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Taxonomic review of living planktonic foraminifera

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Abstract. Applications of fossil shells of planktonic foraminifera to decipher past environmental change and plankton evolution require a robust operational taxonomy. In this respect, extant planktonic foraminifera provide an opportunity for benchmarking the dominantly morphological species concepts and classification of the group by considering ecological, physiological and genetic characters. Although the basic framework of the taxonomy of extant planktonic foraminifera has been stable for half a century, many details have changed, not the least in light of genetic evidence. In this contribution, we review the current taxonomy of living planktonic foraminifera, presenting a comprehensive standard that emerged from the meetings and consultations of the SCOR/IGBP Working Group 138 "Planktonic foraminifera and ocean changes". We present a comprehensive annotated list of 50 species and subspecies recognized among living planktonic foraminifera and evaluate their generic and supra-generic classification. As a result, we recommend replacing the commonly used names *Globorotalia menardii* by *G. cultrata* and *Globorotalia theyeri* by *G. eastropacia*, recognize *Globorotaloides oveyi* as a neglected but valid living species, and propose transferring the three extant species previously assigned to *Tenuitella* into a separate genus, *Tenuitellita*. We review the status of types and designate lectotypes for *Globoturborotalita rubescens* and *Globigerinita uvula*. We further provide an annotated list of synonyms and other names that have been applied previously to living planktonic foraminifera and outline the reasons for their exclusion. Finally, we provide recommendations on how the presented classification scheme should be used in operational taxonomy for the benefit of producing replicable and interoperable census counts.

1 Introduction

Planktonic foraminifera are marine protists with ornate calcite shells, which have inhabited upper ocean waters since the Jurassic. They abound in all oceanic settings, ranging from oligotrophic tropical gyres and productive upwelling regions to the coldest waters of the polar regions (Bé, 1977). Whilst their biomass constitutes only a minor part of the plankton, their calcite shells form a significant portion of the pelagic carbonate flux (Schiebel, 2002). These shells accumulate in marine sediments, where they form a unique archive of climatic and biotic change. This archive can be deciphered because the elemental and isotopic composition of foraminiferal shells contains chemical and physical signals related to the state of the habitat in which they were precipitated (Henderson, 2002). This makes planktonic foraminifera an important tool in paleoceanography and paleoclimatology (Kucera, 2007). However, since the seasonal flux and the calcification depth differ among species, the application of fossil shells of planktonic foraminifera to decipher past environmental change requires species-specific analyses (Jonkers and Kucera, 2017) and is thus contingent on the existence of robust operational taxonomy.

Planktonic foraminifera were initially discovered and studied in sediment samples. Using the richness of morphological characters of their shells, their classification was based entirely on the characters of their skeleton. In this way, living and fossil species concepts are congruent, and the evolutionary origin of living species can be traced in the fossil record (e.g. Aze et al., 2011). In the past two decades,

advances in molecular genetics provided an opportunity to benchmark the classical morphological species concept by analyses of DNA sequence divergence. This new and independent information had two consequences for taxonomy. First, it largely confirmed the choice and interpretation of traits used in species concepts based solely on shell morphology, resulting only in minor amendments (Darling et al., 2006; Aurahs et al., 2011; Weiner et al., 2015; Morard et al., 2019a). Second, it led to the discovery of extensive genetic diversity within most morphologically defined species, which likely signifies the presence of biological (reproductively isolated) species that are morphologically similar or even indistinguishable, i.e. cryptic species (Darling and Wade, 2008).

