

Phylogeny of the Cenozoic planktonic foraminifera

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Here we present a comprehensive revision of the phylogeny of Cenozoic planktonic foraminifera. It integrates stratigraphic ranges, morphological traits and evolutionary relationships, resulting in an updated phylogenetic framework. The work expands the previous taxonomic coverage to include microperforate clades, adding 136 morphospecies and 29 new genera, while removing 15 previously included species. Stratigraphic ranges have been calibrated to the latest Geologic Time Scale (GTS2020), providing a more accurate timeline for evolutionary events. The digital phylogeny visualization using TimeScale Creator allows users to interact with these data, including morphospecies images and ecological information, facilitating further research into macroevolutionary processes. This resource provides a valuable platform for exploring biodiversity dynamics and species responses to environmental change throughout the Cenozoic and serves as a framework for integrating fossil and molecular data.

Keywords: planktonic foraminifera; macroevolution; Cenozoic; biodiversity; phylogeny

Introduction

By examining biodiversity through time, phylogenetic research enables us to explore how evolution influences the development of traits (Revell, 2013), the pace of evolutionary change (Castiglione et al., 2018), and the environmental factors that shape evolutionary processes (Stockdale & Benton, 2021). Phylogenies based on time-calibrated molecular data from modern taxa are widely used to investigate such evolutionary processes (Morard, Füllberg et al., 2019), but are subject to limitations such as a lack of direct evidence for extinction (Harvey et al., 1994) and assumptions related to the estimation of diversification rates (Nee et al., 1994). The fossil record, by comparison, contains a wealth of information about past biodiversity and has long been used as a tool to investigate evolutionary trends (Varela et al., 2018) and the response of biodiversity to changing environments (Lowery et al., 2020). Furthermore, it provides a unique advantage for studying macroevolution, as it can provide a deep-time perspective (Benson, 2018) by comparison to modern phylogenetic approaches (Weiner et al., 2015). Phylogenies based on fossil taxa have provided insight into evolutionary

processes such as morphological and trait evolution (Revell, 2013), diversification rates (Cantalapiedra et al., 2017), biogeography (Floeter et al., 2008; Woodhouse et al., 2023), and how species respond to climate change (Polly, 2019).

Much of the fossil record is notoriously incomplete, and subject to preservation and sampling biases that limit our ability to accurately observe the histories of taxa through time (Benton et al., 2000). A key area of opportunity to circumnavigate these biases is to utilize the marine microfossil record which, due to the environmental controls on deposition and preservation potential, includes some of the richest species-level records throughout deep time (Yasuhara et al., 2017). Planktonic foraminifera (Fig. 1) may possess the most extensive species-level fossil record among all organisms (Aze et al., 2011). Despite variations in sampling intensity over time and space (Lloyd et al., 2012), their abundance (Aze et al., 2011) and high species richness (Yasuhara et al., 2017) and the exceptional recovery rates of continuous sedimentation (Lloyd et al., 2012) together offer one of the most comprehensive species-level fossil records available for research (Ezard et al., 2011). In turn this reduces the impact of sampling biases

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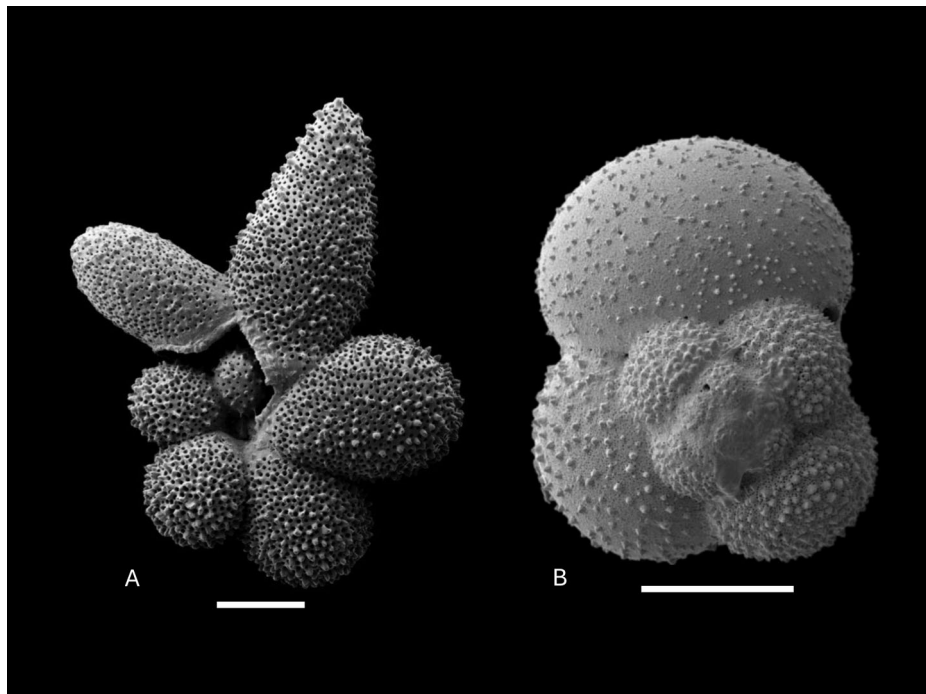


Figure 1. Scanning electron microscope images of the calcite shells of **A**, the macroperforate planktonic foraminifera *Globigerinella adamsi* from the south-west Indian Ocean GLOW Cruise, GLOW 2 Box top, 10°39'07.2"S, 41°46'15.6"E; and **B**, the microperforate planktonic foraminifera *Globigerinita glutinata* from Zone M12, ODP Hole 714 A Core 7 Section 1 100–105 cm, Indian Ocean. Scale bars = 100 μ m.

by showing a continual stretch of time, limiting the number of issues affecting the phylogenetic tree, (e.g. stratigraphic range lengths are revised (as the first and last recorded occurrence of each species can be seen within the same core) for large parts of the fossil record.

There has been a long history of work investigating the evolution of phylogenetic relationships of the planktonic foraminifera, initially due to their utility as biostratigraphic markers (Berggren, 1969; Berggren, Hilgen *et al.*, 1995; Petrizzo *et al.*, 2024; Wade *et al.*, 2011). The most recent Cenozoic phylogenetic compilation was produced by Aze *et al.* (2011) and included the largest clade of planktonic foraminifera, Globigerinoidea. Since that time there have been a number of important synthetic taxonomic updates to this group (Arenillas & Arz, 2017; Wade, Olsson *et al.*, 2018) and many detailed biometric studies (Fabbrini *et al.*, 2023; Latas *et al.*, 2023; Soldan *et al.*, 2014). In light of these efforts we present an updated phylogeny relational database expanded beyond just globigerinids to include all Cenozoic planktonic foraminifera. In this study the database from ‘A Concise Geologic Time Scale 2016’ (GTS2016) (Ogg *et al.*, 2008) and the digital tree (Fordham *et al.*, 2018) derived from the phylogeny of Aze *et al.* (2011) is expanded to include all Cenozoic planktonic foraminifera, recalibrated to GTS2020 (Gradstein *et al.*, 2020)

and linked to biostratigraphic datums, while maintaining pop-up and digital information on species ecologies, biogeographies and key morphological traits, providing an unparalleled resource for empirical analyses aimed at investigating macroevolutionary processes and responses of biodiversity to climate change.

Planktonic foraminifera phylogeny

Planktonic foraminifera are single-celled zooplankton with multiple evolutionary origins, stretching from the Early Jurassic (Hart *et al.*, 2003, Petrizzo *et al.*, 2025). This work focuses on the Cenozoic due to the maturity of the taxonomy during this time period. Planktonic foraminifera can be split into two morphological categories dictated by the porosity of their calcite test wall: macroperforate forms (Superfamily Globigerinoidea) have pores generally at least 1 μ m in diameter (Fig. 1a), while microperforate forms (Superfamilies Globigerinitoidea, Guembelitrioidea, some Bolivinoidea, and the genus *Neogallitellia*) possess pores generally smaller than 1 μ m (Fig. 1b) (Wade, Olsson *et al.*, 2018). The Globigerinoidea, the most abundant group today, are represented by at least 51 extant and 330 extinct morphospecies throughout the last 66 million years. This Cenozoic diversity of Globigerinoidea has been suggested to have evolved from a single common

ancestor, *Muricohedbergella holmdelensis*, which is thought to be one of only two morphospecies to transition the Cretaceous–Paleogene boundary 66 million years ago (Arenillas et al., 2004; Aze et al., 2011; Lui & Olsson, 1994; Olsson et al., 1999). However, alternative stratophenetic phylogenies for the earliest Cenozoic have proposed a benthic origin for the Globigerinoidea (Arenillas & Arz, 2017; Arenillas et al., 2022), rather than from Cretaceous planktonic foraminifera, and recent molecular work has suggested that the spinose and non-spinose Globigerinoidea may have a separate evolutionary origin (Morard et al., 2022). Globigerinoidea, Guembelitrioidea, Bolivinoidea and *Neogallitella* have lower levels of diversity in our modern oceans (at least 21 extant species) and throughout the Cenozoic (69 extinct species) and appear to have originated multiple times from benthic ancestors throughout their evolutionary history (Morard et al., 2022). A partial reason for fewer microperforate species in comparison to macroperforate taxa may be that they are often smaller in size and can more easily be missed and that smaller size fractions are often not looked at in many studies (Huber et al., 2006).

The high-abundance planktonic foraminifera in oceanic environments has resulted in vast accumulations of their biomineralized remains settling on the seafloor (Berger, 1970; de Vargas et al., 1997). The relative quiescence of the deep sea allows for millions of years of evolutionary history to be recorded at individual sites, often capturing a representative range for individual species (Aze et al., 2011). Using material drilled by the Deep-Sea Drilling Project (DSDP) and its successors the Ocean Drilling Program (ODP), Integrated Ocean Drilling Program (IODP) and International Ocean Discovery Program (also abbreviated IODP), the resolution of the record can be as good as 0.001 million years (Hodell et al., 2023), which allows for high-resolution palaeobiological and palaeoceanographic reconstructions (Hernández-Almeida et al., 2013).

The ease of distinguishing morphospecies coupled with their excellent fossil record has resulted in planktonic foraminifera being widely used for biostratigraphy, with a long history of taxonomic and phylogenetic research (see summary in Aze et al., 2011). Due to developments in the field, the taxonomy of this group is under constant revision (e.g. Wade, Olsson et al., 2018). These developments include the erection of new species from core material being accessed in previously understudied regions of our global oceans (Gohl et al., 2021), technological advances in molecular analysis (Morard et al., 2022), and the revision of taxonomic concepts as part of the efforts of the Paleogene Planktonic Foraminifera Working Group (PPFWG) (Olsson et al.,

1999; Pearson et al., 2006; Wade, Olsson et al., 2018). The phylogeny produced in Aze et al. (2011) incorporated the earlier efforts of the PPFWG that were available at the time (Olsson et al., 1999; Pearson et al., 2006), and was restricted to the Cenozoic Globigerinoidea, as this group was considered to be the most well studied and to have the richest fossil record. The recently established Neogene and Quaternary Planktonic Foraminifera Working Group (NQPFWG) will revisit the most comprehensive synthetic taxonomic revision of the Neogene planktonic foraminifera that was completed in the 1980s (Blow, 1979; Bolli et al., 1985; Kennett & Srinivasan, 1983) and the construction of this phylogeny is tasked with providing a phylogenetic framework against which the NQPFWG can test existing evolutionary hypotheses across all groups of planktonic foraminifera.

