUSSION.—A specimen that can be assigned to this morphospecies was first illustrated by Brady (1884, pl. 84, fig. 16; see Banner & Blow, 1967, p. 141). The morphospecies was originally named as a subspecies of *obliquiloculata* but was raised to specific rank by Hays et al. (1969), who did not illustrate it, and then by Lamb & Beard (1972). Lamb & Beard (1972, pl. 30, fig. 1a–f) illustrated a specimen by SEM in which the smooth cortex was partly broken away to reveal the porous nature of the inner test wall. Various authors have chosen to lump *P. finalis* within their concept of *P. obliquiloculata* (e.g., Postuma, 1971; Jenkins & Orr, 1972; Orr & Jenkins, 1980; Kennett & Srinivasan, 1983), some of whom illustrated specimens that are attributed to this morphospecies under the name *obliquiloculata*.

The morphospecies is not generally recognized by biologists but is retained here because it is a useful stratigraphic indicator (see below). No genetic sequence data that are specifically identified as *finalis* have been published. The pseudoplanispiral morphospecies may be a phenotype within the same modern biospecies as *Pulleniatina obliquiloculata*. Specimens lacking the final one or two chambers would generally fall within the concept of *P. obliquiloculata*. Fabbrini et al. (in press) investigated the morphology of a typical specimen using micro-CT and constructed a 3D mesh model to investigate the internal morphology. The proloculus of this specimen was unusually large. The same is true of two specimens of *P. finalis* from Chen et al. (2023), raising the possibility that *P. finalis* may be a megalospheric variant of *P. obliquiloculata*. It is also possible that it is a different biospecies characterized by a larger proloculus, corresponding to one of the genetics types of '*P. obliquiloculata*' (e.g., Ujiié et al., 2012).

(PALEO)ECOLOGY.—*Pulleniatina finalis* presumably has a similar subsurface habitat to *P. obliquiloculata* although it is not generally recognized by biologists, so no specific sediment trap or plankton tow information is available. No stable isotope data are available.

GEOGRAPHIC DISTRIBUTION.—*Pulleniatina finalis* is a tropical form. It may have a more equatorially restricted geographic range than *P. obliquiloculata* (see Fig. 4A).

STRATIGRAPHIC RANGE.—*Pulleniatina finalis* first appeared in the early Pleistocene and persists to the Recent. Biohorizon Base *P. finalis* is a pseudospeciation that depends on a taxonomist being confident that at least one specimen in an assemblage of *Pulleniatina* can be assigned to the *finalis* morphotype. The best constrained calibration is the astronomical age of 2.03±0.03 Ma at ODP Site 925 on Ceara Rise in the tropical Atlantic Ocean (Pearson & Chaisson, 1997), but the bioevent cannot be correlated from site to site with this level of precision. Pearson et al. (2023) suggested a broad age of 1.97±0.17 Ma, which is applicable to the Atlantic and Indo-Pacific Oceans. Our illustrated collection includes a specimen from near the beginning of the range at 1.91 Ma (see Figs. 7.6a–c).

PHYLOGENETIC RELATIONSHIPS.—*Pulleniatina finalis* is the end-stage of the *obliquiloculata* lineage and fully intergrades with the *P. obliquiloculata* morphospecies (Banner & Blow, 1967).

REPOSITORY.—Holotype (Number 1966.2.3.1) deposited in the Natural History Museum, London, UK.

***Pulleniatina obliquiloculata* (Parker & Jones, 1865)**

Figs. 8.1a–8.11

? *Pullenia obliquiloculata* Parker & Jones, in Carpenter et al., 1862, p. 183 (nomen nudum).

? *Pullenia obliquiloculata* Parker & Jones, 1865, p. 365, 368, pl. 19, figs. 4a–b [Dredge sample, probably Recent, probably Abrolhos Bank, South Atlantic Ocean].

Pullenia obliquiloculata Parker & Jones, 1865.—Brady, 1884, p. 618 (partim), pl. 84, figs. 17, 20 [Recent, *Challenger* Station 5, south-west of Canary Islands, North Atlantic Ocean], 18 [plankton net, *Challenger Station* 215, West Pacific Ocean], 19 [Recent, *Challenger* Station 344, near Ascension Island, tropical South Atlantic Ocean] (not pl. 84, fig. 16, = *Pulleniatina finalis*).—Hodgkinson, 1992, p. 61 (description of neotype, not illustrated).

Pullenia sphaeroides var. *obliquiloculata* Parker & Jones, 1865.—Banner & Blow (1960, p. 25, pl. 7, figs. 4a–c) ['lectotype', actually neotype, Abrolhos Bank, South Atlantic Ocean].

Pullenia obliquiloculata Parker & Jones.—Cushman, 1914, p. 22, pl. 10, fig. 3; pl. 12, figs. 2, 3 [surface sediment, North Pacific Ocean, locality unspecified].

Pulleniatina obliquiloculata (Parker & Jones, 1865).—Cushman, 1927b, p. 174 [Pacific coast of America; not illustrated].—Bé, 1959, p. 83, pl. 2, figs. 4–6 [plankton Station VII-FL.3, western North Atlantic Ocean].—Parker, 1962, p. 234, pl. 4, figs. 13–16, 19, 22 [Recent, *Downwind* Station BG 114, tropical west Pacific Ocean].— Postuma, 1971, p. 380, pl. on p.

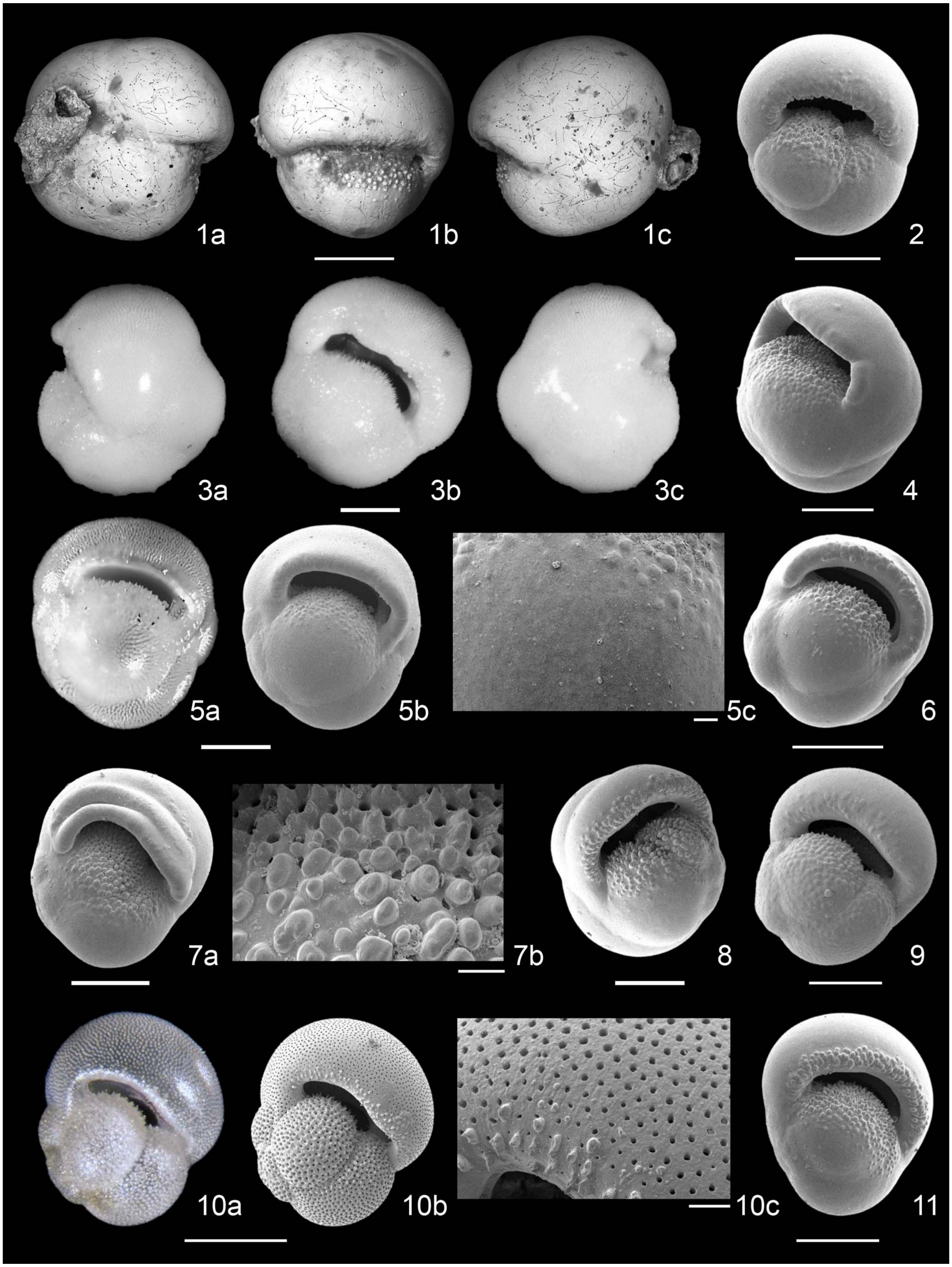


FIGURE 8. *Pulleniatina obliquiloculata* (Parker & Jones, 1865). **1a–c** neotype (ZF3583), environmental SEM, non-standard orientations, note wall surface is affected by scattered surface deposits (?glue), Abrolhos Bank, South Atlantic Ocean. **2** SEM, IODP Site U1483, Indian Ocean, 0.99 Ma. **3a–c** z-stacked LMs, IODP Site U1488, Pacific Ocean, 0.095 Ma (Fabbrini et al., in press, figs. 2aq–as). **4** IODP Site U1483, Indian Ocean, 0.054 Ma. **5a–c** z-stacked LM and SEMs, IODP Site U1483, Indian Ocean, 0.99 Ma. **6** SEM, IODP Site U1483, Indian Ocean, 0.99 Ma, 1.46 Ma. **7a–b** SEMs, IODP Site U1483, Indian Ocean, 0.054 Ma; note crenulated final chamber. **8** SEM, IODP Site U1483, Indian Ocean, 0.99 Ma; sinistral specimen. **9** SEM, ODP Site 925, Atlantic Ocean, 0.245 Ma. **10a–c** z-stacked LM and SEMs, IODP Site U1483, Indian Ocean, 0.054 Ma; pre-gametogenic specimen without cortex. **11** SEM, IODP Site U1483, Indian Ocean, 1.46 Ma. Scale bars = 200 µm, except 5c, 7b, and 10c = 20 µm. For full sample details see Table 1.