In this contribution, we review the current taxonomy of living planktonic foraminifera, with the aim to introduce the comprehensive standard that emerged from the meetings and consultations of the SCOR Working Group 138 "Planktonic foraminifera and ocean changes" (Ganssen and Kucera, 2012). In addition to presenting an annotated list of living species, their generic classification and a review of types, we provide an annotated list of synonyms and other names that have been applied previously but are here considered inappropriate for the use on living planktonic foraminifera. It is not our intention to revise taxonomic descriptions or to provide differential diagnoses or new illustrations apart from the lectotypes designated herein. For these aspects of the taxonomy, the reader is referred to the many existing manuals and classical taxonomic works (Parker, 1962; Saito et al., 1981; Kennett and Srinivasan, 1983; Schiebel and Hemleben, 2017). Instead, our primary intention is to explain the current concepts and (supra-)generic assignment of extant species, justifying the retention or rejection of various taxa and names for better understanding of the diversity of the group through time.

2 History of classification

We begin by briefly commenting on the name of the object of this review, explaining the chosen usage of "planktonic" and "foraminifera". The recommendation that we present is based on a pragmatic approach of *conserving the most common usage*. We do not wish to initiate a detailed linguistic debate nor do we intend to repeat arguments presented at length in the literature, so the justifications are left in their simplest form. With respect to the adjective "planktonic", a second version "planktic" has also been in use. A remarkable body of literature exists advocating each version, using arguments that all seem legitimate (Burckhardt, 1920; Rodhe, 1974; Hutchinson, 1974; Martinsson, 1975, 1979, 1982; Teichert, 1981; Emiliani, 1991a, b). Notwithstanding this debate, the current (year 2021) usage favours "planktonic" by more than an order of magnitude (based on a search in Google or more specifically on Google Scholar). A higher popularity also holds for the combination "planktonic foraminifera". We also note that this distinction has been consistent for over a decade, because the same pattern of usage was noted by Pearson (2012). Therefore, we recommend retaining the adjective "planktonic". This does not mean that we object to the usage of the less popular form, but in the absence of a grammatical consensus, we plead with the community to conserve the more common usage. A similar issue concerns the usage and grammar of "foraminifera". This topic has been exhaustively treated by Lipps et al. (2011). Following that study, we recommend the following usage: capitalized, the word "Foraminifera" is Latin and refers to a taxonomic unit; not capitalized, the word is vernacular and English and can be both singular and plural (like "sheep"), referring to one or more specimens or taxa. Like Lipps et al. (2011), we see no reason to endorse the seemingly "more" English, but far less used, substantive "foraminifer" with its plural form "foraminifers".

Although the oldest illustrations of their shells date to the 18th century (e.g. Soldani, 1791), planktonic foraminifera were first systematically described by Alcide Dessalines d'Orbigny, who is the author of the earliest validly named extant species (d'Orbigny, 1826). The basis of the modern taxonomy has been set in the second half of the 19th century in connection with the exploration of the ocean interior and the deep sea by British and German expeditions. The current classification is the result of the advent of deep-sea drilling and paleoceanography a century later (Fig. 1). A milestone in the development of the current classification is the study by Parker (1962), whose scheme was adopted by Bé (1967a) for studies on living plankton and by the CLIMAP project (1976) to serve as a basis for paleoecological reconstructions by means of geochemical proxies and assemblage census counts in Quaternary sediments. This scheme has prevailed for decades without major amendments, indicating that it succeeded in covering a large part of the diversity of living planktonic foraminifera. Indeed, new species described after Parker (1962) comprise mainly small and (apparently) rare forms. At that time, the higher-level classification of living and fossil planktonic foraminifera began to converge on the current convention, with higher-rank taxa reflecting differences in shell wall texture (Steineck and Fleisher, 1978) and ontogenetic morphology (Brummer et al., 1986), i.e. processes related to biomineralization, metabolism and growth, with genera being defined by differences in shell architecture and aperture modifications (e.g. Loeblich and Tappan, 1984). This choice of characters and their phylogenetic interpretation (Olsson et al., 1999; Pearson et al., 2006; Wade et al., 2018a) has been largely vindicated by genetic data generated in the last two decades (e.g. Aurahs et al., 2009; Morard et al., 2019b).