Terminology

This paper presents phylogenies of the Superfamily Globigerinoidea and several different planktonic groups belonging to Subclass Rotaliana species for the last 66 million years. The phylogenies are presented as both ‘morphospecies’ and ‘evolutionary lineage’ trees.

‘Morphospecies’ are assigned on the basis of morphological characteristics and are the units commonly used to describe taxa in the fossil record using a typological approach (Pearson, 1998a, 1998b). By tracing morphospecies through the stratigraphic record it is possible to determine ancestor–descendant relationships on the basis of morphological similarity and intergradation (Gingerich, 1990). These observed relationships underpin the production of morphospecies phylogenies, and allow populations to be grouped in a consistent way when working through the fossil record and into the modern (Brummer & Kučera, 2022; Wade, Olsson et al., 2018). However, due to the nature of the typological approach for delimiting species based on morphology, arbitrary lines are often drawn through morphological space in order to usefully subdivide fossil populations. This does not necessarily mean that a true cladogenetic (speciation) or extinction event has been captured; rather, it indicates that there has been a notable change in morphology that can be used to define a new morphospecies concept. Where there is full morphological intergradation between a morphospecies ancestor and descendant, despite morphological evolution, this can be termed an anagenetic or ‘pseudospeciation’ event and the subsequent losses of morphospecies throughout these evolutionary clines are identified as ‘pseudoextinctions’. ‘Evolutionary lineages’ are assigned to fossil populations that demonstrate this morphological integration, and are the units used in the

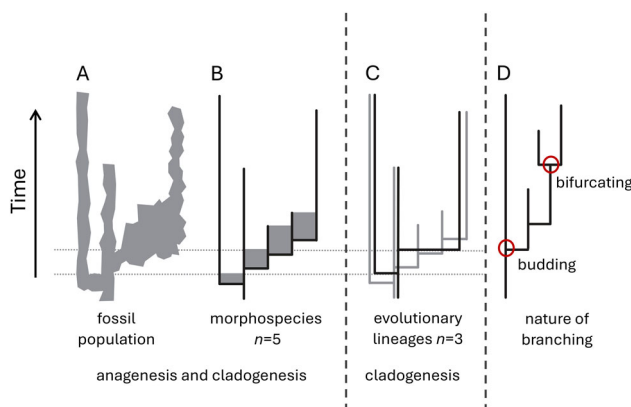


Figure 2. Schematic illustration of anagenetic vs cladogenetic patterns in the fossil record. **A**, Continuous morphological variation within a single population (grey envelope) through time. **B**, Discretization of that continuous variation into five morphospecies ($n=5$) with grey shading representing areas of morphospace that is occupied by morphologies that fully intergrade between two adjacent morphospecies, vertical lines showing species' stratigraphic ranges. In this phylogeny both anagenetic and cladogenetic species events are represented. **C**, Inferred phylogeny under a cladogenetic events only model, recovering three evolutionary lineages ($n=3$). **D**, Simplified depiction of two modes of cladogenesis: budding (lower red circle) and bifurcation (upper red circle), both arising from a single ancestral lineage (vertical line). Adapted from Ezard *et al.* (2012).

lineage phylogenies. The lineage phylogeny aims to retain only true cladogenetic events, thereby removing all cases of anagenesis (Fig. 2).

Speciation events in the morphospecies or lineage phylogenies may be referred to as either 'budding' events, where the ancestor continues to survive after giving rise to its descendant, or 'bifurcating' events when two descendants are produced from one ancestor at the same time with the ancestor not surviving the speciation event (Foote, 1996) (Fig. 2d).

All morphospecies have been assigned to an 'ecogroup' and a 'morphogroup' (Supplementary information: S1. Morphospecies Key Information in Lamyman *et al.*, 2026). Morphogroups represent the assignment of morphospecies to one of 23 groups, based on test architecture and gross morphology. Ecogroups represent the ecological and geographic affinity of morphospecies based on modern-day observations and distributions, fossil distributions and geochemical analysis of their calcite tests (Aze *et al.*, 2011; Schiebel & Hemleben, 2017). The analysis of stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes in foraminiferal calcite allow us to determine water column depth habitats based on the biotic and abiotic processes that influence these signals. $\delta^{18}\text{O}$ is subject to temperature-dependent fractionation and as such increasing values indicate cooler/

deeper depth habitats, whereas $\delta^{13}\text{C}$ is influenced by metabolic processes, photosymbiont activity and ambient water column productivity. Combined, these two parameters can fingerprint ecological preferences.

Scope of the study

The morphospecies and lineage phylogenies of this study expand the taxonomic coverage of those presented in Aze *et al.* (2011) and Fordham *et al.* (2018) (which transferred the phylogenies of Aze *et al.* (2011) onto the TimeScale Creator platform with explicit time-scale calibrations and enhanced database structure) to include all Cenozoic morphospecies which were planktonic for at least a significant part of their life cycle. As with Aze *et al.* (2011), this study is intended primarily as a compilation exercise, designed to gain enough detail (morphospecies with evidenced stratigraphic ranges, proposed relationships, and other pertinent information) in order to put together a phylogeny which is, within the Cenozoic, as fully connected with plausible ancestor–descendant links as practicable. Similarly, corresponding lineages are proposed from both literature and unpublished observations. Note that, as a compilation exercise, our phylogenies have, as much as proved practicable to complete them, attempted to employ genera and morphospecies taxa in current usage. The status of taxa not included in our study will best be sought in taxonomic studies, especially those from the Planktonic Foraminifera Working Groups, both those already available and those to be expected.

Our focus on a phylogeny at finer taxonomic levels (morphospecies and species-level lineage) reflects our view that advancement in taxonomy in our research community is encouraged when a fully specified and connected tree at those finer levels is available for scrutiny. This will raise the risk of 'getting it wrong', but subsequently addressing those mistakes will come with valuable additional information or insights. Alternatively, reliance upon only classifications in which taxa are grouped into broad higher-level groups may be 'safer', but such an approach probably tends to retain knowledge gaps, such as '*incertae sedis*', for much longer, thus impeding progress. The tree is both a synthesis and a hypothesis and we expect future work to lead to further refinements.

Methods

A phylogeny of morphospecies

The morphospecies phylogeny presented in this work represents a summary of existing data from several sources that report the stratigraphic ranges and proposed

evolutionary relationships of Cenozoic species. To maintain taxonomic consistency across the species included in the phylogeny, stratigraphic and evolutionary information was derived mainly from a number of key published works with a focus on a synthetic taxonomic approach and substantial and integrated evidence towards the existence of newly named species. Much of this work has been carried out by the PPFWG for taxa from the first half of the Cenozoic, which is presented in three key atlases (Olsson et al., 1999; Pearson et al., 2006; Wade, Olsson et al., 2018) in addition to the synthetic works that cover the species from the later part of the Cenozoic (Kennett & Srinivasan, 1983; Spezzaferri et al., 2015), as well as living species (Brummer & Kučera, 2022). Taxa were not included on the basis of new molecular genetic information unless formally taxonomically defined, and there have been a number of more detailed studies that have resulted in updates in this synthetic new work (e.g. Fabbrini et al., 2023; Latas et al., 2023; Spezzaferri et al., 2015). The online database mikrotax (Huber et al., 2017) was used in combination with searching published literature to reduce synonyms. Where ancestor–descendant relationship disputes were found in the literature, the relationships from the most up-to-date synthetic taxonomic works were preferred. A cladistic approach has been consciously avoided in this work as it presents several issues when trying to produce a phylogeny of planktonic foraminifera due to the extensive homeomorphy present in this group. Iterative, convergent morphological evolution has resulted in the reoccurrence of species morphologies through time that can result in parsimonious cladistic relationships that significantly conflict with stratigraphic knowledge of species durations (Stewart, 2003). Accordingly, in producing phylogenies of fossil taxa with such a high-resolution and rich fossil record, stratigraphic information can, and should, be incorporated for the range histories of included taxa. An example of this is the ‘stratophenetic’ approach (Gingerich, 1990), whereby ancestor–descendant populations are traced through time based on the occurrence of specific morphological traits observed within the fossil data (e.g. supplementary apertures) being displayed by all taxa in the same group, allowing for the evolutionary relationships between species to be identified (Wiley, 1978).

Conversion to a lineage phylogeny

Following the methodology of Aze et al. (2011), any instances of pseudospeciation or pseudoextinction identified in the phylogeny were examined using literature that documented taxon divergence in morphospace. When such sources were unavailable, qualitative decisions were made regarding the timing and pattern of

species branching based on observed branching events and additional data, including personal observations and discussions with colleagues. Further to Aze et al. (2011) and this study, it is hoped that, as part of a future upgrade to both mikrotax and our relational database, sources and evidence for ancestry for both morphospecies and lineages will be systematically documented (see e.g. evidence for ancestor–descendant proposals in Fordham et al., 2016).

The phylogenetic framework established by Aze et al. (2011) remains unchanged unless new taxonomic evidence has emerged, reflecting revisions in the morphospecies phylogeny incorporated into this updated work. All newly identified instances of pseudospeciation and pseudoextinction, resulting from the inclusion of additional data and the development of the microperforate phylogeny, were evaluated using the same process as in Aze et al. (2011).

Assignment of taxa to morphogroups and ecogroups

All species were assigned to a morphogroup based on the morphological traits possessed by their test e.g. the nature of spinosity, presence/absence of a keel, wall texture, aperture position and number, etc. (see Bolli et al., 1957 for a glossary of morphological terms) (Supplementary information: S1. Morphospecies Key Information in Lamymann et al., 2026).

Ecogroups were also assigned to each morphospecies based upon the geochemical data collected from their tests and known geographic occurrences of each species (Supplementary information: S1. Morphospecies Key Information in Lamymann et al., 2026). The carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopic signatures recorded within the calcite tests allows the reconstruction of the surrounding water column, enabling the study of planktonic foraminifera in relation to their environment. When using this information other factors must be considered including cryptic diversity, migration, algal photosymbiosis, test size, metabolic fractionation, foraminiferal diet, food availability, temperature and reproductive cycle length (Birch et al., 2013). These factors can create a false ecogroup signal unless monitored closely; to account for these features and reduce their impact, known marker species can create a baseline for other species to be compared against and relative ecogroups assigned (Birch et al., 2013). As ours is a phylogeny focusing mainly on extinct taxa, gathering palaeoecological information has been limited to inferences made using geochemical fingerprinting and geographical distributions seen throughout geological time. This is common practice for micropalaeontological research studying past environmental conditions (Birch

et al., 2013; Wade, Olsson *et al.*, 2018). In many cases there is no geochemical information on taxa included in the phylogeny; in such instances we assign to ecogroups based on phylogenetic affinity and geographic information, but detail clearly in the appendix where ecogroups are inferred and not underpinned by data with the qualifier ‘No Data’. The inferred ecological groupings used within this study include (1) open-ocean mixed-layer tropical/subtropical with photosymbionts (based on very high $\delta^{13}\text{C}$ and relatively low $\delta^{18}\text{O}$); (2) open-ocean mixed-layer tropical/subtropical without photosymbionts (based on high $\delta^{13}\text{C}$ and relatively low $\delta^{18}\text{O}$); (3) open-ocean thermocline (based on low $\delta^{13}\text{C}$ and relatively high $\delta^{18}\text{O}$); (4) open-ocean sub-thermocline (based on very low $\delta^{13}\text{C}$ and very high $\delta^{18}\text{O}$); (5) high latitude; (6) upwelling/high-productivity areas (Aze *et al.*, 2011); and (7) benthic or a much deeper part of the water column (based on extremely low $\delta^{13}\text{C}$ and extremely high $\delta^{18}\text{O}$).