381, four specimens [Recent, *Challenger* Station 224, north of Admiralty Islands, western tropical Pacific Ocean].—Lamb & Beard, 1972, p. 58, pl. 29, figs. 1–4 [*Globorotalia tosaensis* Subzone, Gulf of Mexico, North Atlantic Ocean].—Parker, 1973, p. 77, pl. 1, fig. 12 [juvenile specimen, plankton tow, Gulf of California].—Keigwin, 1976, pl. 1, fig. 12 [Pleistocene, DSDP Site 157, Panama Basin, eastern equatorial Pacific Ocean].—Burt & Scott, 1975, pl. 1, figs. 1–7; pl. 2, figs. 1, 2, 6–10; pl. 3, figs. 1–4, 6, 8–12 [Recent, *Challenger* Station 224, north of Admiralty Islands, western tropical Pacific Ocean], pl. 1, figs. 8–12; pl. 2, figs. 11, 12; pl. 3, fig. 5 [Recent, *Mestayer* Station 20, western Pacific Ocean off North Island, New Zealand].—Saito, 1976, p. 305, fig. 1 (upper pair) [probably Pleistocene, *Vema* Core V24–58, central equatorial Pacific Ocean.—Saito et al., 1981, p. 96–100, pl. 30, figs. 1a–c [core top, *Vema* Core V12-126, North Atlantic Ocean], figs. 2a–c [core top, *Vema* Core V3–5, North Atlantic Ocean], pl. 31, figs. 3a–c [core top, *Vema* Core V14-16, North Atlantic Ocean].—Keigwin, 1982, pl. 11, figs. 2–4 [upper Pliocene *Pulleniatina obliquiloculata* Zone, DSDP Site 502, Columbian Basin, western tropical Atlantic Ocean].—Boltovskoy et al., 1982, p. 206, pl. 6, fig. 19, 20 [Quaternary, subsurface core at 32°58′S, 48°58′W, southwestern Atlantic off Brazil].—Moullade, 1983, pl. 9, figs. 8–10 [lower Pleistocene Zone N22/N23, DSDP Site 533, Blake Outer Ridge, North Atlantic Ocean].—Bolli & Saunders, 1985, p. 247–248, fig. 40.4 (‘lectotype’, actually neotype, reproduced from Banner & Blow, 1967), figs. 4.9–12 [Pleistocene *G. truncatulinoides* Zone, DSDP Site 73, Central Pacific Ocean].—Loeblich & Tappan, 1987, pl. 524, figs. 4–8 (reproduced from Brönnimann & Resig, 1971), figs. 9–12 (reproduced from Bolli et al, 1957).—Hemleben et al., 1987, p. 28, figs. 2.7c, d (location not specified).—Loeblich & Tappan, 1994, pl. 187, figs. 8–13, pl. 188, figs. 1–6 [Recent, Timor Sea, tropical Indian Ocean].—Wynn Jones, 1994, p. 132 (partim), pl. 84, figs. 17–20 (reproduced from Brady, 1884) (not pl. 84, fig. 16 = *P. finalis*).—Perembo, 1994, pl. 3, figs. 4–5 [Pleistocene Zone N22, ODP Site 832, Aoba Basin, Vanuatu, western tropical Pacific Ocean].—Chaproniere & Nishi, 1994, p. 225, pl. 3, figs. 22–24 [Pleistocene *Globorotalia (Truncorotalia) crassaformis viola* Subzone, ODP Site 835, Lau Basin, tropical west Pacific Ocean].—Norris, 1998, p. 52, pl. 3, fig. 8 [Pliocene (now lower Pleistocene) Zone PL6, ODP Site 959, eastern equatorial Atlantic Ocean].—Ujiié & Ujiié, 2000, p. 352, pl. 1, figs. 14–16 [Holocene, Pilot Core RN95-PC1, Okinawa Trough, north-western Pacific Ocean].—Hayashi et al., 2011, p. 5, pl. 3, fig. 4a–c [Pleistocene Zone N22, IODP Site C0001, North Pacific Ocean].—Hayashi et al., 2013, fig. 7.13 [Pleistocene Subzone PT1b, IODP Site U1338, eastern equatorial Pacific Ocean].—Singh & Verma, 2014, Fig. 2b(8) [level and site uncertain, northern Indian Ocean].—Schiebel & Hemleben, 2017, p. 66, pl. 2.22, figs. 1–9 [locations not specified].—Takagi et al., 2019, fig. 2.21 [living specimen, locality unspecified].—Stainbank et al., 2019, fig. 5, 7a–f [Holocene, IODP Site U1467, Maldives Inner Sea, tropical Indian Ocean].—Noucoucouk et al., 2021, fig. 4.La–Lb [Pleistocene, Core ANP 1011, Ceará Basin, equatorial Atlantic Ocean].—Singh et al., 2021, p. 18, pl. 2, figs. 9–10, 15 [Pleistocene, DSDP Hole 762B, Exmouth Plateau, southeast Indian Ocean], 11 [Pleistocene, DSDP Hole 763A, Exmouth Plateau, southeast Indian Ocean]. Fabbrini et al., in press, figs. 2ak–ap, 9a–g [Pleistocene, Subzone PT1b, IODP Hole U1488A, Eauripik Rise, western equatorial Pacific Ocean].

Pulleniatina obliquiloculata obliquiloculata (Parker & Jones, 1865).—Banner & Blow, 1967, p. 137–139, pl. 3, figs. 4a–c (‘lectotype’, actually neotype, re-illustrated), pl. 4, fig. 9 [Pleistocene Zone N22, Playa Grande Formation, Venezuela].—Brönnimann & Resig, 1971, pl. 16, figs. 1–2, 4, 10; pl. 17, figs. 1–6; pl. 18, figs. 1–7 [Recent Zone N23, DSDP Site 64, Ontong Java Plateau, western equatorial Pacific Ocean]; pl. 16, figs. 3, 5–9, 11; pl. 19, fig. 6 [Recent Zone N23, DSDP Site 62, Eauripik Rise, western equatorial Pacific Ocean].—Lidz & McNeill, 1995, pl. 2, figs. 29–33 [Pleistocene Zone N22, CLINO borehole, Great Bahama Bank, North Atlantic Ocean].

Pulleniatina obliqueloculata (sic) (Parker & Jones).—Cushman, 1927a, p. 90, pl. 19, figs. 5a–b [locality unknown].—Coryell & Mossman, 1942, p. 239, pl. 36, fig. 31 [Pliocene, Charco Azul Fm., Panama].—Bolli et al., 1957, p. 33 (‘lectotype’, actually neotype, designated but not illustrated), pl. 4, figs. 3a–c (para-neotypes) [Recent, Abrolhos Bank, South Atlantic Ocean], pl. 4, figs. 4a–5 [Recent, location unspecified, Pacific Ocean].—Schnitker, 1971, pl. 8, figs. 6a–b [Recent, North Carolina shelf, North Atlantic Ocean].—Hayward, B.W., 2013 [online image World Register of Marine Species (WoRMS), https://www.marinespecies.org/aphia.php?p=image&pic=38547&tid=221331; accessed 20-06-2024].

Pulleniatina obliqueloculata obliqueloculata (sic) (Parker & Jones).—Iaccarino & Salvatorini (1979, pl. 9, fig. 11) [Pleistocene Zone N22, DSDP Site 398, Vigo Seamount, Iberian Margin, North Atlantic Ocean].

Pulleniatina obliqueloculata [sic] phenon *obliqueloculata* (Parker & Jones).—Fordham, 1986, pl. 20, figs. 2a–4b, 11a–12b [Pliocene *P. obliqueloculata* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean], pl. 20a–23b [Pliocene *P. obliqueloculata* Zone, DSDP Site 77A, eastern equatorial Pacific Ocean].

Globigerina antillensis Bermúdez, 1961, p. 1156, pl. 1, figs. 1a–c [Recent, *Atlantis* Station 2988, Nicholas Channel, Caribbean Sea].

Pulleniatina obliquiloculata finalis Banner & Blow.—Brönnimann & Resig, 1971, pl. 19, figs. 1–3 [Recent Zone N23, DSDP Site 62, Eauripik Rise, western equatorial Pacific Ocean]. (Not Banner & Blow, 1967.)

Pulleniatina okinawaensis Natori, 1976, pl. 5, fig. 5a–6c [Pleistocene *Globorotalia* (*G.*) *truncatulinoides* Zone, Chinen Fm., Okinawa Island, Ryuku Islands, Japan].—Ujiié & Ujiié, 2000, p. 352, pl. 1, fig. 13 [Holocene, Pilot Core RN95-PC1, Okinawa Trough, north-western Pacific Ocean].—Hanagata & Nobuhara, 2015, p. 52, figs. 18.1–2 [Pliocene Zone PL5, Minebari Fm., Miyakojima Island, Ryuku Islands, Japan].

Pulleniatina cf. *okinawaensis* Natori.—Moullade, 1983, pl. 9, figs. 5–7 [lower Pleistocene Zone N22/N23, DSDP Site 533, Blake Outer Ridge, North Atlantic Ocean].

Pulleniatina obliqueloculata [sic] phenon *okinawaensis* (Natori).—Fordham, 1986 (partim), pl. 20, figs. 16–19 [Pliocene *P. obliqueloculata* Zone, DSDP Site 77A, eastern equatorial Pacific Ocean].

Globigerina santamariaensis McCulloch, 1977, p. 416, pl. 172, fig. 7 [Bahia Santa Maria, Baja California, eastern Pacific Ocean].

Pulleniatina sp. 1, Belford, 1988, pl. 3, figs. 17–19 [Dredge DR10, north of New Ireland, Papua New Guinea].

Not *Pulleniatina obliquiloculata* (Parker & Jones, 1865).—Stainforth, 1948, p. 125, pl. 26, figs. 21–23 (= *P. praecursor*).—McTavish, 1966, pl. 5, figs. 6, 13, 25 (= *P. primalis*), pl. 6, figs. 12, 15 (= *P. praecursor*).—Jenkins & Orr, 1972, pl. 39, figs. 1–2 (indicated as *P. finalis* but included in synonymy with *P. obliquiloculata*; = *P. finalis*).—Kennett & Srinivasan, 1983, p. 202, pl. 50, figs. 6–9 (= *P. finalis*).—Wynn Jones, 1994, p. 132 (partim), pl. 84, figs. 16a–b (= *P. finalis*).—Hanagata & Nobuhara, 2015, p. 52, fig. 17.20 (= *P. primalis*).