Because of its geological "roots", the current classification of planktonic foraminifera is based on fully grown specimens, as are typically found in sediment samples. In contrast, specimens found in the living plankton are dominated

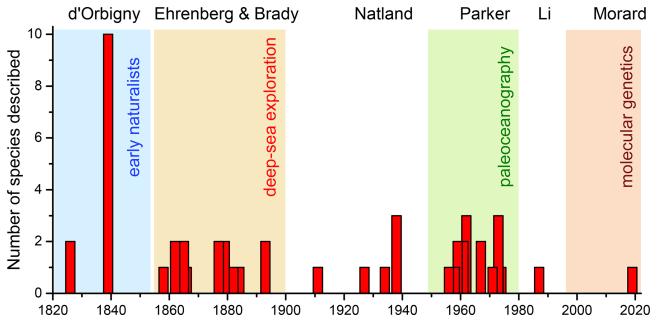

Figure 1. Timeline of the year of original description of 50 extant planktonic foraminifera species and subspecies accepted in this study (including the subspecies *G. ruber albus* described in 2019), highlighting the main "eras" of taxonomy, with names of representative authors.

by maturing forms, which often lack the distinctively shaped final chambers (e.g. the spherical chamber in *Orbulina universa*) and terminal morphological features such as a bulla (e.g. in *Globigerinita glutinata*) or crust (e.g. in *Pulleniatina obliquiloculata*). This reflects the life cycle of planktonic foraminifera, in which the formation of distinctive final chambers and other morphological features ends further shell growth and marks reproductive maturity (terminal stage), after which the shell settles on the seafloor (Brummer et al., 1986). Further complicating conventional taxonomy is the fact that the ontogeny of planktonic foraminifera is associated with substantial transformation of shell architecture, such as in *Trilobatus sacculifer*, and a late ontogenetic emergence of taxonomically important architectural elements, such as chamber elongation, or apertural modifications, such as the presence of supplementary apertures (Brummer et al., 1986). As a result, separate taxa have been proposed for immature and mature specimens of the same species, both in the living plankton and the sediment. Since the transformation of shell morphology through ontogeny is preserved in the early part of the shell, this issue is now largely resolved. However, a lack of diagnostic characters in maturing specimens in the plankton often precludes their species or even genus-level identification, often necessitating (and indeed justifying) the use of open nomenclature.

3 Revised classification

Taxonomy is a communication system which is shared by scientists of different disciplines and which is based on a wide range of data types. In the case of the extant planktonic foraminifera, the involved data sources include morphology, molecular genetics and species ranges observed in the fossil record, and the users include biologists, biostratigraphers, geochemists and paleoceanographers. Inevitably, there are differences in priority and emphasis between these groups, but having a common taxonomy is immensely valuable. This is only possible with compromise, and this has been the guiding principle of our taxonomic work. The most obvious case, where a conflict arises and compromise is required, is the different usage of species concepts between biologists and biostratigraphers. In biostratigraphy, emphasis is on the emergence and demise of a certain morphology, which needs a formal label. Such a typological approach is useful in biostratigraphic practice, but it cannot be transferred on extant taxa, whose taxonomic identity can be confirmed by independent, genetic evidence and which must represent evolutionarily significant units. Conversely, species concepts circumscribed strictly by genetic evidence or defined by discontinuity in morphospace (morphospecies) cannot be easily transferred in the fossil record in the presence of anagenetic change (as noted and explained in detail by Aze et al., 2011) and fail to stabilize by name many biostratigraphically useful morphologies. Being confronted with the task of classifying extant taxa, we here must adhere to the biological understanding of a species, but we do so without claiming that such a system must be transferred onto the fossil record. Instead, we highlight key cases where names that must be rejected for extant taxa may be retained when classifying fossil species. This problem is illustrated by cases like the usage in fossil and extant material of *Trilobatus trilobus* and *T. sacculifer* (Spezzaferri et al., 2015) or the nature of the fossil taxon *Pulleniatina finalis*, which describes a morphology that ranges to the present, but whose existence as a biological taxon cannot be substantiated (Pearson and Penny, 2021).