Species age range determination

Following on from the databased version of Aze *et al.* (2011) as presented in Fordham *et al.* (2018), all ages for stratigraphic ranges that are expressed in Ma (millions of years ago) are explicitly recorded against standard time scales (e.g. Gradstein *et al.*, 2020), and dates that have been updated are retained in our database so that a history of date assignments is accumulated (Supplementary information: S3. Supporting Information and S4. Relational Database in Lamyman *et al.*, 2026). However, for the revision of many ranges presented in this work, specific age tables have been introduced into the database (one table each for morphospecies and lineages) allowing easier and more-transparent selection when more than one date was available in the literature for each morphospecies or lineage. This also eases the use of ranges which contain multiple separate dates (in different range-line styles), depicting less reliable stratigraphic occurrences and conjectured ranges. The updated morphospecies dating table primarily uses ages expressed as percentages within specific stratigraphic zones (%-up zones). When calibrated age data were unavailable, species' ages were estimated directly from published range charts, such as those provided by Kennett and Srinivasan (1983) where species occurrences are represented as percentages of the way through a particular zone. Wherever possible, however, we have used more explicit and preferred methods involving defined time-stratigraphic units. For lineages, we have followed the approach of Aze *et al.* (2011), either providing a direct numerical age (Ma) for lineage origination or extinction or linking lineage events directly to morphospecies-level occurrences.

With regard to transparency and consistency of date choices, a significant improvement in this work is its introduction of datum lists from sources additional to Wade *et al.* (2011), though it is currently only a short list including other planktonic foraminifera biogeochronological zonations (Berggren, Hilgen *et al.*, 1995; Berggren, Kent *et al.*, 1995; Huber & Quillévéré, 2005; King *et al.*, 2020), relevant sections in The Geological Timescale publications (Gradstein *et al.*, 2012; Ogg *et al.*, 2008; Raffi *et al.*, 2020), and studies focused on a particular site(s) (Berggren *et al.*, 2000; Luciani & Giusberti, 2014). All these datums have been compiled against a single list of datum names, and then those relevant to the morphospecies events in this work have been judged (with reasons recorded in the database) for their phylogenetic plausibility, given the ancestry built into the tree – e.g. a datum may be inapplicable for this work if it is markedly affected by palaeogeographic controls, given that the tree is intended to reflect globally relevant timing. A separate table lists, for each datum, its single or multiple sources and the Ma value from each source; the table then records which source has been adopted (as for Aze *et al.*, 2011, the time scale for each source is recorded in a separate table). Those datums selected then override the corresponding already adopted date(s).

Calibration to GTS2020 of adopted dates that were expressed in Ma against Cande and Kent (1995) (CK95) or the Geological Time Scales (GTS2004, GTS2012, GTS2016) was made directly against geomagnetic polarity chrons. Prior to this, dates originally given against Berggren, Kent *et al.* (1995) (BKSA95) or Berggren and Pearson (2005) (BP05) were calibrated to CK95 using all shared datums (not only markers) from Wade *et al.* (2011) [WPBP11(CK95): 110 datums for BKSA95; 46 datums for BP05].

Completeness analysis

The completeness and accuracy of our phylogeny depend on the fossil record being sufficiently complete that the stratigraphic ranges assigned to morphospecies can be trusted. We used these data in the Triton database (Fenton *et al.*, 2021) to generate a minimum estimate of the completeness of the record for Cenozoic planktonic foraminifera.

We matched 501,629 macroperforate and 40,673 microperforate occurrence records from Triton (downloaded on 21 April 2021) to the 480 morphospecies in the phylogeny. Where Triton was based on the phylogeny of Aze *et al.* (2011), all records are now updated to the new phylogeny presented here. Of the 390 macroperforate morphospecies in the tree, 43 have no occurrence records in Triton, whilst 9 species have records

within Triton but their recorded occurrences fall outside of the assigned ranges in this study. Amongst the microperforate forms, 38 have no occurrence records in Triton, whilst 6 are present in Triton but not within their ranges. Amongst these absent planktonic foraminiferal morphospecies, some are recently described species (e.g. *Globoturborotalita eolabiocrassata* [Spezzaferri, Olsson et al., 2018]) that had not been documented on ocean drilling biostratigraphic reports, and so are not included in Triton, whereas other taxa are often from the early Cenozoic with shorter stratigraphic ranges, where scientific drilling often encounters operational issues that make it harder to recover complete cores and accurately assign ages to samples from this time. For each of the remaining 384 morphospecies, we calculated the proportion of its duration (according to the phylogeny) that is represented in the database, as the proportion of time bins containing at least one recorded occurrence.

At a bin length of 1 million years, 233 species (60.7%) have complete fossil records, i.e. every bin contains a record. Across the 384 species, the mean completeness is 86.4% (macroperforate = 88.4%, microperforate = 71.2%) and the median completeness is 100% (macroperforate = 100%, microperforate = 89.4%) (see Supplementary information: S3. Supporting Data for full completeness data for each species in Lamyman et al., 2026). These results, especially when the limitations of Triton are considered, suggest that the species-level fossil record of Cenozoic macroperforate planktonic foraminifera is at least as good as the genus-level records of the best-preserved macroinvertebrate groups (quantified by Foote & Sepkoski, 1999). Further, note the mean completeness for macroperforate taxa is now 5% higher than that calculated by Aze et al. (2011). This indicates substantial improvements in the known recorded occurrences of planktonic foraminifera even with the addition of another 51 macroperforate morphospecies. However, it is important to recognize that this value is likely to represent a conservative underestimate of true completeness, as the shipboard biostratigraphic data that largely underpin Triton were not collected with the primary aim of exhaustively recording species occurrences; sampling and reporting have historically focused on biostratigraphically informative taxa, with non-target species recorded more opportunistically.

Visualization and systematics listing

The preferred visualization of the phylogenies presented in this work are morphospecies and lineage trees drawn directly (without editing) from TimeScale Creator datapacks output from our database (Supplementary

information: S2. Morphospecies and Lineage Phylogeny Visualizations in Lamyman et al., 2026).

Pop-ups in this work have been designed to be easier to follow and more colourful and engaging (see Supplementary information: S5. Evolutionary Trees in Lamyman et al., 2026): genus, morphogroup and ecogroup names are coloured; now that Chronos (an online planktonic foraminifera taxonomy database) has been decommissioned, morphospecies links are to the World Register of Marine Species (WoRMS) and mikrotax; source details for the stratigraphic range are now colour-coded to highlight those dates adopted, or replaced by a datum, and details of associated datums are introduced; references specific to that morphospecies are now given a separate subsection.

Results

A revised phylogeny of the Cenozoic planktonic foraminifera is presented (Fig. 3), incorporating several significant adjustments to taxonomy, phylogenetic relationships, stratigraphic ranges, and age calibrations since Aze et al. (2011). Notable changes include the addition of 141 morphospecies, comprising 90 microperforate and 51 macroperforate species, which has led to an increase in species richness over time, particularly in the Oligocene and lower Miocene (Fig. 4). Furthermore, 32 genera have been added, while 15 morphospecies now considered synonyms have been removed from the phylogeny (Table 1). In this expanded tree, 65 taxonomic names have been updated from the Aze et al. (2011) version. All stratigraphic ranges have been recalibrated to align with GTS2020. Some species, such as *Globigerinella radians*, have undergone changes based on molecular evidence. Additionally, the family Hastigerinidae has been incorporated into the Globigerinoidea phylogeny, and *Bolivina* has been included in the microperforate group as some members of this genus are now recognized to have a planktonic phase in their life cycle.

Completeness

Our completeness analysis demonstrated a mean completeness of 88% and a median completeness of 100% for 1 Myr time bins (Table 1). However, it should be noted that species could have sparse records within their stratigraphic ranges for three reasons: they might have a very incomplete fossil record; they might have a complete record, but these data are from cores not in Triton; or they might be underrepresented in Triton because of taxonomic changes or due to the lack of observation during shipboard analyses due to certain species falling

Table 1. A table showing the differences in morphospecies, lineages and genera included in this work compared to that of Aze et al. (2011) (please see Supplemental materials S3. Supporting Information, for full completeness data for each species in Lamyman et al., 2026). The morphospecies (MS) completeness represents the proportion of a species' duration shown as both mean and median values (according to the phylogeny) that is represented by at least one recorded occurrence in the Triton database at a bin length of one million years.

	Aze et al. (2011)	This study	% increase
Morphospecies (MS)	339	480	42
Lineages (L)	210	268	28
Genera	48	80	67
%Completeness MS (mean)	83	88	5
%Completeness MS (median)	100	100	0

including the phylogeny presented by Aze et al. (2011). Genus abbreviations, as much as practicable, follow those used in previous sources (see S3. Supporting Data in Lamyman et al., 2026).

Discussion

Superfamily Globigerinoidea

In this study, the major changes to the Globigerinoidea of Aze et al. (2011) come from the 2018 release of the Oligocene Atlas (Wade, Olsson et al., 2018). This includes the addition of two new genera, *Quiltyella* (Spezzaferri, Coxall et al., 2018) and *Ciperoella* (Olsson et al., 2018), new species (e.g. *Globoturborotalita pseudopraebuloides*, *Dentoglobigerina eotripartita* and *Subbotina projecta*), alterations to stratigraphic ranges (e.g. *Acarinina echinata* and *Paragloborotalia birnagae*) and name changes (e.g. *Globigerinoides trilobus* to *Trilobatus trilobus* [Spezzaferri et al., 2015]). The Oligocene Atlas (Wade, Olsson et al., 2018) also favoured some changes to the ancestral relationships incorporated into the Globigerinoidea evolutionary tree of Aze et al.'s (2011) ancestry of the Globigerinoidea (see Data Repository anudc:6398, Figures: Slides 54–59). These changes, which had major phylogenetic implications, highlighted the limited understanding of the origins of some important genera e.g.: *Dentoglobigerina* – Blow's (1979, p. 1299) original descent from *Subbotina*, rather than *Acarinina* (Olsson, Hemleben et al., 2006, p. 404), was termed 'probable' (Wade, Pearson et al., 2018, p. 335); *Globorotaloides* – Coxall and Spezzaferri (2018, p. 103) favoured *Subbotina* as ancestor, rather than *Parasubbotina* (Olsson et al., 2006, p. 83), but still considered this uncertain; and *Turborotalita* – Pearson and Kučera (2018, p. 387) proposed the earliest-Paleocene '*Praemurica nikolasi*' as its initial species, informed by its 'possibly spinose wall' rather than the Olsson et al. (2006) middle-Eocene origin from *Globoturborotalita*. For *Paragloborotalia* and immediate descendants (*Fohsella*, *Globorotalia*,

Neogloboquadrina), the Oligocene Atlas (Wade, Olsson et al., 2018) provided a firmer, if still not well understood, ancestry. Aze et al. (2011, p. 907) had provisionally descended their two '*Paragloborotalia*' species ('*P.*' *pseudokugleri* and '*P.*' *kugleri*) from *Dentoglobigerina*, which thus became an eventual ancestor for *Fohsella*, *Globorotalia* and the other 'globorotaliine' genera, and also for *Neogloboquadrina*, given their choice of '*P.*' *kugleri* as ancestor to their *N.* (not *Paragloborotalia*) *continua*. However, Leckie et al. (2018) provided a somewhat simpler and more plausible phylogeny. They returned *pseudokugleri* (and descendant *kugleri*) and *continua* to *Paragloborotalia*, these species descended from *P. nana*, and, with the other *Paragloborotalia*, ultimately descended from *Parasubbotina*, thus consolidating the Globorotaliidae.