Not *Pulleniatina obliquiloculata obliquiloculata* (Parker & Jones, 1865).—Belford, 1988, pl. 3, fig. 5, pl. 3, figs. 6–8 (all recorded as "strongly involute forms" = *P. finalis*).

DESCRIPTION.—Nonspinose, porous and weakly cancellate, pustulose on the chamber shoulders around and within the aperture. In the terminal stage, test covered in a translucent non-porous cortex with a smooth reflective surface that can be degraded by diagenesis to a dull glossy sheen. Large, inflated test, subspherical; ventrally involute coiling, initially trochospiral, then streptospiral; 3 to 4 globular chambers in final whorl, moderately or rapidly increasing in size, final chamber sometimes flattened or undulatory. Chambers appressed and embracing, sutures gently curving, weakly depressed to indistinct beneath the dense cortex. Test lacks a true umbilicus because of the enveloping final chamber. Aperture a broad low arch extending to the equatorial periphery and sometimes onto the spiral side, often irregular; no lip but a thickened pustulose rim. Coiling exclusively dextral in Recent but variable downcore.

DISTINGUISHING FEATURES.—*Pulleniatina obliquiloculata* is distinguished from *P. praecursor* by having more globular chambers, tighter and more streptospiral coiling, less well-defined sutures, and a larger, more globular test. It is not pseudo-planispiral like *P. finalis*. Parker (1967, p. 173) differentiated *P. obliquiloculata* from *P. primalis*/*praecursor* (which she lumped) by the presence of what she called a "linear suture", defined as a "single suture formed by the meeting of the final two sutures prior to reaching the umbilical area", although she recognized this was an arbitrary distinction. While an interesting observation, we have found this definition difficult to apply due to ambiguity as to what represents the umbilical area, but in essence Parker's criterion is a function of the more streptospiral coiling mode. This species can be confused with *Globoconella inflata* which also has a glossy reflective surface (Fenton et al., 2018, p. 438–440) but *G. inflata* is more compact with a smaller adult size, has trochospiral coiling, slightly better-defined sutures, and a low aperture with a more distinct umbilicus.

DISCUSSION.—The taxon *Pullenia obliquiloculata* first appeared in Carpenter et al. (1862, p. 183) where it was attributed to Parker and Jones but not illustrated. The single specimen illustrated by Parker & Jones (1865) as *Pullenia obliquiloculata* is lost. It is probably from the Abrolhos Bank off Brazil, although the plate caption refers to three different locations (Parker & Jones, 1865, p. 421; see also discussion in Hodgkinson, 1992, p. 61). Parker & Jones (1865, p. 368) noted that their species "has the chambers set on obliquely", hence the specific name *obliquiloculata*. Parker & Jones's original illustration appears to have a pseudo-planispiral chamber arrangement that, in our opinion, may better fit the modern concept of *P. finalis*. However, it would be gratuitous to upset the taxonomy based on a drawing of a lost specimen that is inadequate by modern standards, and after a neotype has been selected and widely accepted (see below), so Parker & Jones's specimen is here placed in questionable synonymy with *obliquiloculata*.

A stable concept for the species developed around the excellent illustrations in the HMS *Challenger* report (Brady, 1884), one of which is assigned to *P. finalis* in this study. A 'lectotype' (actually a neotype as the specimen is not from the original syntype series; see Hodgkinson, 1992, p. 61) was designated by A.R. Loeblich from the original Abrolhos Bank sediment sample curated in the Natural History Museum, London, as reported by Bolli et al. (1957, p. 33). Unfortunately, Bolli et al. (1957) misspelled the species name *obliqueloculata* following earlier usage (e.g., Cushman, 1927a) and this misspelling has propagated through part of the literature. The neotype specimen was illustrated for the first time by Banner & Blow (1960) with good quality line drawings and with a new set of drawings by Banner & Blow (1967). It is shown here in SEM on Figures 8.1a–c. The neotype specimen is not an especially close match to Parker & Jones's original illustration as discussed above.

Globigerina antillensis Bermúdez 1961 has been proposed as an adult pre-gametogenic specimen of *P. obliquiloculata* (Banner & Blow, 1967; Saito et al., 1981; Brummer & Kučera, 2022). The original illustrations (reproduced in Figs. 6.1a–c) are inadequate, but we have confirmed this with new environmental SEMs of the holotype (compare Figs. 6.1d–f with Figs. 8.10a–b). It has not been recognized by any other author. *Pulleniatina okinawaensis* Natori 1976 (reproduced in Figs. 6.2a–c) appears to be a similar case (Brummer & Kučera, 2022), although it has been recognized as a separate taxon by various authors (Fordham, 1986; Ujiié & Ujiié, 2000; Hanagata & Nobuhara, 2015). *Globigerina santamariaensis* McCulloch 1977 (reproduced in Figures 6.4a–c) is regarded as a probable juvenile or pre-adult ontogenetic stage of *P. obliquiloculata* as occur frequently in subtropical settings (Saito et al., 1981).

(PALEO)ECOLOGY.—Modern *P. obliquiloculata* is an asymbiotic herbivore that grazes algae at depth around the Deep Chlorophyll Maximum. Stable isotope evidence (relatively light δ^{13}C and heavy δ^{18}O compared to mixed-layer dwelling species) suggests that it has always had a similar life habit, perhaps becoming progressively deeper on average through time (see discussion above).

GEOGRAPHIC DISTRIBUTION.—*Pulleniatina obliquiloculata* is a tropical to subtropical species with highest abundance in the equatorial Pacific Ocean (see Fig. 4B). Away from its core area, abundance levels fluctuate seasonally and with climatic change. Rare individuals occur as far as 45°N in the Gulf Stream (Bé, 1959). Concentrations of *P. obliquiloculata* in the sediment have been used to track Quaternary climatic changes related to the influence of the Kurushio Current (Li et al., 1997; Xu et al., 2005; Lin et al., 2006; see also discussion in Sijinkumar et al., 2011). It is also sensitive to El Niño oscillations (Watkins et al., 1998; Yamasaki et al., 2008). It was absent from the Atlantic Ocean for an extended period in the late Pliocene and early Pleistocene between 3.37 and 2.24 Ma (Pearson et al., 2023). Local disappearances from the Caribbean Sea and parts of the Atlantic Ocean in the Quaternary have also been related to climate (Prell & Damuth, 1978).

STRATIGRAPHIC RANGE.—The first appearance of *P. obliquiloculata* has been recorded at various levels, partly because of differing species concepts. The full literature was reviewed by Pearson et al. (2023) who suggested a global biochronological calibration of 4.22±0.12 Ma (see Table 2). It persists to the Recent. In the Atlantic record there is a long interval in which *Pulleniatina* is mostly absent (see Table 2).

PHYLOGENETIC RELATIONSHIPS.—*Pulleniatina obliquiloculata* intergrades with the *Pulleniatina praecursor* and *P. finalis* morphospecies as part of the same evolutionary lineage. Its distinction from both forms can be somewhat arbitrary because of full intergradation.

REPOSITORY.—Neotype (ZF 3583, ex. *HMS Challenger* Sample 94.4.3.1045) deposited in the Natural History Museum, London, UK.

***Pulleniatina praecursor* Banner & Blow, 1967**

Figs. 9.1a–9.12b

Pulleniatina obliquiloculata (Parker & Jones, 1865).—Stainforth, 1948, p. 125, pl. 26, figs. 21–23 ['upper Miocene' (= probably Pliocene), Ecuador].— McTavish, 1966 (partim), pl. 6, figs. 12, 15 [Miocene to Pliocene Malaita Group, Solomon Islands] (not pl. 5, figs. 6, 13, 25 = *P. primalis*). (Not Parker & Jones, 1865.)

Pulleniatina praeobliquiloculata Lloyd, 1961, p. 115–118 [Subsurface 'Miocene' (probably Pliocene), Wreck Island, Queensland, Australia] (nomen nudum).

? *Pulleniatina obliqueloculata* var. *trochospira* Hartono, 1964, p. 10, pl. 8, figs. a–c [upper Miocene – Pliocene, Bali, Indonesia].

Pulleniatina semiinvoluta Germeraad.—Parker, 1965 (partim), figs. 5a–c [Pliocene, Core LSDH 78P, central tropical Pacific Ocean]. (Not Germeraad, 1946.)

Pulleniatina obliquiloculata praecursor Banner & Blow, 1967, p. 139–140, pl. 3, figs. 3a–c [upper part of Pliocene Zone N19, Borbón Fm., Ecuador].—Kadar, 1972, p. 64, pl. 4, figs. 22a–c ['upper Miocene' (=probably Pliocene), Bali, Indonesia].

Pulleniatina praecursor Banner & Blow.—Postuma, 1971, p. 382, pl. on p. 382, 2 specimens [Pliocene, Bodjonegoro Well, Java, Indonesia].—Kennett & Srinivasan, 1983, p. 200, pl. 49, figs. 6–8 [lower Pliocene Zone N19, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean].—Bolli & Saunders, 1985, p. 247, fig. 40.5 (holotype, reproduced from Banner & Blow, 1967), figs. 41.1–2, 13–17 ['upper Pliocene' (now lower Pleistocene) *G. tosaensis* Zone, DSDP Site 148, Aves Ridge, Caribbean Sea], pl. 41.18–19 [lower Pliocene *G. margarita margaritae* Zone, Cubagua Fm., Venezuela].—Chaproniere, 1991, pl. 3, figs. 13–15 [Pliocene, *Rig Seismic* Gravity Core 51GC22-214, Queensland Plateau, offshore Queensland, Australia].—Chaproniere & Nishi, 1994, p. 225, pl. 3, figs. 19–21 [Pliocene *Globorotalia crassaformis viola* Zone, ODP Hole 835A, Lau Basin, tropical western Pacific Ocean].—Perembo, 1994, pl. 3, fig. 3 [Pliocene Zone N19 (lower part), ODP Site 832, Aoba Basin, Vanuatu, western tropical Pacific Ocean].—Singh & Verma, 2014, fig. 2b(7) [level and site uncertain, northern Indian Ocean].—Singh et al., 2021, p. 18, pl. 2, figs. 5–8 (Note: listed as *precursor* (sic) on p. 18) [Pliocene, DSDP Hole 762B, Exmouth Plateau, southeast Indian Ocean].—Permana et al., 2021, figs. 7.13a–c [Pliocene, Limboto Limestone, Sulawesi, Indonesia].