What we cannot endorse is a continued formal taxonomic treatment of morphological variants, referring to a subset of specimens within the range of variability of the constituent taxon without evolutionary or biostratigraphic significance, or any artificial taxa referring to adventitious characters, aberrations or separate names for adult and pre-adult specimens of the same taxon. Having said that, we have to admit that in the fossil record it is not always possible to determine which characters only represent facultative ontogenetic developments or aberrations and which do not. This means that in the fossil record, we will always be left with artificial taxa, creating obstacles to a full unification of the taxonomy of fossil and extant species.

With respect to taxa beyond the rank of species, we believe that the spirit of compromise is served best by accepting taxa of higher rank, such as genera, that are paraphyletic, i.e. which do not include all descendants of the nearest common ancestor. Whilst we should strive, both for extant and fossil material, to create and use monophyletic taxa, we believe it is impossible and impractical to ensure strict monophyly at all taxonomic levels. Paraphyletic taxa arise because morphological innovations used to circumscribe genera and higher-rank taxa arise within single lineages, with their surviving sister taxa retaining the ancestral morphology. Indeed, in the notable case of *G. siphonifera*, even the species concept is paraphyletic, because the named sister taxa *G. radians* and *G. calida* clearly originate from different lineages within the

genetically diverse but otherwise morphologically homogenous *G. siphonifera* (Weiner et al., 2015).

3.1 Species classification

At the species level, our taxonomy includes 48 holoplanktonic species and subspecies, which are phylogenetically coherent (monophyletic or paraphyletic) and are known to occur alive in the plankton. In addition to the 48 holoplanktonic taxa, we also include two forms with serially arranged chambers, which live in the plankton but may not follow a holoplanktonic lifestyle. The scheme builds on the classification as presented in Hemleben et al. (1989) who recognized 43 holoplanktonic species, with *Neogloboquadrina incompta*, *Globigerinoides elongatus* and *Globigerinella radians* being added later based on genetic confirmation of their different morphologies (Darling et al., 2006; Aurahs et al., 2011; Weiner et al., 2015) and accepted by Schiebel and Hemleben (2017). Recently, *Globigerinoides ruber albus* was established as a subspecies name necessary to differentiate the two genetically distinct lineages within *G. ruber* (Morard et al., 2019a). Finally, we reviewed all species names known to us that were established for living foraminifera collected from the plankton. As a result, next to the elusive *Globorotalia cavernula*, which we provisionally retain, we here also recognize the species *Globorotaloides oveyi*. With respect to the names used for the accepted taxa, unlike Schiebel and Hemleben (2017), we retain *T. fleisheri* and reject *T. compressa* as an invalid synonym. Like Hemleben et al. (1989) and Schiebel and Hemleben (2017), and in line with André et al. (2013) we prefer the use of "*sacculifer*" as the name for the morphologically variable but genetically homogenous single living species of the genus *Trilobatus* (Spezzaferri et al., 2015). In our research on the history of classification we came to the conclusion that the name "*menardii*" has been used incorrectly for the extant taxon, whose appropriate name must be *Globorotalia cultrata*. We also discovered that *Globorotalia theyeri* must be considered a junior synonym of *G. eastropacia*.

Next to the inventory of accepted taxa, we provide a list of species names that have been used previously in association with living planktonic foraminifera or with fossil material from the late Quaternary, but which are here excluded (Table 3). We provide an opinion for each name in terms of its likely (or certain) counterpart in our classification and the reason why it is not recognized as appropriate for the classification of living planktonic foraminifera. In constructing the list, we made use of the comprehensive review of species-level names by Saito et al. (1981), including the numerous names proposed by McCulloch (1977). We also considered the names of species ranging to the present as presented by Aze et al. (2011) and the synonyms highlighted by Siccha and Kucera (2017) as well as names listed in internet inventories (Hayward et al., 2020; Young et al., 2020; Huber et al., 2016). Our decisions are based on observations of type material as well as cross-referencing with original (re)descriptions and major monographs. Although we do not formally establish new taxa or names in this review, this work has been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID alphanumeric component to the prefix http://zoobank.org/. The LSID for this publication is urn:lsid:zoobank.org:pub:9864F738-9F9C-482B-8EEA-D1ED4B189B5D.