More-specific changes to the Globigerinoidea of Aze et al. (2011) have also been implemented. Within *Dentoglobigerina*, Fayolle and Wade (2021) evidenced a likely origin from *Acarinina* for two sub-quadrant to sub-circular species, informally referred to as '*D.*' *eotripartita* and '*D.*' *tripartita*, each considered a distinct lineage, extending the Truncorotaloididae into the middle Miocene. *Globigerina megastoma* is returned to *Globigerina* from *Beella*, influenced by the variability of its type collection (Holmes, 1984) and that of the *G. bulloides* group (Rögl & Bolli, 1973). *Globigerina pseudobesa* ('*Turborotalia pseudobesa* Salvatorini, 1967'), included in *Globigerinella obesa* by Aze et al. (2011), is here also considered descended from *G. bulloides*, acknowledging the quite strong descriptive and illustrative evidence from Tjalsma (1971) (see also Spaak, 1981 and Fordham, 1986). Aze et al. (2011) included '*Globigerinoides bulloideus* Crescenti, 1966' within *Globigerina bulloides* but, influenced especially by Zachariasse (1975) and Molina (1979), and following Popescu and Crihan (2011), we now include it as *Globoturborotalita bulloidea*, descended from *G. woodi* and possibly ancestral to *G. apertura*. Also related to *Globoturborotalita*, we now include the suggestion of Brönnimann et al. (1987) that *Soldaniella toscanae* is

possibly descended from *G. druryi* based on the small illustrated collection in Fordham (1986) showing similarities to his phenas *druryi*, *opsionepenthoides* and *columbae*. For now it is considered a separate lineage, but note that the collections so far are too meagre to interpret intergradation with confidence (Fordham, 1986, p. 113). *Globigerinoides rublobatus* (Latas *et al.*, 2023), including both pink and white morphotypes, is added as a short-lived lineage offshoot from *G. conglobatus*. Two morphospecies of *Neogloboquadrina* additional to the phylogeny of Aze *et al.* (2011) are now included: *N. atlantica* and, as its descendant, *N. inglei*. However, the early history of *Neogloboquadrina* remains unclear (Weitkamp *et al.*, 2023) but, of the proposals made, we particularly note the suggestion of Hilgen *et al.* (2000) that *N. atlantica* intergrades with *N. acostaensis sensu lato*, and their speculation that they are ancestor and descendant, respectively. However, for now we assign both *N. atlantica* and *N. acostaensis* as descendants of *Paragloborotalia continuosa*. The subsequent evolution of *Neogloboquadrina* is also not well understood and our current recognition of morphospecies and lineages will probably prove to be simplistic.

Our inclusion of *Globorotalia panda* ('*G. menardii panda* Jenkins, 1960') largely follows Cifelli and Scott (1986), but with a provisional inclusion of both '*G. magnifica* Bizon and Glaçon, 1978' and '*G. (G.) ichinosekiensis* Takayanagi and Oda, 1976', and with, for now, probably overly simplistic relative timings during the Langhian which result in *G. archeomenardii* giving rise to our more-inclusive *G. panda* prior to the origin of *G. praemenardii*. The restoration of *Globoconella triangula* ('*Globorotalia inflata triangula* Theyer, 1973') in Lam and Leckie (2020) is adopted as a descendant of *Globoconella inflata*; its recognition may encourage investigation of evolutionary histories such as biogeographical isolation and absorption or incipient speciation (Scott *et al.*, 1990, p. 91). Also related to *G. inflata*, *Neoacarinina blowi* Thompson, 1973 ranges from Zone PL3 and so would most plausibly descend from *G. puncticulata* and is considered to then eventually bud as a separate lineage. *Neoacarinina* is retained as a monospecific genus in recognition of its distinctive pustules (Poore & Berggren, 1975; Saito *et al.*, 1981).

A few additional select adjustments to the Globigerinoidea tree have been adopted from recent studies in record-rich stratophenetics (Fabbrini *et al.*, 2021, 2023, 2024; Pearson & Penny, 2021; Wade *et al.*, 2021). Several changes have also been made where molecular studies have provided strong evidence that stratophenetic placement of morphospecies has been misplaced or unrecognized. Examples of these involve: *Neogloboquadrina incompta*, now recognized as a

lineage separate from *Neogloboquadrina pachyderma* (Darling *et al.*, 2006); *Globigerinella radians* (Weiner *et al.*, 2015); *Globigerinoides elongatus* (Aurahs *et al.*, 2011); *Globigerinoides tenellus* (Morard, Füllberg *et al.*, 2019); *Globorotaloides oveyi*; and the widely known *Globorotalia menardii*, now revised as a Mediterranean species separate to *Globorotalia cultrata* (Brummer & Kučera, 2022; Stainforth *et al.*, 1975, 1978).

The Globigerinoidea remains the most likely home for a few difficult-to-place genera. Based on (albeit weak) stratophenetic evidence, it is suggested that *Turborotalita* is an ancestor worth investigating for both *Berggrenia* and *Orcadia*, for want of a better alternative (Fordham, 1986). The stratophenetic evidence tying these three genera together is based on morphological similarities including the possession of small macroperforate low-trochospiral tests, tightly coiled with $4\frac{1}{2}$ to $5\frac{1}{2}$ chambers in the final whorl of *Turborotalita quinqueloba* (Pearson & Kučera, 2018) and 5 in the final whorl of both *Berggrenia primoripumilio* (Fordham, 1986) and *Orcadia riedeli* (Kennett & Srinivasan, 1983). All taxa are observed to possess slowly enlarging sub-globular to globular chambers towards the final whorl (Fordham, 1986; Kennett & Srinivasan, 1983; Pearson & Kučera, 2018). This evidence is classed as weak due to the lack of physical observational data showing the transition between these genera.

Building on the hypothesis that *Turborotalita* is an ancestor of *Berggrenia* and *Orcadia* (Fordham, 1986), along with Pearson and Kučera's (Pearson & Kučera, 2018) suggestion that *Praemurica nikolasi* was the first *Turborotalita*, Koutsoukos (2014) presented detailed stratophenetic observations that place this long-lived Cenozoic group within the explosive radiation of Globigerinoidea in the earliest Cenozoic. This positioning helps explain the "extremely long-branched" (Aurahs *et al.*, 2009) nature of living *Turborotalita quinqueloba* in molecular trees. Speculatively, this phylogeny also assigns the even more deeply divergent (Aurahs *et al.*, 2009) *Hastigerina* a similar, albeit stratigraphically unsupported, origin within the earliest Globigerinoidea.

Other than Globigerinoidea

The Cenozoic planktonic groups recognized in this study, additional to the Superfamily Globigerinoidea, are the Superfamily Globigerinitoidea, Superfamily Guembelitrioidea, and select members of the genera *Bolivina* and *Neogallitellia* of Subclass Rotaliana (higher level names follow the World Foraminifera Database [Hayward *et al.*, 2022]). For these groups, the sources most useful for construction of the phylogenies presented in Aze *et al.* (2011) could usually be

redeployed (e.g. *Atlas of Paleocene planktonic foraminifera* [Olsson et al., 1999], *Atlas of Eocene planktonic foraminifera* [Pearson et al., 2006] and *Neogene planktonic foraminifera: A phylogenetic atlas* [Kennett & Srinivasan, 1983]).

Appreciation of the fossil record of many planktonic morphospecies in the Rotaliana tends to be poorer, partly due to their typically more fragile and/or smaller tests, the latter sometimes below the standard sieve sizes employed (Brönnimann & Resig, 1971; Darling et al., 2009; Smart & Thomas, 2007). This sampling bias is exacerbated by the still only rare use in the discipline of representative sampling (e.g. complete picking from a microsplitter [Fordham, 1986; Hayward et al., 2010; Resig, 1989; Thomas, 1987]), resulting in the larger and/or more-distinctive specimens receiving most of the attention in a typical study. These sampling biases have the potential to affect the construction of the phylogenetic tree, as taxa may be missed whilst completing assemblage counts due to the destruction of the foraminifera (if fragile) or smaller specimens not being studied in average micropalaeontological size fractions (which these groups tend to be), leading to reduced stratigraphic ranges and taxa missing from the fossil record.

Another issue in the study of planktonic Rotaliana is the frequent use of a single (or very limited range of) magnification(s) in taxonomic illustrations, which tends to obscure the substantial size differences that exist among species. This contributes to a reduced appreciation of the relevance of size difference between morphospecies, further compromising phylogenetic understanding of especially the taxa with smaller tests (an issue mirrored in molecular studies [Morard, Füllberg et al., 2019; Morard et al., 2018]) and compounding the sampling biases already discussed.

Bolivina. In this study the Neogene ‘*Streptochilus*’ morphospecies represented in previous synthetic taxonomic works (Huber et al., 2006; Smart & Thomas, 2018) have been included in *Bolivina*. At this provisional stage of integrating the long list of ‘*Streptochilus*’ morphospecies into *Bolivina* lineages, there appears to be a case for most of the taxa to be closely related to one of two highly variable species (*B. variabilis* and *B. inflata*), each of which for now is lumped into a single lineage. With this approach, the lineage with *B. variabilis* encompasses highly variable morphology (especially with regard to the test surface) and the lineage with *B. inflata* has a much more consistently smooth-walled appearance. By choosing these taxa, this study is supporting the ‘*Streptochilus*’ phylogeny of Fordham (1986), rather than those presented by Resig (1993). These and the other *Bolivina* lineages provisionally recognized in this study can for now only speculatively

and somewhat vaguely be assigned as coming from a *Bolivina* clade, which is also the case for the Maastrichtian–Paleogene *Rectoguembelina* and *Zeauvigerina*.

Superfamily Guembelitrioidea

This study places *Cassigerinella eocaenica* as the eventual ancestor of *Dentigloborotalia anfracta* based on morphological similarity (Brummer, 1988; Pearson, Spezzaferri et al., 2018), given that *Riveroinella martinipicoi* has been considered a likely descendant of *C. eocaenica* (Pearson, Spezzaferri et al., 2018). As part of this proposal, Quilty’s (1976) suggested ancestry, ‘*Globorotalia* (*Turborotalia*) *bauerensis*’ – ‘*Globorotalia* (*Turborotalia*) *akersi*’ – ‘*Globorotalia* (*Turborotalia*) *anfracta*’, seems worthy of consideration, though further detailed investigation is required to provide convincing evidence for the ancestries of *Riveroinella* and *Dentigloborotalia* (Brummer, 1988).

Superfamily Globigerinitoidea

The Paleogene portion of our tree for the Globigerinitoidea is derived mainly from the Eocene and Oligocene atlases (Huber et al., 2006; Pearson, Wade et al., 2018); we have not attempted a comprehensive update of the Paleogene Globigerinitoidea, though *Antarcticella*, now considered planktonic (Huber et al., 2020), has been added. The post-Paleogene portions of the tree, available from Kennett and Srinivasan (1983, text-fig. 8, 18, 25) and Li (1987, fig. 8A, B), have required some further input, summarized here (for further details of the changes, See S3. Supporting Information). *Tenuitella minutissima* is herein considered a laterally compressed morphospecies, close to its primary type, descended from *T. gemma* (with its range questionably extended to the early Miocene), and ancestral to the short-lived *T. pieste*. *Tenuitella angustiumbilocata* is dubiously expanded into the middle Miocene, incorporating Li’s ‘*Tenuitellinata* cf. *T. pseudoeedita*’. It gives rise to *T. jamesi* (Li et al., 1992), *T. cf. minutissima* (Li’s version of the morphospecies, which is less laterally compressed, bearing more-inflated chambers than its holotypic namesake), which, following Li, is in turn ancestral to *T. neobrevispira*. Li et al. (1992) have *T. selleyi*, as an even smaller morphospecies, that appears to survive to the Pleistocene; a living presence awaits confirmation.