Pulleniatina obliqueloculata [sic] phenon *praecursor* Banner & Blow.—Fordham, 1986 (partim), pl. 19, figs. 17a–b, 19a–21b, 30a–b [Pliocene *S. dehiscens* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean], figs. 32a–b, 39a–40b [Pliocene *G. fistulosus* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean], figs. 43a–45b [Pliocene *P. obliqueloculata* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean], pl. 20, figs. 7a–b [Pliocene *P. obliqueloculata* Zone DSDP Site 77B, eastern equatorial Pacific Ocean], pl. 20, figs. 14a–b [Pliocene *P. obliqueloculata* Zone DSDP Site 77A, eastern equatorial Pacific Ocean] (not pl. 19, figs. 18a–b, = *P. praespectabilis*, pl. 20, figs. 5a–6b = *P. primalis*).

Pulleniatina primalis Banner & Blow 1967.—Jenkins & Orr, 1972 (partim), pl. 39, figs. 5–7 [Pliocene *S. dehiscens* Zone, DSDP Site 82, eastern equatorial Pacific], figs. 8–10 [Pliocene *S. dehiscens* Zone, DSDP Site 83, eastern equatorial Pacific].—Kadar, 1972, p. 64 (partim), pl. 4, figs. 20a–c ['upper Miocene' (probably Pliocene), Bali].—Singh & Verma, 2014, figs. 2b(5, 6) [level and site uncertain, northern Indian Ocean].— (Not Banner & Blow, 1967.)

Pulleniatina alticuspis Carreño 1985, p. 154–156, pl. 2, figs. 18–20, text-fig. 7a–c [Pliocene, Arroyo-Hondo section, Isla Maria Madre, eastern Pacific Ocean offshore Mexico].

Not *Pulleniatina* aff. *Pulleniatina praecursor* Banner & Blow, 1967.—Brönnimann & Resig, 1971, fig. 22 [Pleistocene Zone N22, DSDP Site 62, Eauripik Rise, western equatorial Pacific Ocean] (=*P. obliquiloculata*).

Not *Pulleniatina praecursor* Banner & Blow, 1967.—Saito et al., 1981, p. 101, pl. 32, figs. 1a–2b (= *P. obliquiloculata*).—Hanagata & Nobuhara 2015, p. 52, figs. 18.3–4 (=*P. primalis*).

DESCRIPTION.—Nonspinose, porous and weakly cancellate, pustulose on the chamber shoulders around and within the aperture and on apertural face. In the terminal stage, test covered in a translucent non-porous cortex with a smooth

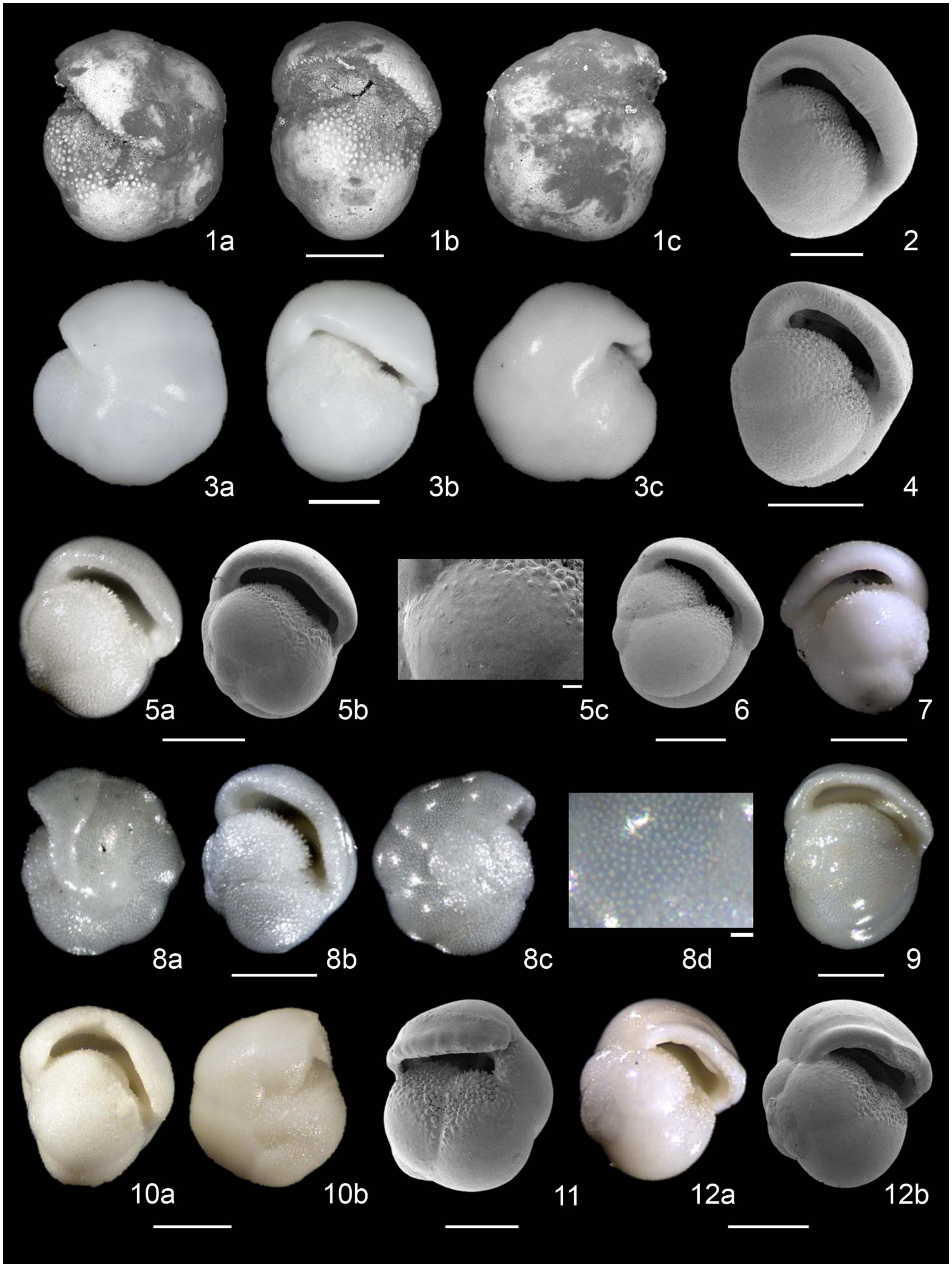


FIGURE 9. *Pulleniatina praecursor* Banner & Blow, 1967. **1a–c** holotype (P46423), environmental SEM, note wall surface is affected by scattered surface deposits (?glue), upper part of Pliocene Zone N19, Borbón Fm., Ecuador. 2 SEM, IODP Site U1488, Pacific Ocean, 3.14 Ma. **3a–c** z-stacked LMs, IODP Site U1488, Pacific Ocean, 3.28 Ma (Fabbrini et al., in press, figs. 2ae–aj). **4, 5a–c** SEMs and z-stacked LM, IODP Site U1482, Indian Ocean, 3.36 Ma. **6** SEM, IODP Site U1488, Pacific Ocean, 3.42 Ma. **7** z-stacked LM, IODP Site U1488, Pacific Ocean, 3.14 Ma. **8a–d, 9** z-stacked LMs, RV *Pelagia* Station GLOW 22, Indian Ocean, 4.4 Ma, exceptionally well-preserved, note translucent cortex with visible pore channels. **10a–b** z-stacked LMs, IODP Site U1488, Pacific Ocean, 3.28 Ma. **11, 12a–b** SEMs and z-stacked LM, IODP Site U1482, Indian Ocean, 3.36 Ma, high-spired variants. Scale bars = 200 µm, except 5c, 8d = 20 µm. For full sample details see Table 1.

reflective surface that is often degraded by diagenesis to a dull glossy sheen. Test medium sized, somewhat inflated, oblate subspherical; ventrally involute coiling, initially trochospiral, then slightly streptospiral; 4 to 6 globular chambers in final whorl, increasing moderately in size. Chambers appressed and embracing, sutures gently curving, weakly depressed. Umbilicus generally obscured because of the enveloping final chamber which typically extends over it in a loose, flap-like manner. Aperture a broad low arch extending to the equatorial periphery, except on some high-spired streptospiral variants that intergrade with *P. obliquiloculata*. Coiling direction varies down-core.

DISTINGUISHING FEATURES.—*Pulleniatina praecursor* intergrades with both *P. primalis* and *P. obliquiloculata*, so its distinction from both forms can be somewhat arbitrary. It differs from *P. primalis* by possessing an aperture that extends at least as far as the equatorial periphery and its more irregular coiling in some specimens. It differs from *P. obliquiloculata* by being generally smaller, thinner-walled and less distinctly streptospiral and globular than *P. obliquiloculata*, usually with more chambers in the final whorl. Populations of *P. praecursor* may vary in their average number of chambers per whorl or spire height. It is similar to *Globoconella inflata*, which also has a glossy reflective surface, but *G. inflata* is more compact and regularly trochospiral.

DISCUSSION.—Although *Pulleniatina* was long regarded as a monospecific genus (e.g., Bolli et al., 1957), it gradually become evident that Pliocene populations were morphologically distinct from modern assemblages, especially in being more regularly trochospiral. Stainforth (1948) illustrated a specimen of '*P. obliquiloculata*' from the 'upper Miocene' (probably Pliocene) of Ecuador, noting that it did not tend to involute planispiral coiling like modern forms; this is now clearly referable to *P. praecursor*. Germeraad (1946) named a trochospiral species called *Pulleniatina semiinvoluta* from sediments exposed on the island of Ceram (or Seram), Indonesia, but Banner & Blow (1967) showed that this is in fact a smooth-walled benthic foraminifer with an areal aperture and transferred it to their new genus *Rotaliatinopsis*. Lloyd (1961, p. 115–118) named *Pulleniatina praeobliquiloculata* in an unpublished thesis (now available online via mikrotax.org) in which the repository is not given and the species is not illustrated; the name is hence regarded as nomen nudum. Parker (1965, text-figs. 5a–6c) illustrated two specimens of Pliocene *Pulleniatina* as '*P. semiinvoluta*'. One of these is now referable to *P. praecursor* and the other to *P. primalis*.