An extensive list of other species names for possibly living taxa, most of them proposed in the 19th century by Ehrenberg but rarely (or never) used since, is given in Saito et al. (1981, pp. 16–18). Apart from the 12 *nomina nuda* (originally listed without description or illustration), which are taxonomically neither valid nor available, another 66 names are given many of which should be regarded as *nomina dubia*, e.g. of which the type material is lost and without a description and/or illustration that would allow them to be identified as conspecific with any taxa described later. Some of these names may well prove useful in future revisions, in the manner of *G. radians* that was reinstated by Weiner et al. (2015); others are likely lost to science. Even if some of the names could represent senior synonyms, most names have not been used by any later authors (except in listings such as Saito's et al., 1981), so that probably all later proposed species names should effectively be considered as *nomina conservanda* against the names listed by Saito et al. (1981). Therefore, most of the Ehrenberg's names listed on pp. 16–18 of Saito et al. (1981) are not included here. Similarly, we have systematically avoided new names (including generic and suprageneric) proposed in Fordham (1986), as this publication does not follow the principles of binomial nomenclature and the names described therein should thus be regarded as unavailable (see Loeblich and Tappan, 1988; Haman, 1988).

In general, we identify four reasons why a species name has not been accepted by us for living planktonic foraminifera:

a. name referring to a morphological variant within an accepted species, whose taxonomic status as a species is in doubt (example: *Biorbulina bilobata* used for an aberrant form of *Orbulina universa*);

b. junior synonym of a valid species (example: *Globigerinella aequilateralis* for *G. siphonifera*);

c. invalid (for a formal reason) or suppressed name for a valid species (example: *Tenuitella compressa* for *T. fleisheri*);

d. name referring to an extinct species, erroneously applied to a valid extant species (example: *Neogloboquadrina humerosa* used for *N. dutertrei*) or to a morphological variant of a valid extant species (example: *Orbulina suturalis* used for an aberrant form of living *Orbulina universa*).

Among the 128 names listed (Table 3), 51 are considered synonymous, 24 refer to extinct taxa, and 10 are invalid or informal names. The remaining 42 names refer to morphological variants within accepted species, and we note that a significant number of such names may prove useful in future revisions, since the morphological distinction associated with this name, here considered as taxonomically not significant, may later prove to be associated with consistent genetic divergence. Indeed, cryptic genetic diversity is prevalent among planktonic foraminifera (Darling and Wade, 2008), and many of the involved morphospecies are known to harbour substantial and systematic phenotypic variability.

3.2 Genus-level classification

The generic classification of living planktonic foraminifera (Fig. 2) follows a convention where genera are established to demarcate a significant difference in shell architecture (Olsson et al., 1999; Pearson et al., 2006; Wade et al., 2018a). Such demarcations are often present in single lineages, which may contain several fossil species but are represented by a sole survivor. As a result, the classification of modern planktonic foraminifera appears to be cluttered with monotypic genera (genera containing only one species). To remain consistent with the fossil taxonomy, we here retain most of the commonly used monotypic genera, including all those which comprise additional fossil species (such as *Beella, Globoquadrina*, *Globoturborotalita*, *Orbulina* or *Pulleniatina*). Unlike Schiebel and Hemleben (2017), our classification does not recognize *Bolliella*, which is here subsumed under *Globigerinella*. This is because *Bolliella* has always been strictly monotypic and defined by a trait that is recurrent in the clade and thus does not constitute a large and singular transition in shell architecture needed to justify its own genus. Nevertheless, we stress that *Bolliella* would be monophyletic and the remaining *Globigerinella* paraphyletic, and should the use of *Bolliella* prove useful to elucidate the diversity of fossil or living pseudocryptic taxa, the name may be reinstated.