Broadly following Kennett and Srinivasan (1983), *Globigerinatella insueta*, *Globigerinita parkerae* (their ‘*G. parkerae*’), and *Candeina nitida* are derived from *G. glutinata*, though we employ *Globigerinatella* sp. of Pearson (1995) as the intermediary ancestor for *G. insueta*, and return

to Blow (1969) with *C. praenitida* as that for *C. nitida*. *Globigerinita minuta* is also needed as an intermediary ancestor between *G. glutinata* and the high-spired *G. uvula*, given that its highly divergent molecular results (Morard, Vollmar *et al.*, 2019) support its distinction in living populations (Brummer, 1988c; Hemleben *et al.*, 1989); a provisional survey of fossil illustrations to attempt to distinguish *G. minuta* and *G. uvula* suggests the latter succeeds the former in the early Miocene (Spezzaferri, 1994). Our compilation suggests changes to relationships usually envisaged among the three living ‘tenuitelliform’ morphospecies. The suggestion of Parker (1967) that *Globigerinita iota* descended from *G. glutinata* appears well supported by illustrated Pliocene–Pleistocene sequences (Fordham, 1986), so there seems little reason to transfer it from *Globigerinita*. Regarding Brönnimann and Resig’s (1971) ‘*Globorotalia (Turborotalia) parkerae*’, we support Li’s doubt that it was a *Tenuitella* by somewhat speculatively pointing to ancestral forms previously considered part of the main *G. glutinata* lineage sequence; we nomenclaturally resurrect that ancestor as *G. polypetala* (Fordham, 1986) and so assign Brönnimann and Resig’s morphospecies to *Globigerinita*, noting that it would then be a junior homonym in need of a new name. Finally, despite the almost absent nominal fossil record of Boltovskoy *et al.*’s (1982) South Atlantic ‘*Globigerina atlantisae brasiliensis*’ (= ‘*Toddella grata ph. compressa*’ [Fordham, 1986], ‘*T. fleisher*’ [Li, 1987]), we find enough (albeit scattered and small) possible precursors to suggest an early Oligocene origin from *T. munda*, firstly to the poorly understood *T. brevispira* (‘*Globigerina brevispira*’ Subbotina [Subbotina *et al.*, 1960]), and then to the living *T. brasiliensis* by the middle Miocene (see S3. Supporting information in Lamyman *et al.*, 2026).

Polyphyletic taxa

At present this work includes a polyphyletic genus retained from recent synthetic works. *Neogloboquadrina* descends from *Paragloborotalia continua* four times: to *Neogloboquadrina pachyderma*, *Neogloboquadrina incompta*, *Neogloboquadrina atlantica*, and *Neogloboquadrina acostaensis* (Aze *et al.*, 2011). It is anticipated that a resolution to this issue will come from more detailed study of these taxa as part of the NQPFWG taxonomic and phylogenetic revisions.

Conclusions

This study presents the most comprehensive revision to date of the Cenozoic planktonic foraminifera phylogeny, integrating stratigraphy, morphology, ecology and evolutionary relationships into a unified, updated framework. Taxonomic coverage is expanded to include all

Cenozoic clades, with the addition of 141 morphospecies and 32 genera and the removal of outdated or redundant taxa, yielding markedly improved resolution and accuracy. All stratigraphic ranges are recalibrated to the GTS2020 timescale, ensuring temporal consistency and enabling evolutionary events to be placed within a robust global chronostratigraphical context. Parallel morphospecies and lineage phylogenies further strengthen evolutionary inference by distinguishing cladogenetic events from anagenetic change.

Completeness analyses confirm that the fossil record of Cenozoic planktonic foraminifera is among the most complete known, providing an exceptionally detailed record of origination and extinction and establishing the group as an outstanding model system for macroevolutionary studies of biodiversity dynamics, trait evolution and environmental response.

Delivered as a digital, interactive resource, the phylogeny functions as both a synthesis and a platform for future research, linking morphological, ecological and stratigraphic data and enabling integration with molecular datasets. It will underpin the work of the Neogene and Quaternary Planktonic Foraminifera Working Group by providing a robust phylogenetic baseline for taxonomic revision and hypothesis testing, while more broadly advancing macroevolutionary analyses and reinforcing planktonic foraminifera as a premier system for studying biodiversity–environment interactions through deep time.

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Author contributions

CRedit: **Grace S. Lamyman**: Data curation, Investigation, Writing – original draft; **Barry G. Fordham**: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software,

Supervision, Visualization, Writing – original draft, Writing – review & editing; **Paul N. Pearson**: Conceptualization, Data curation, Methodology, Writing – original draft, Writing – review & editing; **Bridget S. Wade**: Data curation, Writing – original draft, Writing – review & editing; **Adam Woodhouse**: Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing; **Jeremy R. Young**: Data curation, Writing – review & editing; **Tracy Aze**: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Disclosure statement

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

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Data availability statement

All Supplementary Information is available from Zenodo at <https://doi.org/10.5281/zenodo.18854731> (Lamyman et al., 2026).

All code used to generate the completeness analysis is available in the Tree Mk II repository on github (<https://github.com/foradamifera/Tree-MkII>), and Triton is available to download in the figshare supplementary material of Fenton & Woodhouse et al. (2021). The relational database TSCEvolTree_CenoPIForam2 contains all tables, queries and subroutines used to generate the TimeScale Creator, data, datapacks and charts, graphs and spreadsheets, which is available from Zenodo at <https://doi.org/10.5281/zenodo.18854730> (Lamyman et al., 2026).

References

Arenillas, I., & Arz, J. A. (2017). Benthic origin and earliest evolution of the first planktonic foraminifera after the Cretaceous/Palaeogene boundary mass extinction.

Historical Biology, 29, 25–42. <https://doi.org/10.1080/08912963.2015.1119133>

Arenillas, I., Arz, J. A., & Gilabert, V. (2022). An updated suprageneric classification of planktic foraminifera after growing evidence of multiple benthic–planktic transitions. *Spanish Journal of Palaeontology*, 37, 1–34. <https://doi.org/10.7203/sjp.22189>

Arenillas, I., Arz, J., & Molina, E. (2004). A new high-resolution planktic foraminiferal zonation and subzonation for the lower Danian. *Lethaia*, 34, 79–95. <https://doi.org/10.1080/00241160310005097>

Aurahs, R., Göker, M., Grimm, G. W., Hemleben, V., Hemleben, C., Schiebel, R., & Kučera, M. (2009). Using the multiple analysis approach to reconstruct phylogenetic relationships among planktonic foraminifera from highly divergent and length-polymorphic SSU rDNA sequences. *Bioinformatics and Biology Insights*, 3, BBI.S3334. <https://doi.org/10.4137/bbi.s3334>

Aurahs, R., Treis, Y., Darling, K., & Kucera, M. (2011). A revised taxonomic and phylogenetic concept for the planktonic foraminifer species *Globigerinoides ruber* based on molecular and morphometric evidence. *Marine Micropaleontology*, 79, 1–14. <https://doi.org/10.1016/j.marmicro.2010.12.001>

Aze, T., Ezard, T. H. G., Purvis, A., Coxall, H. K., Stewart, D. R. M., Wade, B. S., & Pearson, P. N. (2011). A phylogeny of Cenozoic macroperforate planktonic foraminifera from fossil data. *Biological Reviews*, 86, 900–927. <https://doi.org/10.1111/j.1469-185X.2011.00178.x>

Benson, R. B. J. (2018). Dinosaur macroevolution and macroecology. *Annual Review of Ecology, Evolution, and Systematics*, 49, 379–408. <https://doi.org/10.1146/annurev-ecolsys-110617-062231>

Benton, M. J., Wills, M. A., & Hitchin, R. (2000). Quality of the fossil record through time. *Nature*, 403, 534–537. <https://doi.org/10.1038/35000558>

Berger, W. H. (1970). Planktonic foraminifera: Selective solution and the lysocline. *Marine Geology*, 8, 111–138. [https://doi.org/10.1016/0025-3227\(70\)90001-0](https://doi.org/10.1016/0025-3227(70)90001-0)

Berggren, W. A. (1969). Paleogene biostratigraphy and planktonic foraminifera of Northwestern Europe. In P. Brönnimann & H. H. Renz (Eds.), *Proceedings of the First International Conference on Planktonic Microfossils, Geneva, 1967* (pp. 121–160). E. J. Brill.

Berggren, W. A., Aubry, M. P., Van Fossen, M., Kent, D. V., & Norris, R. D. (2000). Integrated Paleocene calcareous plankton magnetobiochronology and stable isotope stratigraphy: DSDP Site 384 (NW Atlantic Ocean). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 159, 1–51. [https://doi.org/10.1016/S0031-0182\(00\)00031-6](https://doi.org/10.1016/S0031-0182(00)00031-6)

Berggren, W. A., Hilgen, F., Langereis, C., Obradovich, J., Raffi, I., Raymo, M., & Shackleton, N. (1995). Late Neogene chronology: New perspective in high resolution stratigraphy. *Geological Society of America Bulletin*, 107, 1272–1287.

Berggren, W. A., Kent, D. V., Swisher, C. C. III, & Aubry, M.-P. (1995). A revised Cenozoic geochronology and chronostratigraphy. In W. A. Berggren, D. V. Kent, M.-P. Aubry, & J. Hardenbol (Eds.), *Geochronology, time scales and global stratigraphic correlations* (pp. 129–212). Society for Sedimentary Geology, Special Publication No. 54.