Hartono (1964) described *Pulleniatina obliqueloculata* [sic] var. *trochospira* from the 'upper Miocene to Pliocene' of Bali, Indonesia (illustration reproduced here in Figs. 6.3a–c). He distinguished this from typical *P. obliquiloculata* by being "more trochospiral than streptospiral" with an aperture that extends "the whole length of the base of the apertural face" (Hartono, 1964, p. 10). Banner & Blow (1967) regarded Hartono's taxon as a synonym of *P. obliquiloculata*, albeit exhibiting "primitive features" for that taxon, including the less obviously streptospiral coiling mode. In our opinion Hartono's illustration falls closer to *P. praecursor* than *P. obliquiloculata* and thus might be regarded as a senior synonym of *P. praecursor*. However, the name has never been used (to our knowledge) since Hartono's (1964) publication, unlike *P. praecursor*, which has been used many times, and to reinstate it now would cause instability; moreover, the case is questionable because the type illustration is poor by modern standards. *Pulleniatina obliqueloculata* var. *trochospira* is therefore listed as a questionable synonym of *P. praecursor*.

Pulleniatina alticuspis Carreño 1985 from the Pliocene of Mexico seems not to have been used by any other author since its initial description. One view of the holotype is re-illustrated here in Figure 6.5. A fine suite of paratypes is deposited at the U.S. National Museum and was examined as part of this study. Here it is regarded as a high-spired variant of *P. praecursor*. We have observed much variation in the spire height of *Pulleniatina* populations throughout their range, especially *P. praecursor*. A good example of a published image of a high-spired variant is the specimen illustrated in three views by Postuma (1971), and we illustrate two specimens in Figures 9.11–9.12. At this stage we see no good reason geographically or stratigraphically to formally separate these forms.

A complete description of *P. praecursor* was provided by Banner & Blow (1967). Some authors (e.g., Kaneps, 1973; Orr & Jenkins, 1980) have regarded it as a synonym of *P. primalis* while others (e.g., Beckmann, 1971; Chaisson & Leckie, 1993) have combined it with *P. obliquiloculata* or simply omitted it, but it is separated here to try to achieve consistency with Banner & Blow (1967) and the majority of studies that have followed them.

PALEOECOLOGY.—Pearson & Shackleton (1995) and Boscolo-Galazzo et al. (2021) found that *P. praecursor* had very similar stable isotope ratios to *P. obliquiloculata* (relatively light δ^{13}C and heavy δ^{18}O compared to mixed-layer dwelling species) suggesting a similar habitat as a subsurface herbivore living around the Deep Chlorophyll Maximum.

GEOGRAPHIC DISTRIBUTION.—Globally distributed in the tropics and subtropics. It was absent from the Atlantic Ocean for an extended period in the late Pliocene and early Pleistocene between 3.37 and 2.24 Ma (Pearson et al., 2023).

STRATIGRAPHIC RANGE.—Both the base and top occurrence are based on gradual transitions and precise determination is subjective and depends on species concepts. Neither biohorizon has been used widely for biostratigraphic correlation. The bottom occurrence is at 4.52±0.10 Ma and top occurrence at 1.90±0.15 Ma (see Table 2).

PHYLOGENETIC RELATIONSHIPS.—Evolved from *P. primalis* and gave rise to *P. obliquiloculata*, apparently as part of a single unbroken evolutionary lineage.

REPOSITORY.—Holotype (P 46423) deposited in the Natural History Museum, London, UK.

Pulleniatina praespectabilis Parker, 1965

Figs. 10.1a–10.14

Pulleniatina sp. ex. interc. *primalis* Banner & Blow and *spectabilis* Parker.—Banner & Blow, 1967, pl. 2, fig. 1 [upper Miocene Zone N18, Moenoek River section, west Irian, New Guinea].

Pulleniatina spectabilis praespectabilis Brönnimann & Resig, 1971, p. 1286–1287, pl. 19, figs. 4, 7 [Pliocene Zone N19–N20, DSDP Site 62, Eauripik Rise, western equatorial Pacific

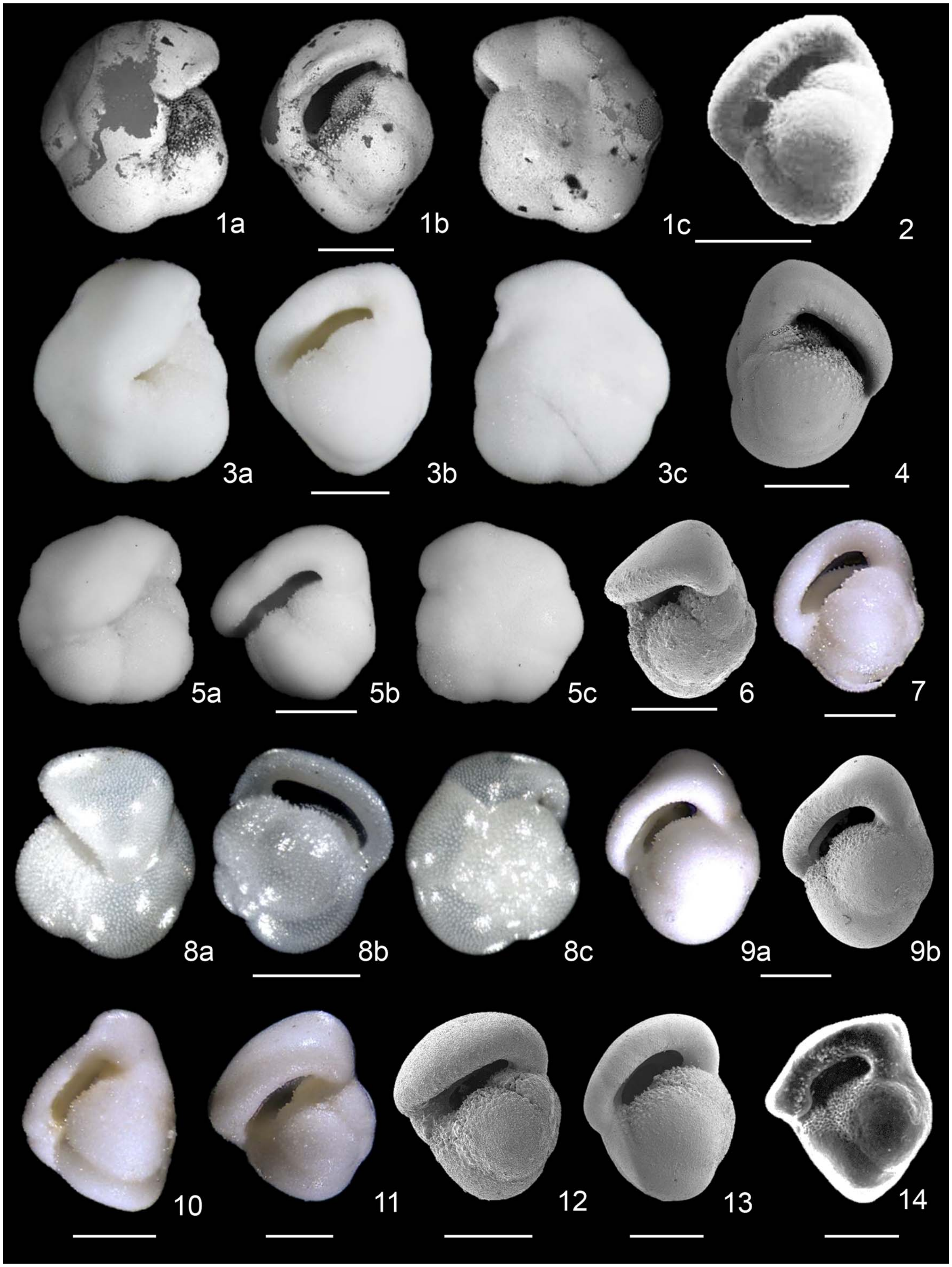


FIGURE 10. *Pulleniatina praespectabilis* Brönnimann & Resig, 1971. **1a–c** holotype (USNM-219449), environmental SEM, note wall surface is affected by scattered surface deposits (?glue), Pliocene Zone N19–N20, DSDP Site 62, Eauripik Rise, western equatorial Pacific Ocean. **2** SEM, Zone N17, DSDP Site 219, Sample 219/8/6, 70–72 cm, Arabian Sea (reproduced from Fleisher, 1974, pl. 15, fig. 3). **3a–c** z-stacked LMs, IODP Site U1488, Pacific Ocean, 5.28 Ma (Fabbrini et al., in press, figs. 2ae–aj). **4** SEM, IODP Site U1482, Indian Ocean, 5.26 Ma, dextral specimen. **5a–c** z-stacked LMs, IODP Site U1488, Pacific Ocean, 5.28 Ma. **6, 7** SEM and z-stacked LM, ODP Site 873, Pacific Ocean, 4.6 Ma. **8a–c** z-stacked LMs, RV *Pelagia* Station GLOW-22, Indian Ocean, 4.4 Ma, exceptionally well-preserved specimen with translucent cortex. **9a–12** z-stacked LMs and SEMs, ODP Site 873, Pacific Ocean, 4.6 Ma. **13** SEM, ODP Site 873, Pacific Ocean, 4.6 Ma, transitional to *P. primalis*. **14** SEM, lower Pliocene *Sphaeroidinella dehiscens* Zone, DSDP Hole 503B, eastern equatorial Pacific Ocean, transitional to *P. spectabilis* (reproduced from Keigwin, 1982, pl. 11, fig. 1). Scale bars = 200 µm. For full sample details see Table 1.

Ocean].—Belford, 1988, pl. 3, figs. 14–16 [Pliocene, New Ireland, Papua New Guinea].

Pulleniatina praespectabilis Brönnimann & Resig, 1971.—Fleisher, 1974, p. 1031, pl. 15, fig. 2 [lower Pliocene Zone N17, DSDP Site 219, Arabian Sea].—Bolli & Saunders, 1985, p. 250, fig. 40.1 (holotype, reproduced from Brönnimann & Resig, 1971).—Chaisson & Leckie, 1993, p. 165, pl. 8, fig. 2 [Pliocene Zone N18–N19, DSDP Site 806, Ontong Java Plateau, western equatorial Pacific Ocean].

Pulleniatina obliqueloculata [sic] phenon *praespectabilis* Brönnimann & Resig.—Fordham, 1986, pl. 19, figs. 22a–b, 31a–b [Pliocene *S. dehiscens* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean].