We retain the monotypic *Hastigerinella* alongside *Hastigerina*, originally established to account for the large change in chamber architecture associated with the bifurcating digitate chambers of *Hastigerinella*. The retention of *Hastigerinella* is essential to avoid confusion in assigning the species name "*digitata*" to *Hastigerina*, because the same combination has been wrongly used in the past for the species that is now classified as *Beella digitata*. The genus *Hastigerinella* has been subject to formal ICZN rulings that were necessary to stabilize the nomenclature of fossil taxa (Coxall, 2003: ICZN Case 3245; ICZN Opinion 2105, 2005). Similarly, the application of a phylogenetically consistent taxon concept at the level of genera leads us to accept the genus *Trilobatus*, which is necessary to avoid a polyphyletic *Globigerinoides* (Spezzaferri et al., 2015), and following Morard et al. (2019a), we return the species "*tenella*" to *Globigerinoides*, where it was placed originally by Parker (1962). In addition, we note that the name *Tenuitella*, commonly applied to three distinct extant small microperforate taxa with extraumbilical apertures, is typified by the latest Eocene to late Oligocene species *Globorotalia gemma*, and there is at present no consensus on how the extant taxa are related to the Paleogene and early Neogene representatives of this group (Pearson et al., 2018). Genetic data indicate that the extant taxa are relatively recently derived from *Globigerinita* (Morard et al., 2019b), and there exists a conspicuous Messinian–Zanclean gap between the known range of the extant taxa and the extinction of *T. clemenciae* as the sole Neogene survivor of the Paleogene group (e.g. Kennett and Srinivasan, 1983). Therefore, we here propose to use *Tenuitellita* for the clade comprising the three extant species. This is because *Tenuitellita* Li, 1987, is typified by *Globigerinita iota* Parker, 1962, and there is thus no doubt that this validly established genus name is referring to the extant clade (Haman, 1988).

Like Schiebel and Hemleben (2017) and most other workers, we retain a broad concept of *Globorotalia*, but we highlight here that the existing genus level names in this clade such as *Globoconella*, *Truncorotalia*, *Menardella* and *Hirsutella* (Table 1) are phylogenetically consistent and their use may have merit especially when considering the taxonomy of extinct lineages. However, should any of these names be reinstated in future revisions, we caution about the complexities involved with homonymy and synonymy issues associated with these names as detailed in Table 1. Finally, four monotypic genera are retained because the taxonomic position of the involved species is unclear, precluding their assignment to other existing genera. This refers to the spinose *Orcadia*, as well as the non-spinose *Dentigloborotalia* and *Berggrenia* and the triserial *Neogallitellia*. Their morphology differs from other planktonic foraminifera in unique ways,, and their fossil record is as yet too poorly documented to reconstruct their ancestry. As a result, the phylogenetic assignment of these four species cannot be resolved at present, and they must remain assigned to their idiosyncratic genera.

3.3 Suprageneric classification

The suprageneric classification adopted in this study (Fig. 2) follows a phylogenetically consistent concept in which we assign all extant planktonic foraminifera to the order Rotaliida but no longer assign the microperforate planktonic foraminifera to the same suborder as the macroperforate globigerinids and globorotaliids. Instead, we assign the three clades to different superfamilies. This distinction accounts for the possibility of separate origin of each clade from different benthic ancestors (Morard et al., 2019b). At the same time, should it transpire that some of the clades share a common ancestor, the superfamilies will remain valid, albeit at the cost of one of them, or their common ancestor, becoming paraphyletic. Unlike in the recent revision presented in

Table 1. Annotated list of genera previously used in the taxonomy of living planktonic foraminifera but rejected in the present revision.