- Berggren, W. A., & Pearson, P. N. (2005). A revised tropical to subtropical Paleogene planktonic foraminiferal zonation. *Journal of Foraminiferal Research*, 35, 279–298. <https://doi.org/10.2113/35.4.279>
- Birch, H., Coxall, H. K., Pearson, P. N., Kroon, D., & O'Regan, M. (2013). Planktonic foraminifera stable isotopes and water column structure: Disentangling ecological signals. *Marine Micropaleontology*, 101, 127–145. <https://doi.org/10.1016/j.marmicro.2013.02.002>
- Blow, W. H. (1969). Late middle Eocene to Recent planktonic foraminiferal biostratigraphy. In P. Brönnimann & H. H. Renz (Eds.), *Proceedings of the 1st International Conference on Planktonic Microfossils, Geneva, 1967* (pp. 199–422). E. J. Brill.
- Blow, W. H. (1979). *The Cainozoic Globigerinida: A study of the morphology, taxonomy, evolutionary relationships and stratigraphical distribution of some Globigerinida (mainly Globigerinacea)*. E. J. Brill.
- Bolli, H. M., Loeblich, A. R., & Tappan, H. (1957). Planktonic foraminiferal families Hantkeninidae, Orbulinidae, Globorotaliidae and Globotruncanidae. In Loeblich, A. R., Jr., Tappan, H., Beckmann, J. P., Bolli, H. M., Montanaro Gallitelli, E., & Troelsen, J. C. (Eds.), *Studies in foraminifera*. US Government Printing Office, Washington, DC.
- Bolli, H. M., Saunders, J. B., & Perch-Nielsen, K. (1985). *Plankton stratigraphy. Volume 1: Planktic foraminifera, calcareous nannofossils and calpionellids*. Cambridge University Press.
- Boltovskoy, E., Madeira-Falcetta, M., & Thiesen, Z. V. (1982). Foraminiferos del Testigo 22 (talud de Brasil meridional). *Ameghiniana, Revista de la Asociación Paleontológica Argentina*, 19, 179–208.
- Brönnimann, P., Parisi, G., & Whittaker, J. E. (1987). *Soldaniella toscanae* n. gen., n. sp., a new planktonic foraminifer (Globigerinacea) from the Pliocene of southern Tuscany, central Italy. *Revue de Paléobiologie*, 6, 169–175.
- Brönnimann, P., & Resig, J. M. (1971). A Neogene globigerinacean biochronologic time-scale of the southwestern Pacific. In E. L. Winterer, W. R. Riedel, & Others (Eds.), *Initial reports of the Deep Sea Drilling Project*. US Government Printing Office.
- Brummer, G.-J. (1988). Comparative ontogeny and species definition of planktonic foraminifers: A case study of *Dentogloborotalia anfracta* n. gen. In G.-J. A. Brummer & D. Kroon, *Planktonic foraminifers as tracers of ocean-climate history* (pp. 51–75). Free University Press.
- Brummer, G.-J. A. (1988c). Comparative ontogeny of modern microporiferate planktonic foraminifers. In G.-J. A. Brummer & D. Kroon (Eds.), *Planktonic foraminifers as tracers of ocean-climate history: Ontogeny, relationships and preservation of modern species and stable isotopes, phenotypes and assemblage distribution in different water masses*. Free University Press for Vrije Universiteit te Amsterdam.
- Brummer, G. J. A., & Kučera, M. (2022). Taxonomic review of living planktonic foraminifera. *Journal of Micropalaeontology*, 41, 29–74. <https://doi.org/10.5194/jm-41-29-2022>
- Cande, S., & Kent, D. (1995). Revised calibration of the geomagnetic polarity time scale for the late Cretaceous and Cenozoic. *Journal of Geophysical Research*, 100, 6093–6095. <https://doi.org/10.1029/94JB03098>
- Cantalapiedra, J. L., Prado, J. L., Hernández Fernández, M., & Alberdi, M. T. (2017). Decoupled ecomorphological evolution and diversification in Neogene–Quaternary horses. *Science*, 355, 627–630. <https://doi.org/10.1126/science.aag1772>
- Castiglione, S., Tesone, G., Piccolo, M., Melchionna, M., Mondanaro, A., Serio, C., Di Febbraro, M., & Raia, P. (2018). A new method for testing evolutionary rate variation and shifts in phenotypic evolution. *Methods in Ecology and Evolution*, 9, 974–983. <https://doi.org/10.1111/2041-210X.12954>
- Cifelli, R., & Scott, G. H. (1986). *Stratigraphic record of the Neogene globorotalid radiation (planktonic Foraminiferida)*. Smithsonian Contributions to Paleobiology 58. Smithsonian Institution Press. <https://doi.org/10.5479/si.00810266.58.1>
- Coxall, H. K., & Spezzaferri, S. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene *Catapsydrax*, *Globorotaloides*, and *Protentelloides*. In B. S. Wade, R. K. Olsson, P. N. Pearson, B. T. Huber, & W. A. Berggren (Eds.), *Atlas of Oligocene planktonic foraminifera* (pp. 79–124). Cushman Foundation for Foraminiferal Research Special Publication 46.
- Darling, K. F., Kučera, M., Kroon, D., & Wade, C. M. (2006). A resolution for the coiling direction paradox in *Neoglobobulimina pachyderma*. *Paleoceanography*, 21, PA2011. <https://doi.org/10.1029/2005PA001189>
- Darling, K. F., Thomas, E., Kasemann, S. A., Secars, H. A., Smart, C. W., & Wade, C. M. (2009). Surviving mass extinction by bridging the benthic/planktic divide. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 12629–12633. <https://doi.org/10.1073/pnas.0902827106>
- De Vargas, C., Zaninetti, L., Hilbrecht, H., & Pawlowski, J. (1997). Phylogeny and rates of molecular evolution of planktonic foraminifera: SSU rDNA sequences compared to the fossil record. *Journal of Molecular Evolution*, 45, 285–294. <https://doi.org/10.1007/pl00006232>
- Ezard, T. H. G., Aze, T., Pearson, P. N., & Purvis, A. (2011). Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science*, 332, 349–351. <https://doi.org/10.1126/science.1203060>
- Ezard, T. H. G., Pearson, P. N., Aze, T., & Purvis, A. (2012). The meaning of birth and death (in macroevolutionary birth–death models). *Biology Letters*, 8(1), 139–142. <https://doi.org/10.1098/rsbl.2011.0699>
- Fabbrini, A., Greco, M., Iacoviello, F., Kučera, M., Ezard, T. H. G., & Wade, B. S. (2023). Bridging the extant and fossil record of planktonic foraminifera: Implications for the Globigerina lineage. *Palaeontology*, 66(6), e12676. <https://doi.org/10.1111/pala.12676>
- Fabbrini, A., Petrizzo, M. R., Silva, I. P., Foresi, L. M., & Wade, B. S. (2024). Rediscovering *Globigerina bollii* Cita and Premoli Silva 1960. *Journal of Micropalaeontology*, 43, 121–138. <https://doi.org/10.5194/jm-43-121-2024>
- Fabbrini, A., Zaminga, I., Ezard, T. H. G., & Wade, B. S. (2021). Systematic taxonomy of middle Miocene *Sphaeroidinellopsis* (planktonic foraminifera). *Journal of Systematic Palaeontology*, 19, 953–968. <https://doi.org/10.1080/14772019.2021.1991500>
- Fayolle, F., & Wade, B. S. (2021). The evolution of Eocene planktonic foraminifera *Dentoglobigerina*. *Journal of Systematic Palaeontology*, 19, 333–376. <https://doi.org/10.1080/14772019.2021.1904021>

- Fenton, I. S., Woodhouse, A., Aze, T., Lazarus, D., Renaudie, J., Dunhill, A. M., Young, J. R., & Saupe, E. E. (2021). Triton, a new species-level database of Cenozoic planktonic foraminiferal occurrences. *Scientific Data*, 8, 1–9. <https://doi.org/10.1038/s41597-021-00942-7>
- Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J. C., Smith-Vaniz, W. F., Wirtz, P., Edwards, A. J., Barreiros, J. P., Ferreira, C. E. L., Gasparini, J. L., Brito, A., Falcón, J. M., Bowen, B. W., & Bernardi, G. (2008). Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, 35, 22–47. <https://doi.org/10.1111/j.1365-2699.2007.01790.x>
- Footo, M. (1996). On the probability of ancestors in the fossil record. *Paleobiology*, 22, 141–151. <https://doi.org/10.1017/S0094837300016146>
- Footo, M., & Sepkoski, J. J. (1999). Absolute measures of the completeness of the fossil record. *Nature*, 398, 415–417. <https://doi.org/10.1038/18872>
- Fordham, B. G. (1986). *Miocene–Pleistocene planktic foraminifers from DSDP Sites 208 and 77, and phylogeny and classification of Cenozoic species*, University of Chicago Evolutionary Monographs, 6.
- Fordham, B. G., Aze, T., Haller, C., Zehady, A. K., Pearson, P. N., Ogg, J. G., & Wade, B. S. (2018). Future-proofing the Cenozoic macroperforate planktonic foraminifera phylogeny of Aze & others (2011). *PLoS ONE*, 13, e0204625. <https://doi.org/10.1371/journal.pone.0204625>
- Fordham, B. G., Huber, B. T., & Haynes, J. R. (2016). Evidence for ancestry in taxonomic studies: Lessons from mid-Cretaceous biserial planktonic foraminifera. International Geological Congress, Abstracts vol. 35(2462), 2016 Geological Congress, Cape Town, South Africa, 27 August–4 September.
- Gingerich, P. D. (1990). Stratophenetics. In D. E. G. Briggs & P. R. Crowther (Eds.), *Paleobiology: A synthesis*. Blackwell Scientific.
- Gohl, K., Uenzelmann-Neben, G., Gille-Petzoldt, J., Hillenbrand, C.-D., Klages, J. P., Bohaty, S. M., Passchier, S., Frederichs, T., Wellner, J. S., Lamb, R., Leitchenkova, G., & IODP Expedition 379 Scientists. (2021). Evidence for a highly dynamic West Antarctic Ice Sheet during the Pliocene. *Geophysical Research Letters*, 48, e2021GL093103. <https://doi.org/10.1029/2021GL093103>
- Gradstein, F., Ogg, J., Schmitz, M., & Ogg, G. (2012). *The geologic time scale 2012*. Elsevier.
- Gradstein, F. M., Ogg, J. G., Schmitz, M., & Ogg, G. (Eds.). (2020). *The geologic time scale 2020*. Elsevier Science.
- Hart, M. B., Hylton, M. D., Oxford, M. J., Price, G. D., Hudson, W., & Smart, C. W. (2003). The search for the origin of the planktic Foraminifera. *Journal of the Geological Society*, 160, 341–343. <https://doi.org/10.1144/0016-764903-003>
- Harvey, P. H., May, R. M., & Nee, S. (1994). Phylogenies without fossils. *Evolution*, 48, 523–529. <https://doi.org/10.1111/j.1558-5646.1994.tb01341.x>
- Hayward, B. W., Da Encarnação, S. C., Le Coze, F., Mamo, B., Vachard, D., & Gross, O. (2022). *World Foraminifera Database, World Register of Marine Species (WoRMS)* [Online]. Oostende (Belgium). <https://doi.org/10.14284/305>; WoRMS Editorial Board, Vlaams Instituut voor de Zee (Flanders Marine Institute). <http://www.marinespecies.org/foraminifera>
- Hayward, B. W., Grenfell, H. R., Sabaa, A. T., Neil, H., & Buzas, M. A. (2010). *Recent New Zealand deepwater benthic foraminifera: Taxonomy, ecology distribution, biogeography, and use in paleoenvironmental assessment*, Lower Hutt, New Zealand, GNS Science Monograph 26 (New Zealand Geological Survey Paleontological Bulletin 77).
- Hemleben, C., Spindler, M., & Anderson, O. R. (1989). *Modern planktonic foraminifera*, Springer-Verlag.
- Hernández-Almeida, I., Sierro, F. J., Flores, J.-A., Cacho, I., & Filippelli, G. M. (2013). Palaeoceanographic changes in the North Atlantic during the Mid-Pleistocene Transition (MIS 31–19) as inferred from planktonic foraminiferal and calcium carbonate records. *Boreas*, 42, 140–159.
- Hilgen, F. J., Krijgsman, W., Raffi, I., Turco, E., & Zachariasse, W. J. (2000). Integrated stratigraphy and astronomical calibration of the Serravallian/Tortonian boundary section at Monte Gibliscemi (Sicily, Italy). *Marine Micropaleontology*, 38, 181–211. [https://doi.org/10.1016/S0377-8398\(00\)00008-6](https://doi.org/10.1016/S0377-8398(00)00008-6)
- Hodell, D. A., Abrantes, F., Alvarez Zarikian, C.A., & Expedition 397 Scientists. (2023). Expedition 397 Preliminary Report: Iberian Margin Paleoclimate. International Ocean Discovery Program.
- Holmes, N. A. (1984). An emendation of the genera *Beella* Banner and Blow 1959, and *Turborotalita* Banner and Blow, 1962, with notes on *Orcadia* Boltovskoy and Watanabe, 1982. *Journal of Foraminiferal Research*, 14, 101–110. <https://doi.org/10.2113/gsjfr.14.2.101>
- Huber, B. T., Olsson, R. K., & Pearson, P. N. (2006). Taxonomy, biostratigraphy, and phylogeny of Eocene microperforate planktonic foraminifera (*Jenkinsina*, *Cassigerinelloita*, *Chiloguembelina*, *Streptochilus*, *Zeauvigerina*, *Tenuitella*, and *Cassigerinella*) and Problematica (*Dipsidripella*). In P. N. Pearson, R. K. Olsson, B. T. Huber, C. Hemleben, & W. A. Berggren (Eds.), *Atlas of Eocene planktonic foraminifera* (pp. 461–508). Cushman Foundation for Foraminiferal Research Special Publication 41.
- Huber, B. T., Petrizzo, M. R., & Macleod, K. G. (2020). Planktonic foraminiferal endemism at southern high latitudes following the terminal Cretaceous extinction. *Journal of Foraminiferal Research*, 50, 382–402. <https://doi.org/10.2113/gsjfr.50.4.382>
- Huber, B. T., Petrizzo, M. R., Young, J., Falzoni, F., Gilardoni, S., Bown, P., & Wade, B. (2017). Pforams@microtax: A new online taxonomic database for planktonic foraminifera. *Micropaleontology*, 62(6), 429–438. <https://doi.org/10.47894/mpal.62.6.02>
- Huber, B. T., & Quillevéré, F. (2005). Revised Paleogene planktonic foraminiferal biozonation for the Austral Realm. *The Journal of Foraminiferal Research*, 35, 299–314. <https://doi.org/10.2113/35.4.299>
- Kennett, J. P., & Srinivasan, M. S. (1983). *Neogene planktonic foraminifera: A phylogenetic atlas*. Hutchinson and Ross.
- King, D. J., Wade, B. S., Liska, R. D., & Miller, C. G. (2020). A review of the importance of the Caribbean region in Oligo–Miocene low latitude planktonic foraminiferal biostratigraphy and the implications for modern biochronological schemes. *Earth-Science Reviews*, 202, 102968. <https://doi.org/10.1016/j.earscirev.2019.102968>