Pulleniatina spectabilis Parker, 1965.—Parker, 1965, p. 151–152 (partim), figs. 3–4 [Pliocene, Core LSDH 78P, central tropical Pacific Ocean] (=*Pulleniatina praespectabilis*).—Keigwin, 1982, pl. 11, fig. 1 [lower Pliocene *Sphaeroidinella dehiscens* Zone, DSDP Site 503, eastern equatorial Pacific Ocean].—Kennett & Srinivasan, 1983, p. 202 (partim), pl. 50, fig. 5 (reproduced without attribution from Keigwin, 1982, pl. 11, fig. 1; wrongly identified as from DSDP Site 504; labelled as "transitional from *primalis* to *spectabilis*"). (Not Parker, 1965).

Pulleniatina obliqueloculata [sic] phenon *praecursor* Banner & Blow.—Fordham, 1986 (partim), pl. 19, fig. 18 [Pliocene *S. dehiscens* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean] (not pl. 19, figs. 17a–c, 19a–21 = *P. praecursor*). (Not Banner & Blow, 1967).

DESCRIPTION.—Nonspinose, porous and weakly cancellate wall, pustulose on the chamber shoulders around and within the aperture. Wall moderately thick, test covered in the terminal stage in a translucent non-porous cortex with a smooth reflective surface that is usually degraded by diagenesis to a dull glossy sheen. Test small to medium sized, biconvex with ventrally involute trochospiral coiling; outline slightly petaloid. Typically 4–5 chambers in final whorl, increasing moderately in size; earlier chambers globular, becoming wedge-shaped in umbilical view in last few adult chambers with an acute rounded periphery; chambers appressed and embracing, sutures gently curving, weakly depressed. Test lacks a true umbilicus because of the umbilically encroaching chambers. Aperture a broad sub-rectangular to slightly arched opening in an intra-extraumbilical position extending to the periphery in some specimens.

DISTINGUISHING FEATURES.—*Pulleniatina praespectabilis* intergrades with both *P. primalis* and *P. spectabilis*. It is distinguished from *P. primalis* by the slightly petaloid biconvex test, more triangular umbilical chamber shape and acute, periphery, especially of the last chamber. It is distinguished from *P. spectabilis* by being less anguloconical, less petaloid in outline and lacking the distinctly pinched rim of the last few chambers.

DISCUSSION.—Banner & Blow (1967) illustrated a specimen that they regarded as intermediate between their species *P. primalis* and Parker's *P. spectabilis*. In their investigation of DSDP Site 62 (Eauripik Rise, west Pacific Warm Pool), Brönnimann & Resig (1971) recorded further such specimens and named *praespectabilis* as the connecting form. The holotype was illustrated by them in one view in SEM. New SEM images in three views are given here (Figs. 10.1a–c). The holotype specimen is quite an 'advanced' form with a petaloid outline. Earlier *P. praespectabilis* have less acute margins and less petaloid outlines. Populations are sinistrally dominated throughout its range (Pearson et al., 2023).

PHYLOGENETIC RELATIONSHIPS.—Descended from *P. primalis* and gave rise to *P. spectabilis*.

STRATIGRAPHIC RANGE.—Brönnimann & Resig (1971) depicted their new taxon as arising about halfway through their Zone N17 in the upper Miocene, and its topmost occurrence was recorded at the same level as *P. spectabilis*. Appearance calibrated to 5.98 ± 0.05 Ma and disappearance calibrated to 4.27 ≤ 0.05 Ma by Pearson et al. (2023).

GEOGRAPHIC DISTRIBUTION.—Mostly restricted to the tropical Pacific Ocean (e.g., Bolli & Saunders, 1985) but with rare occurrences in the Indian Ocean (this study) and Arabian Sea (Fleisher, 1974).

PALEOBIOLOGY.—No stable isotope data are available for this species.

REPOSITORY.—Holotype (USNM PAL 219449) deposited in the Smithsonian Museum of Natural History, Washington, D.C.

Pulleniatina primalis Banner & Blow, 1967

Figs. 11.1a–11.11e

Pulleniatina semiinvoluta Germeraad, 1946.—Parker, 1965, p. 152 (partim), figs. 6a–c [Pliocene, Core LSDH 78P, central tropical Pacific Ocean]. (Not Germeraad, 1946.)

Pulleniatina obliquiloculata (Parker & Jones, 1865).—McTavish, 1966 (partim), pl. pl. 5, figs. 6, 13, 25 [Miocene to Pliocene Malaita Group, Solomon Islands] (not pl. 6, figs. 12, 15 = *P. primalis*).—Hanagata & Nobuhara 2015, p. 52, fig. 17.20 [Pliocene Zone PL2, Yonohama Fm., Miyakojima Island, Ryuku Island Arc, western Pacific Ocean]. (Not Parker & Jones, 1865.)

Gen. et spp. ex interc. *Globorotalia (Turborotalia) acostaensis* Blow – *Pulleniatina primalis* Banner and Blow, n. sp.—Banner & Blow, 1967, pl. 1, figs. 1–2 [upper Miocene Zone N17, lower part, Kariava, Papua New Guinea].

Pulleniatina primalis Banner & Blow, 1967, p. 142–143, pl. 1, figs. 3–4 [upper Miocene Zone N17, Wana No. 1 well, Papua New Guinea], 5–6 [upper Miocene Zone N17, upper part, Cubagua No. 1 well, Venezuela], 7 [upper Miocene Zone N18, upper part, Bowden Fm., Buff Bay, Jamaica], 8 [dissected paratype, upper Miocene Zone N17, upper part, Cubagua Fm., Venezuela], pl. 3, fig. 2a–c [holotype, upper Miocene Zone N18, upper part, Bowden Fm., Buff Bay, Jamaica].—Parker, 1967, p. 173–174, pl. 27, figs. 5a–c [upper Pliocene Zone N19, Core CAP 38 BP, eastern tropical Pacific Ocean], figs. 6a–c [upper Miocene Zone N17, Core CAP 38 BP, eastern tropical Pacific Ocean].—Postuma, 1971, p. 384, pl. opposite p. 384, four specimens [unspecified level, Araya, Estado Sucre, Venezuela].—Brönnimann & Resig, 1971, pl. 20, fig. 7 [Pliocene Zone N18, DSDP Site 62, Eauripik Rise, western equatorial Pacific Ocean].—Jenkins & Orr, 1972 (partim), pl. 39, figs. 3–4 (not figs. 5–10, = *P. praecursor*) [Pliocene *S. dehiscens* Zone, DSDP Site 83, eastern equatorial Pacific].—Lamb & Beard, 1972, p. 58, pl.

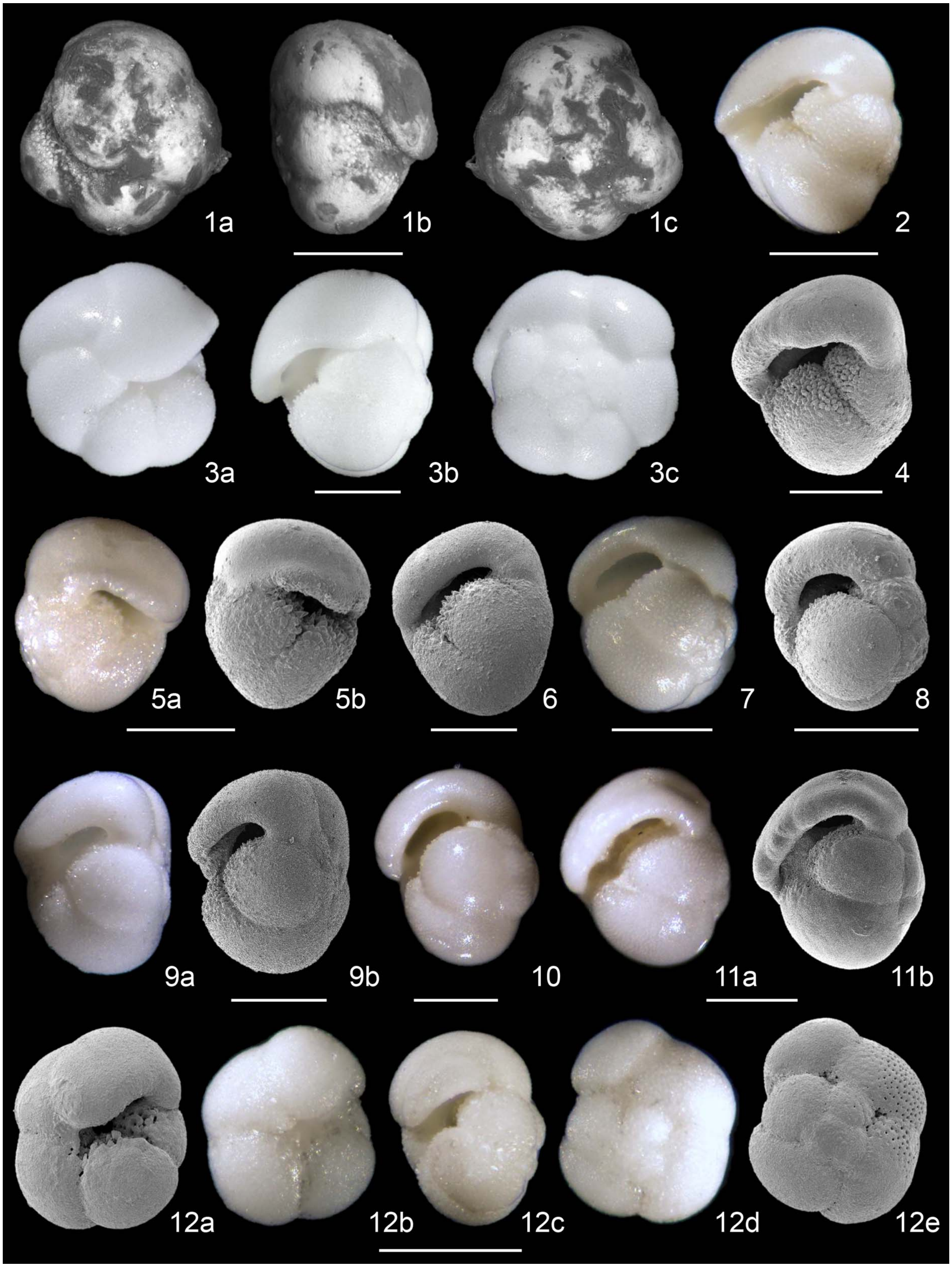


FIGURE 11. *Pulleniatina primalis* Banner & Blow, 1967. **1a–c** holotype (P.46416), environmental SEM, note wall surface is affected by scattered surface deposits (?glue), upper Miocene Zone N18, upper part, Bowden Fm., Buff Bay, Jamaica. **2**, **3a–c** z-stacked LMs, IODP Site U1488, Pacific Ocean, 4.33 Ma (Fabbrini et al., in press, figs. 2m–o). **4** SEM, ODP Site 873, Pacific Ocean, 4.95 Ma. **5a–6** z-stacked LM and SEM, IODP Site U1488, Pacific Ocean, 6.09 Ma. **7** z-stacked LM, IODP Site U1488, Pacific Ocean, 4.33 Ma. **8-9b** z-stacked LM and SEM, ODP Site 873, Pacific Ocean, 4.60 Ma **10–11b** z-stacked LMs and SEM, IODP Site U1482, Indian Ocean, 5.03 Ma. **12a–e** early specimen with incomplete cortex, z-stacked LMs and SEMs, IODP Site U1488, Pacific Ocean, 6.59 Ma (Fabbrini et al., in press, figs. 13ba–be). Scale bars = 200 μm. For full sample details see Table 1.