Alloglobigerinoides **Huang, 1986**, type species *Globigerina conglobata* Brady, 1879
A monotypic genus erected by Huang (1986) to account for a presumed absence of an umbilical primary aperture on the final chamber in the type species. Whilst there are specimens where the final chamber does obscure the aperture, there are also many specimens where the primary aperture is visible, making the diagnostic character of the genus obsolete in lieu of *Globigerinoides*.
Biorbulina **Blow, 1956**, type species *Globigerina bilobata* d'Orbigny, 1846
A monotypic genus based on a species representing a morphological variant found in living *Orbulina universa*, which generally forms only one spherical chamber but may occasionally form a second, hemispherical chamber partially encompassing the previous spherical chamber, as observed during laboratory cultures (Caron et al., 1987; Bonnin et al., 2019), in the living plankton and in down-core sediments ranging into the Miocene. The genus (and species) is rejected as a junior synonym of *Orbulina* d'Orbigny, 1839a.
Bolliella **Banner and Blow, 1959**, type species *Hastigerina* (*Bolliella*) *adamsi* Banner and Blow, 1959
A monotypic genus originally proposed as a subgenus of *Hastigerina*, later as a (sub)genus of *Globigerinella*. Phylogenetically not incorrect, but unnecessary and therefore here rejected to avoid strictly monotypic genera.
Coscinosphaera Stuart, 1866, type species *Coscinosphaera ciliosa* Stuart, 1866
Mistaken by the author for a radiolarian, the depiction of the species in the original publication shows a beautifully drawn living specimen of *Orbulina universa* with spines, pseudopodia and algal symbionts.
Gallitellia **Loeblich and Tappan, 1986**, ***non*** **Cuif, 1977**, type species *Guembelitria vivans* Cushman, 1934
Established as a monotypic genus to account for the peculiar taxonomic position of the only triserial species among extant planktonic foraminifera, with unknown relationship to the serial planktonic foraminifera of the Cretaceous period to which its original generic classification alluded. The genus name is a junior homonym of the coral *Gallitellia* Cuif, 1977, and has been consequently replaced by *Neogallitellia* by Özdikmen (2009).
Globoconella **Bandy, 1975**, type species *Globorotalia conomiozea* Kennett, 1966*
Originally described as a subgenus of *Globorotalia* referring to species of the distinct lineage within the genus leading to the living *G. inflata*. Later also used as genus name, including for living *G. inflata* (e.g. Morard et al., 2011). Whilst we here refrain from retaining *Globoconella* for the classification of living planktonic foraminifera, we note that the concept of *Globoconella* as a monophyletic clade may have merit when classifying the Miocene to earliest Pliocene precursors leading to the living *G. inflata*. However, we note that if a future revision including fossil taxa will decide to use a genus-level name for this clade, the name *Neoacarinina* Thompson, 1973 may have priority over *Globoconella* Bandy, 1975.
Hastigerinopsis **Saito and Thompson, 1976**, type species *Hastigerinopsis digitiformans* Saito and Thompson, 1976
Proposed as a replacement name for *Hastigerinella* Cushman, 1927, because the type species, *Hastigerina digitata* Rhumbler, 1911, was considered not valid. This proposal was overruled by opinion 2105 (case 3245) of the ICZN (2005) based on the proposal by Coxall (2003).
Hirsutella **Bandy, 1972,** ***non*** **Cooper and Muir-Wood, 1951**, type species *Globorotalia hirsuta* (d'Orbigny, 1839a) with basionym *Rotalina hirsuta* d'Orbigny 1839
Originally described as a subgenus of *Globorotalia*, it has also been later used as genus name for extant species of the distinct lineage leading to *G. hirsuta*. Whilst we here refrain from retaining *Hirsutella* for the classification of living planktonic foraminifera, we note that the concept of the genus may have merit when classifying fossil taxa. However, according to Haman et al. (1981), *Hirsutella* is a junior objective homonym pre-occupied by the brachiopod genus *Hirsutella* Cooper and Muir-Wood, 1951, that should be replaced by their new name *Obandyella*.
Menardella **Bandy, 1972**, type species *Globorotali menardii* Parker et al., 1865, as typified by Banner and Blow (1960a) with basionym *Rotalia menardii* Parker et al., 1865
Proposed as a subgenus of *Globorotalia*, later also used as genus name for extant species of the distinct lineage including *G. cultrata*. Whilst we here refrain from retaining *Menardella* for the classification of living planktonic foraminifera, we note that the concept of the genus as a monophyletic clade may have merit when classifying the Miocene to earliest Pliocene precursors leading to the living *G. cultrata*. We also note that the typification of the genus is potentially confusing, because at the time of the establishment of the genus, the type species *Globorotalia menardii* was in its concept identical with *G. cultrata* and different from *G. menardii* as emended and newly typified by Stainforth et al. (1975) and Stainforth et al. (1978).