- Koutsoukos, E. (2014). Phenotypic plasticity, speciation, and phylogeny in Early Danian planktic foraminifera. *Journal of Foraminiferal Research*, 44, 109–142. <https://doi.org/10.2113/gsjfr.44.2.109>
- Lam, A. R., & Leckie, R. M. (2020). Late Neogene and Quaternary diversity and taxonomy of subtropical to temperate planktic foraminifera across the Kuroshio Current Extension, northwest Pacific Ocean. *Micropaleontology*, 66, 177–268. <https://doi.org/10.47894/mpal.66.3.01>
- Lamyman, G., Fordham, B., Pearson, P., Woodhouse, A., Wade, B., Young, J., & Aze, T. (2026). Lamyman_et_al_2026_PForamPhylogeny_Supplementary_Data [dataset]. Zenodo. <https://doi.org/10.5281/zenodo.18854731>
- Latas, M., Pearson, P. N., Poole, C. R., Fabbri, A., & Wade, B. S. (2023). *Globigerinoides rublobatus* – a new species of Pleistocene planktonic foraminifera. *Journal of Micropaleontology*, 42, 57–81.
- Leckie, R. M., Wade, B. S., Pearson, P. N., Fraass, A. J., King, D. J., Olsson, R. K., Premoli Silva, I., & Spezzaferri, S. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene *Catapsydrax*, *Globorotaloides*, and *Protentelloides*. In Wade, B. S., Olsson, R. K., Pearson, P. N., Huber, B. T., & Berggren, W. A. (Eds.), *Atlas of Oligocene planktonic foraminifera* (pp. 125–178). Fredericksburg [Virginia, USA]: Cushman Foundation for Foraminiferal Research Special Publication 46.
- Li, Q.-Y. (1987). Origin, phylogenetic development and systematic taxonomy of the *Tenuitella plexus* (Globigerinitidae Globigerinina). *Journal of Foraminiferal Research*, 17, 298–320.
- Li, Q.-Y., Radford, S. S., & Banner, F. T. (1992). Distribution of microporiferate tenuitellid planktonic foraminifera in Holes 747a and 749b, Kerguelen Plateau. In Wise, S. W., JR., Schlich, R., & Others (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*, 120 (pp. 569–594). Ocean Drilling Program.
- Lloyd, G. T., Pearson, P. N., Young, J. R., & Smith, A. B. (2012). Sampling bias and the fossil record of planktonic foraminifera on land and in the deep sea. *Paleobiology*, 38, 569–584. <https://doi.org/10.1666/11041.1>
- Lowery, C., Bown, P., Fraass, A., & Hull, P. (2020). Ecological response of plankton to environmental change: Thresholds for extinction. *Annual Review of Earth and Planetary Sciences*, 48, 403–429. <https://doi.org/10.1146/annurev-earth-081619-052818>
- Luciani, V., & Giusberti, L. (2014). Reassessment of the early–middle Eocene planktic foraminiferal biomagnetochronology: New evidence from the Tethyan Possagno section (NE Italy) and western North Atlantic Ocean ODP Site 1051. *The Journal of Foraminiferal Research*, 44, 187–201. <https://doi.org/10.2113/gsjfr.44.2.187>
- Lui, C. J., & Olsson, R. K. (1994). On the origin of Danian normal perforate planktonic foraminifera from Hedbergella. *Journal of Foraminiferal Research*, 24, 61–74.
- Molina, E. (1979). *Oligoceno–Mioceno inferior por medio de foraminíferos planctónicos en el sector central de las Cordilleras Béticas (España)*. Tesis doctoral, Departamento de Paleontología, Universidad de Granada, Granada. Granada y Zaragoza, Publicación de los Departamentos de Paleontología de las Universidades de Granada y Zaragoza.
- Morard, R., Füllberg, A., Brummer, G.-J. A., Greco, M., Jonkers, L., Wizemann, A., Weiner, A. K. M., Darling, K., Siccha, M., Ledevin, R., Kitazato, H., De Garidel-Thoron, T., De Vargas, C., & Kučera, M. (2019). Genetic and morphological divergence in the warm-water planktonic foraminifera genus *Globigerinoides*. *PLoS ONE*, 14, 1–30. <https://doi.org/10.1371/journal.pone.0225246>
- Morard, R., Garet-Delmas, M.-J., Mahé, F., Romac, S., Poulain, J., Kučera, M., & De Vargas, C. (2018). Surface ocean metabarcoding confirms limited diversity in planktonic foraminifera but reveals unknown hyper-abundant lineages. *Scientific Reports*, 8, 2539. <https://doi.org/10.1038/s41598-018-20833-z>
- Morard, R., Hassenrück, C., Greco, M., Fernandez-Guerra, A., Rigaud, S., Douady, C. J., & Kučera, M. (2022). Renewal of planktonic foraminifera diversity after the Cretaceous Paleogene mass extinction by benthic colonizers. *Nature Communications*, 13, 7135. <https://doi.org/10.1038/s41467-022-34794-5>
- Morard, R., Vollmar, N. M., Greco, M., & Kučera, M. (2019). Unassigned diversity of planktonic foraminifera from environmental sequencing revealed as known but neglected species. *PLoS ONE*, 14, e0213936. <https://doi.org/10.1371/journal.pone.0213936>
- Nee, S., May, R. M., & Harvey, P. H. (1994). The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 344, 305–311. <https://doi.org/10.1098/rstb.1994.0068>
- Ogg, J., Ogg, G., & Gradstein, F. M. (2016). *The Concise Geologic Time Scale*. Cambridge University Press.
- Olsson, R. K., Hemleben, C., Berggren, W., & Huber, B. (1999). *Atlas of Paleocene planktonic foraminifera*.
- Olsson, R. K., Hemleben, C., Coxall, H. K., & Wade, B. S. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene *Ciperoella*. In Wade, B. S., Olsson, R. K., Pearson, P. N., Huber, B. T., & Berggren, W. A. (Eds.), *Atlas of Oligocene planktonic foraminifera* (pp. 215–230).
- Olsson, R. K., Hemleben, C., & Pearson, P. N. (2006). Taxonomy, biostratigraphy, and phylogeny of Eocene *Dentoglobigerina*. In Pearson, P. N., Olsson, R. K., Huber, B. T., Hemleben, C., & Berggren, W. A. (Eds.), *Atlas of Eocene planktonic foraminifera* (pp. 401–412). Fredericksburg [Virginia, USA]: Cushman Foundation for Foraminiferal Research Special Publication, vol. 41.
- Olsson, R. K., Pearson, P. N., & Huber, B. T. (2006). Taxonomy, biostratigraphy, and phylogeny of Eocene *Catapsydrax*, *Globorotaloides*, *Guembelitrioides*, *Paragloborotalia*, *Parasubbotina*, and *Pseudoglobigerinella* n. gen. In Pearson, P. N., Olsson, R. K., Huber, B. T., Hemleben, C., & Berggren, W. A. (Eds.), *Atlas of Eocene planktonic foraminifera* (pp. 67–110). Fredericksburg [Virginia, USA]: Cushman Foundation for Foraminiferal Research Special Publication, vol. 41.
- Parker, F. L. (1967). Late Tertiary biostratigraphy (planktonic foraminifera) of tropical Indo-Pacific deep-sea cores. *Bulletins of American Paleontology*, 52, 115–208.
- Pearson, P. N. (1995). Planktonic foraminiferal biostratigraphy and the development of pelagic caps on guyots in the Marshall Islands Group. In J. Haggerty, I. Premoli Silva, F. Rack, & M. K. McNutt (Eds.), *Proceeding of the Ocean Drilling Program: Scientific Results*, 144 (pp. 21–59). Ocean Drilling Program.