28, figs. 5, 7–9 [Pliocene *Pulleniatina primalis* Subzone, Gulf of Mexico].—Kadar, 1972, p. 64 (partim), pl. 3, fig. 21 [upper Miocene, Bali] (not pl. 4, figs. 20a–c = *P. praecursor*).—Keigwin, 1976, pl. 1, fig. 10 [lower Pliocene, DSDP Site 157, Panama Basin, eastern equatorial Pacific Ocean].—Saito et al., 1981, p. 101, pl. 32, fig. 1a–2b [unknown level, Vema Station V16-205, North Atlantic Ocean].—Keigwin, 1982, pl. 10, figs. 10–12 [lower Pliocene *Sphaeroidinella dehiscens* Zone, DSDP Site 503, eastern equatorial Pacific Ocean].—Kennett & Srinivasan, 1983, p. 200, pl. 49, figs. 1, 3, 5 [lower Pliocene Zone N19, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean], fig. 4 (reproduced without attribution from Keigwin, 1982, pl. 10, fig. 11).—Bolli & Saunders, 1985, p. 247, fig. 40.6 (holotype reproduced from Banner & Blow, 1967), figs. 41.20–27 [lower Pliocene *G. margaritae margaritae* Zone, Cubagua Fm., Venezuela].—Jenkins, 1986, p. 101, pl. 2, figs. 7, 8 [Pliocene *Globorotalia inflata* Zone, St, Erth beds, Cornwall, UK] (from material collected and described by Millett, 1898, as *Pullenia obliqueloculata* Parker & Jones).—Chaisson & Leckie, 1993, p. 165, pl. 8, fig. 1 [Pliocene Zone N18–N19, DSDP Site 806, Ontong Java Plateau, western equatorial Pacific Ocean].—Perembo, 1994, pl. 3, fig. 2 [Pliocene Zone N20 (lower part), ODP Site 832, Aoba Basin, Vanuatu, western tropical Pacific Ocean].—Pearson, 1995, p. 52, pl. 5, fig. 1 [Pliocene Zone N18, ODP Site 873, Wodejebato Guyot, western tropical Pacific Ocean].—Norris, 1998, p. 52, pl. 3, fig. 9 [Pliocene Zone PL1b, ODP Site 959, eastern equatorial Atlantic Ocean].—Hayashi et al., 2011, p. 5, pl. 3, figs. 4a–c [upper Miocene Zone N18, IODP Site C0001, North Pacific Ocean].—Singh et al., 2021, p. 18, pl. 2, figs. 1, 3, 13 [Pliocene, DSDP Hole 762B, Exmouth Plateau, southeast Indian Ocean], 2 [Pliocene, DSDP Hole 763A, Exmouth Plateau, southeast Indian Ocean].—Permana et al., 2021, figs. 7.14a, b [upper Miocene Zone M14, Limboto Limestone, Sulawesi, Indonesia].

Pulleniatina obliquiloculata primalis Banner and Blow, 1967.—Lidz & McNeill, 1995, pl. 2, figs. 22–28 [Pliocene Zone N19, CLINO borehole, Great Bahama Bank, North Atlantic Ocean].

Pulleniatina obliqueloculata [sic] phenon *primalis* Banner and Blow.—Fordham, 1986, pl. 19, figs. 9a–11b [Pliocene *G. tumida* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean], figs. 13a–16b, 28a–b [Pliocene *S. dehiscens* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean], figs. 34–38 [Pliocene *G. fistulosus* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean], fig. 42 [Pliocene *P. obliqueloculata* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean].

Pulleniatina obliqueloculata [sic] phenon *okinawaensis* Natori.—Fordham, 1986 (partim), pl. 19, figs. 23a–25b, 29a–b [Pliocene *S. dehiscens* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean], figs. 41a–b [Pliocene *G. fistulosus* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean],? figs. 46a–b, pl. 20, figs. 1a–b, 8a–b, 10a–b [Pliocene *P. obliqueloculata* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean] (not pl. 19, figs. 33a–b, pl. 20, figs. 9a–b = *Globoconella inflata*). (Not Natori, 1976).

Pulleniatina obliqueloculata [sic] phenon *praecursor* Banner & Blow—Fordham, 1986 (partim), pl. 20, figs. 5a–6b [Pliocene *P. obliqueloculata* Zone DSDP Site 77B, eastern equatorial Pacific Ocean]. (Not Banner & Blow, 1967.)

Pulleniatina praecursor Banner and Blow.—Hanagata & Nobuhara, 2015, p. 52, fig. 18.3–4 [Pliocene Zone PL2, Yonohama Fm., Miyakojima Island, Ryuku Island Arc, western Pacific Ocean]. (Not Banner & Blow, 1967.)

Not *Pulleniatina primalis* Banner and Blow, 1967.—Singh & Verma, 2014, Fig. 2b(5, 6) (= *P. praecursor*).

DESCRIPTION.—Nonspinose, porous and weakly cancellate wall, pustolose on the chamber shoulders around and within the aperture. In the terminal stage, test covered in a translucent nonporous cortex with a smooth reflective surface that is usually degraded by diagenesis to a dull glossy sheen. The cortex is less well-developed and often incomplete in the earliest populations. Test small to medium sized, subglobular, trochospiral, slightly involute ventrally; typically 4 to 5 chambers in final whorl, increasing moderately in size. Earlier chambers globular, becoming slightly wedge-shaped with a rounded periphery. Umbilicus narrow or obscured by encroaching final chamber. Chambers appressed and embracing, sutures gently curving, depressed. Aperture a broad low arch in an intra-extraumbilical position, not quite extending to the periphery.

DISTINGUISHING FEATURES.—*Pulleniatina primalis* is distinguished from *Neogloboquadrina acostaensis* by its larger size, more inflated ventral side with a final chamber that partly obscures the umbilicus, lack of an apertural lip or flange, and the presence of a reflective cortex. It fully intergrades with *P. praecursor* and *P. praespectabilis*. It is distinguished from *P. praecursor* by its more regular trochospiral coiling, slightly smaller adult size, and less spherical morphology with an aperture that does not extend to the periphery. It is distinguished from *P. praespectabilis* by the rounded rather than acute periphery and less triangular umbilical chambers.

DISCUSSION.—The holotype of *Pulleniatina primalis* is a relatively ‘advanced’ form for the species with a somewhat aberrant, flattened final chamber that covers the umbilicus to a greater extent than is normally encountered in populations. The earliest populations have less umbilically encroaching chambers and less complete cortex coverage (e.g., Figs. 11.12a–e). They show greater affinity to the ancestral form, *Neogloboquadrina acostaensis*, but fully intermediate morphologies have yet to be described. Sub-adult *Pulleniatina* can resemble *P. primalis* up to the present day, but without the cortex.

PALEOECOLOGY.—Van Eijden (1995), Pearson & Shackleton (1995), and Boscolo-Galazzo et al. (2021) showed stable isotope data (relatively light δ^{13}C and heavy δ^{18}O compared to mixed-layer dwelling species) that indicate *P. primalis* was probably an asymbiotic sub-surface form like all other species of the genus. It may have occupied a shallower subsurface habitat than modern *P. obliquiloculata*, possibly because the Deep Chlorophyll Maximum was generally shallower in the Miocene than it is today (see Fig. 1).

GEOGRAPHIC DISTRIBUTION.—Initially restricted to the tropical Indo-Pacific, then expanding globally in low to mid latitudes (Pearson et al., 2023; see Fig. 2).

STRATIGRAPHIC RANGE.—First appeared in the Indo-Pacific in the late Miocene at 6.50±0.10 Ma. First appeared in the Atlantic Ocean and mid-latitudes at 5.33±0.25 Ma. Global disappearance level at 4.0±0.6 Ma is a pseudoextinction caused by gradual evolution into *P. praecursor*.

PHYLOGENETIC RELATIONSHIPS.—*Pulleniatina primalis* is first species of the genus to have evolved and is the root of both the *spectabilis* and *obliquiloculata* lineages.

REPOSITORY.—Holotype (P 46416) deposited in the Natural History Museum, London, UK

Pulleniatina spectabilis **Parker, 1965**

Figs. 12.1a–12.9b

Pulleniatina spectabilis Parker, 1965 (partim), p. 151–152, figs. 1–2 [Pliocene, Core LSDH 78P, central tropical Pacific Ocean], not figs. 3–4 (=*Pulleniatina praespectabilis*).—Banner & Blow, 1967, p. 143–144, pl. 2, fig. 2 [lower Pliocene Zone N19, Core Cap BP38, central tropical Pacific Ocean], figs. 3a–b (dissected specimen) [lower Pliocene Zone N19, Core LSDH 78P, central tropical Pacific Ocean].—Brönnimann & Resig, 1971, pl. 19, fig. 5 [Sample LSDH-78 P, 100–102 cm, central tropical Pacific Ocean], pl. 16, figs. 3, 5–9, 11 [Recent Zone N23, DSDP Site 62, Eauripik Rise, western equatorial Pacific Ocean].—Jenkins & Orr, 1972, pl. 39, figs. 11–13 [Pliocene *S. dehiscens* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean].—Keigwin, 1976, pl. 1, fig. 11 [lower Pliocene, DSDP Site 158, Panama Basin, eastern equatorial Pacific Ocean].—Kennett & Srinivasan, 1983, p. 202, pl. 50, figs. 1–5 [lower Pliocene Zone N19, DSDP Site 504, Costa Rica Rift, eastern equatorial Pacific Ocean].—Bolli & Saunders, 1985, p. 250, fig. 40.1 (holotype, reproduced from Parker, 1965).—Chaisson & Leckie, 1993, p. 165, pl. 8, fig. 3 [Pliocene Zone N18–N19, DSDP Site 806, Ontong Java Plateau, western equatorial Pacific Ocean].—Pearson, 1995, p. 52, pl. 5, figs. 2–3 [Pliocene Zone N18, ODP Site 873, Wodejebato Guyot, western tropical Pacific Ocean].