- Pearson, P. N. (1998a). Evolutionary concepts in biostratigraphy. In P. Doyle & M.R. Bennett (Eds.), *Unlocking the stratigraphical record: Advances in modern stratigraphy* (pp. 123–144). John Wiley and Sons Ltd.
- Pearson, P. N. (1998b). Speciation and extinction asymmetries in paleontological phylogenies: Evidence for evolutionary progress. *Paleobiology*, 24, 305–335.
- Pearson, P. N., & Kučera, M. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene *Turborotalita*. In B. S. Wade, R. K. Olsson, P. N. Pearson, B. T. Huber, & W. A. Berggren (Eds.), *Atlas of Oligocene planktonic foraminifera*. Cushman Foundation for Foraminiferal Research Special Publication 46.
- Pearson, P. N., Olsson, R. K., Huber, B. T., Hemleben, C., & Berggren, W. A. (2006). *Atlas of Eocene planktonic foraminifera*. Cushman Foundation for Foraminiferal Research.
- Pearson, P. N., & Penny, L. (2021). Coiling directions in the planktonic foraminifer Pulleniatina: A complex eco-evolutionary dynamic spanning millions of years. *PLoS ONE*, 16, e0249113. <https://doi.org/10.1371/journal.pone.0249113>
- Pearson, P. N., Spezzaferri, S., & Huber, B. T. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene Cassigerinella. In B. S. Wade, R. K. Olsson, P. N. Pearson, B. T. Huber, & W. A. Berggren (Eds.), *Atlas of Oligocene planktonic foraminifera*. Cushman Foundation for Foraminiferal Research Special Publication 46.
- Pearson, P. N., Wade, B. S., & Huber, B. T. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene Globigerinitidae (*Dipsidripella*, *Globigerinita*, and *Tenuitella*). In B. S. Wade, R. K. Olsson, P. N. Pearson, B. T. Huber, & W. A. Berggren (Eds.), *Atlas of Oligocene planktonic foraminifera*. Cushman Foundation for Foraminiferal Research Special Publication 46.
- Petrizzo, M. R., King, D. J., Pearson, P. N., Huber, B. T., & Wade, B. S. (2024). Planktonic foraminifera in biostratigraphy and biochronology. *Newsletters on Stratigraphy*, 59, 1–37.
- Petrizzo, M. R., Wade, B. S., & Gradstein, F. M. (2025). Planktonic foraminifera. In F. M. Gradstein, J. Zalasiewicz, M. Williams, & A. Wałkowska (Eds.), *Fossils and Earth time: Evolution and biostratigraphy* (pp. 119–134). Elsevier.
- Polly, P. D. (2019). Climate, diversification and refugia in the common shrew: Evidence from the fossil record. In J. B. Searle, P. D. Polly, & J. Zima (Eds.), *Shrews, chromosomes and speciation*. Cambridge University Press.
- Poore, R. Z., & Berggren, W. A. (1975). Late Cenozoic planktonic foraminiferal biostratigraphy and paleoclimatology of Hatton-Rockall Basin: DSDP Site 116. *Journal of Foraminiferal Research*, 5, 270–293. <https://doi.org/10.2113/gsjfr.5.4.270>
- Popescu, G., & Crihan, I.-M. (2011). Middle Miocene Globigerinas of Romania. *Acta Palaeontologica Romaniaae*, 7, 291–314.
- Quilty, P. G. (1976). Planktonic foraminifera DSDP Leg 34–Nazca Plate. *Initial Reports of the Deep Sea Drilling Project*, 34, 629–703.
- Raffi, I., Wade, B. S., & Palike, H. (2020). The Neogene Period. *Geologic Time Scale 2020*, 2, 1141–1215.
- Resig, J. M. (1989). Stratigraphic distribution of late Neogene species of the planktonic foraminifer *Streptochilus* in the Indo-Pacific. *Micropaleontology*, 35, 49–62. <https://doi.org/10.2307/1485536>
- Resig, J. M. (1993). Cenozoic stratigraphy and paleoceanography of biserial planktonic foraminifers, Ontong Java Plateau. In W. H. Berger, L. W. Kroenke, L. A. Mayer, & Others (Eds.), *Initial reports of the Deep Sea Drilling Project*. US Government Printing Office.
- Revell, L. J. (2013). Two new graphical methods for mapping trait evolution on phylogenies. *Methods in Ecology and Evolution*, 4, 754–759. <https://doi.org/10.1111/2041-210X.12066>
- Rögl, F., & Bolli, H. M. (1973). Holocene to Pleistocene planktonic foraminifera of Leg 15, Site 147 (Cariaco Basin (Trench), Caribbean Sea) and their climatic interpretation. In N. T. Edgar, & Others (Eds.), *Initial Reports of the Deep Sea Drilling Project*. US Government Printing Office.
- Saito, T., Breger, D., & Thompson, P. R. (1981). *Systematic index of Recent and Pleistocene planktonic foraminifera*. University of Tokyo Press.
- Schiebel, R., & Hemleben, C. (2017). *Planktic foraminifers in the modern ocean*. Springer-Verlag.
- Scott, G. H., Bishop, S., & Burt, B. J. (1990). *Guide to some Neogene globorotalids (Foraminiferida) from New Zealand*. New Zealand Geological Survey Paleontological Bulletin 61.
- Smart, C. W., & Thomas, E. (2007). Emendation of the genus *Streptochilus* Brönnimann and Resig 1971 (Foraminifera) and new species from the lower Miocene of the Atlantic and Indian Oceans. *Micropaleontology*, 53, 73–103. <https://doi.org/10.2113/gsmicropal.53.1-2.73>
- Smart, C. W., & Thomas, E. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene *Streptochilus*. In B. S. Wade, R. K. Olsson, P. N. Pearson, B. T. Huber, & W. A. Berggren (Eds.), *Atlas of Oligocene planktonic foraminifera*. Cushman Foundation for Foraminiferal Research Special Publication.
- Soldan, D. M., Petrizzo, M. R., & Silva, I. P. (2014). *Pearsonites*, a new Paleogene planktonic foraminiferal genus for the broedermanni lineage. *Journal of Foraminiferal Research*, 44, 17–27. <https://doi.org/10.2113/gsjfr.44.1.17>
- Spaak, P. (1981). Accuracy in correlation and ecological aspects of the planktonic foraminiferal zonation of the Mediterranean Pliocene. *Utrecht Micropaleontological Bulletin*, 28, 1–159.
- Spezzaferri, S. (1994). *Planktonic foraminiferal biostratigraphy and taxonomy of the Oligocene and lower Miocene in the oceanic record. An overview*. Palaeontographica Italica, Pubblicata a cura della società Toscana di scienze naturali, LXXXI.
- Spezzaferri, S., Coxall, H. K., Olsson, R. K., & Hemleben, C. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene *Globigerina*, *Globigerinella*, and *Quiltyella* n. gen. In B. S. Wade, R. K. Olsson, P. N. Pearson, B. T. Huber, & W. A. Berggren (Eds.), *Atlas of Oligocene planktonic foraminifera*.
- Spezzaferri, S., Kučera, M., Pearson, P. N., Wade, B. S., Rappo, S., Poole, C. R., Morard, R., & Stalder, C. (2015). Fossil and genetic evidence for the polyphyletic nature of the planktonic foraminifera ‘Globigerinoides’, and description of the new genus *Trilobatus*. *PLoS ONE*, 10(5), e0128108. <https://doi.org/10.1371/journal.pone.0128108>

- Spezzaferri, S., Olsson, R. K., Hemleben, C., Wade, B. S., & Coxall, H. K. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene and Lower Miocene Globoturborotalita. In B. S. Wade, R. K. Olsson, P. N. Pearson, B. T. Huber, & W. A. Berggren (Eds.), *Atlas of Oligocene planktonic foraminifera*.
- Stainforth, R. M., Lamb, J. L., & Jeffords, R. M. (1978). *Rotalia menardii* Parker, Jones and Brady, 1865 (Foraminiferida): Proposed suppression of lectotype and designation of neotype Z.N.(S.) 2145. *Bulletin of Zoological Nomenclature*, 34, 251–262.
- Stainforth, R. M., Lamb, J. L., Luterbacher, H., Beard, J. H., & Jeffords, R. M. (1975). *Cenozoic planktonic foraminiferal zonation and characteristics of index forms*. University of Kansas Paleontological Contributions. The Paleontological Institute, The University of Kansas.
- Stewart, D. R. M. (2003). *Evolution of Neogene globorotaliid foraminifera and Miocene climate change*. University of Bristol.
- Stockdale, M. T., & Benton, M. J. (2021). Environmental drivers of body size evolution in crocodile-line archosaurs. *Communications Biology*, 4, 38. <https://doi.org/10.1038/s42003-020-01561-5>
- Subbotina, N. N., Pishvanova, L. S., & Ivanova, L. V. (1960). Stratigrafiya oligotsenovykh i miotsenovykh otlozheniy predkarpat'ya po foraminiferam. In N. N. Subbotina (Ed.), *Mikrofauna SSSR XI. Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta (VNIGRI)* (Vol. 153, pp. 157–307).
- Thomas, E. (1987). Late Oligocene to Recent benthic foraminifers from Deep Sea Drilling Project Sites 608 and 610, northeastern North Atlantic. In W. F. Ruddiman, R. B. Kidd, E. Thomas, & Others (Eds.), *Initial Reports of the Deep Sea Drilling Project*. US Government Printing Office.
- Tjalsma, R. C. (1971). Stratigraphy and foraminifera of the Neogene of the eastern Guadalquivir Basin (southern Spain). *Utrecht Micropaleontological Bulletin*, 4, 1–161.
- Varela, L., Tambusso, P. S., McDonald, H. G., & Farina, R. A. (2018). Phylogeny, macroevolutionary trends and historical biogeography of sloths: Insights from a Bayesian morphological clock analysis. *Systematic Biology*, 68, 204–218. <https://doi.org/10.1093/sysbio/syy058>
- Wade, B. S., Aljadhali, M. H., Mufreih, Y. A., Memesh, A. M., Alsoubhi, S. A., & Zalmout, I. S. (2021). Upper Eocene planktonic foraminifera from northern Saudi Arabia: Implications for stratigraphic ranges. *Journal of Micropaleontology*, 40, 145–161. <https://doi.org/10.5194/jm-40-145-2021>
- Wade, B. S., Olsson, R., Pearson, P., Huber, B., & Berggren, W. (2018). *Atlas of Oligocene planktonic foraminifera*. Cushman Foundation for Foraminiferal Research, Special Publication.
- Wade, B. S., Pearson, P. N., Berggren, W. A., & Pälike, H. (2011). Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth-Science Reviews*, 104, 111–142. <https://doi.org/10.1016/j.earscirev.2010.09.003>
- Wade, B. S., Pearson, P. N., Olsson, R. K., Fraass, A. J., Leckie, R. M., & Hemleben, C. (2018). Taxonomy, biostratigraphy, and phylogeny of Oligocene and lower Miocene *Dentoglobigerina* and *Globoquadrina*. In B. S. Wade, R. K. Olsson, P. N. Pearson, B. T. Huber, & W. A. Berggren (Eds.), *Atlas of Oligocene planktonic foraminifera*. Cushman Foundation for Foraminiferal Research Special Publication 46.
- Weiner, A., Weinkauf, M., Kurasawa, A., Darling, K., & Kucera, M. (2015). Genetic and morphometric evidence for parallel evolution of the *Globigerinella calida* morphotype. *Marine Micropaleontology*, 114, 19–35. <https://doi.org/10.1016/j.marmicro.2014.10.003>
- Weitkamp, T. M., Razmjooei, M. J., Pearson, P. N., & Coxall, H. K. (2023). Upper Oligocene to Pleistocene planktonic foraminifera stratigraphy at North Atlantic DSDP Site 407, Reykjanes Ridge: Diversity trends and biozonation using modern Neogene taxonomic concepts. *Journal of Micropaleontology*, 44, 1–78. <https://doi.org/10.5194/jm-44-1-2025>
- Wiley, E. O. (1978). The evolutionary species concept reconsidered. *Systematic Biology*, 27, 17–26. <https://doi.org/10.2307/2412809>
- Woodhouse, A., Swain, A., Fagan, W. F., Fraass, A. J., & Lowery, C. M. (2023). Late Cenozoic cooling restructured global marine plankton communities. *Nature*, 614, 713–720. <https://doi.org/10.1038/s41586-023-05694-5>
- Yasuhara, M., Tittensor, D. P., Hillebrand, H., & Worm, B. (2017). Combining marine macroecology and palaeoecology in understanding biodiversity: Microfossils as a model. *Biological Reviews*, 92, 199–215. <https://doi.org/10.1111/brv.12223>
- Zachariasse, W. J. (1975). Planktonic foraminiferal biostratigraphy of the late Neogene of Greece. *Utrecht Micropaleontological Bulletin*, 11, 1–171.

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