Pulleniatina spectabilis spectabilis Parker, 1965.—Belford, 1988, pl. 3, figs. 10–13 [Dredge sample DR6A, Manus Basin, western tropical Pacific Ocean].

Pulleniatina obliqueloculata [sic] phenon *spectabilis* Parker.—Fordham, 1986, pl. 19, figs. 26a–27b [Pliocene *S. dehiscens* Zone, DSDP Site 77B, eastern equatorial Pacific Ocean].

Not *Pulleniatina spectabilis* Parker, 1965.—Keigwin, 1982, pl. 11, fig. 1 (= *P. praespectabilis*).—Kennett & Srinivasan, 1983, p. 202 (partim), pl. 50, fig. 5 (reproduced without attribution from Keigwin, 1982; wrongly identified as from DSDP Site 504; labelled as "transitional from *primalis* to *spectabilis*" (= *P. praespectabilis*).

DESCRIPTION.—Nonspinose, porous, thin, and weakly cancellate wall, pustolose on the chamber shoulders around and within the aperture. In the terminal stage, test covered in a translucent non-porous cortex with a smooth reflective surface that is usually degraded by diagenesis to a dull glossy sheen. Test medium sized, lenticular to anguloconical, with a petaloid peripheral outline and ventrally involute trochospiral coiling; 5 chambers in final whorl, increasing moderately in size. Chambers wedge-shaped with a distinctly pinched but unkeeled periphery; pinching disjunct between chambers. Chambers closely appressed and embracing, sutures gently curving to sigmoidal, weakly depressed. Umbilicus narrow or obscured by the involute, successively encroaching chambers. Aperture a broad sub-rectangular to slightly arched opening, sometimes irregular, in an intra-extraumbilical position extending to the periphery in some specimens.

DISTINGUISHING FEATURES.—*P. spectabilis* intergrades with *P. praespectabilis* from which it is distinguished by having a more petaloid outline and at least one chamber with a pinched periphery; in typical specimens all chambers in the final whorl are pinched and the spiral side is relatively flat giving an anguloconical shape.

DISCUSSION.—*Pulleniatina spectabilis* is a very distinctive species (the name means 'showy' or 'remarkable') with an almost globorotaliiform morphology. Parker's original broad concept was divided when Brönnimann & Resig (1971) named *praespectabilis* for forms that are morphologically intermediate to the ancestral form, *P. primalis*.

PALEOECOLOGY.—Stable isotope data indicate a similar ecology and depth habitat to other co-occurring *Pulleniatina* species (Boscolo-Galazzo et al., 2021; Fig. 1G). It was likely herbivorous and lived around the Deep Chlorophyll Maximum.

GEOGRAPHIC DISTRIBUTION.—Restricted to the tropical Pacific Ocean (see Fig. 3C).

STRATIGRAPHIC RANGE.—The first occurrence of *P. spectabilis* is sensitive to the taxonomic criteria used to distinguish it from *P. praespectabilis*. Pearson et al. (2023) estimated it at 5.14±0.10 Ma based on Expedition 320/321 Scientists (2010b; see Table 2). The extinction of *P. spectabilis* occurred at 4.27±0.05 Ma (see Table 2).

PHYLOGENETIC RELATIONSHIPS.—Descended from *P. praespectabilis* by gradual transition, later becoming extinct without descendants.

REPOSITORY.—Holotype (642379) deposited in the Smithsonian Museum of Natural History, Washington, D.C.

ACKNOWLEDGMENTS

This paper is Contribution Number 1 to a planned Atlas of Neogene and Quaternary Planktonic Foraminifera. Dr. Brian Huber of the Smithsonian Museum of Natural History, Washington, D.C., provided SEM images of the holotypes of *P. finalis*, *P. obliquiloculata*, *P. praecursor*, *P. praespectabilis*, *P. primalis*, *P. spectabilis*, *G. antillensis* and *G. atlantis*. Dr. Monika Doubrawa of the Naturhistorisches Museum Basel provided light microscope images of the type series of *Globigerinopsis* Bolli. Nikol Staikidou assisted with z-stacked light microscopy images. Samples from deep sea drill sites were provided by the International Ocean Discovery Program (IODP) and Netherlands Institute for Sea Research (NIOZ). Michal Kucera and Lukas Jonkers commented on an earlier draft. For IODP Expedition 363 sites, we acknowledge U.K.

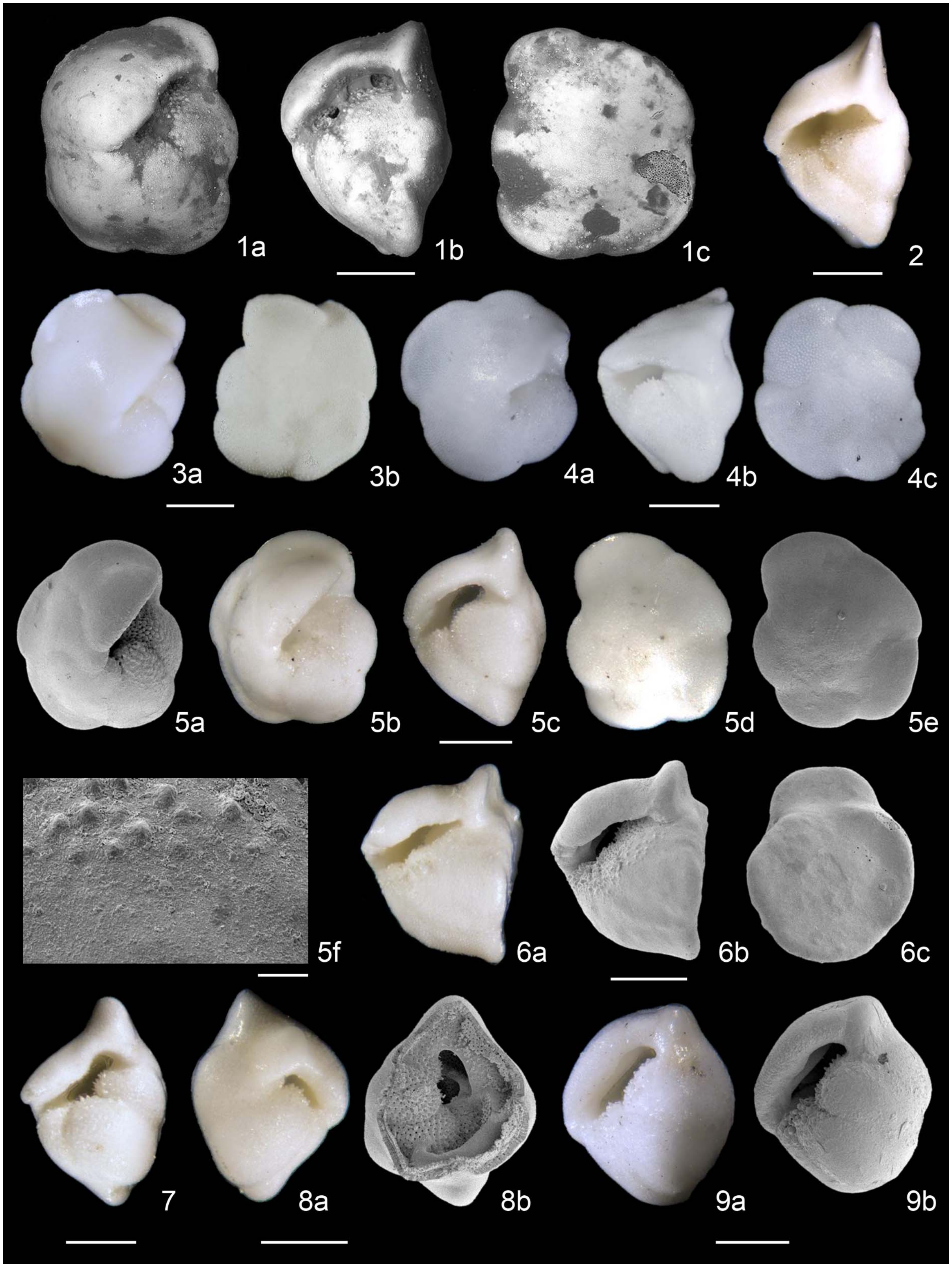


FIGURE 12. *Pulleniatina spectabilis* Parker, 1965. **1a–c** holotype (USNM 642379), environmental SEM, note wall surface is affected by scattered surface deposits (?glue), Pliocene, Core LSDH 78P, central tropical Pacific Ocean. **2** z-stacked LM, ODP Site 873, Pacific Ocean, 4.40 Ma. **3a–b** z-stacked LMs, IODP Site U1488, Pacific Ocean, 4.33 Ma (Fabbrini et al., in press, figs. 2y–aa). **4a–c, 5a–e, 6a–c** SEMs and z-stacked LMs, IODP Site U1488, Pacific Ocean, 4.33 Ma. **7** z-stacked LM, ODP Site 873, Pacific Ocean, 4.40 Ma. **8a–b** dextral specimen, z-stacked LM and SEM, IODP Site U1488, Pacific Ocean, 4.33 Ma, SEM shows specimen after breakage revealing interior morphology. **9a–b** z-stacked LM and SEM, ODP Site 873, Pacific Ocean, 4.40 Ma. Scale bars = 200 μm, except 5f = 20 μm. For full sample details see Table 1.

National Environment Research Council (NERC) Grant NE/P016375/1 to PNP. For NIOZ 'GLOW' sites, we acknowledge NERC Grant NE/F523292/1 to PNP. This research was supported by NERC Grant NE/P019013/1 to BW.

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Received 24 December 2024
Accepted 20 February 2025

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Foraminiferal
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Est. 1950