Table 1. Continued.

Neoacarinina **Thompson, 1973**, type species *Neoacarinina blowi* Thompson, 1973
Established to highlight the prominent branching pustules distinguishing it from *Globorotalia*. In our opinion, *N. blowi* is congeneric with living *G. inflata*, if not conspecific, perhaps pseudocryptic. As a result, *Neoacarinina* may be considered the senior objective synonym of *Globoconella* Bandy, 1975, and thus, in case the concept of *Globorotalia* is to be split into the constituent lineages, the nature of *Neoacarinina* would have to be clarified.
Obandyella **Haman, Huddleston and Donahue, 1981**, type species *Globorotalia hirsuta* (d'Orbigny, 1839b) with basionym *Rotalina hirsuta* d'Orbigny, 1839b
A replacement name for *Hirsutella* Bandy, 1972, that is a junior objective homonym of the brachiopod genus *Hirsutella* Cooper and Muir-Wood, 1951. See Haman et al. (1981).
Parkerina **Fordham, 1986**, type species *Globigerinita iota* Parker, 1962
Invalid name as it lacks a description (see Haman, 1988).
Streptochilus **Brönnimann and Resig 1971**, type species *Bolivina tokelaue* Boersma, 1969
Extant biserial species previously assigned to this genus are identical with *Bolivina variabilis* (Williamson, 1858) based on molecular genetic evidence (Darling et al., 2009; Kucera et al., 2017) and must be classified as *Bolivina*. The identity of other Cenozoic biserial foraminifera in the plankton cannot be constrained by genetic data and if these are considered to belong to a distinct lineage, they may remain to be assigned to *Streptochilus*.
Tenuitella **Fleisher, 1974**, type species *Globorotalia gemma* Jenkins, 1966 *
The genus concept as emended by Li (1987) and further by Huber at al. (2006) and accepted by Pearson et al. (2018) comprises Eocene to Miocene microperforate species with extraumbilical aperture and tendency towards various modifications of chamber shape. Since the continuity between these taxa and the extant clade with similar morphology cannot be established, we here propose to limit this name to the Miocene and older species that can be linked to the type species *Tenuitella gemma* and use *Tenuitellita* for the extant species and any related fossil forms that can be phylogenetically linked to them.
Tinophodella **Loeblich and Tappan, 1957**, type species *Tinophodella ambitacrena* Loeblich and Tappan, 1957
Considered a junior synonym of *Globigerinita*, based on a species probably conspecific with *G. glutinata* (Egger, 1893), overstating the importance of the presence of a bulla.
Toddina **Fordham, 1988**, type species *Todella grata* subsp. *compressa* Fordham, 1986
Invalid replacement name for *Toddella* Fordham, 1986, that is a junior objective homonym pre-occupied by *Toddella* Brönnimann and Zaninetti, 1984 (see Haman, 1988), erected for a fossil taxon in replacement for a genus initially erected for an invalidly described taxon that is here considered *Tenuitellita fleisheri.*
Toddella **Fordham, 1986**, type species *Todella grata* subsp. *compressa* Fordham, 1986
Invalid name, initially erected for what is here considered *Tenuitellita fleisheri*, later shown to be a junior objective homonym pre-occupied by *Toddella* Brönnimann and Zaninetti, 1984, that should be replaced by the new name *Toddina* Fordham, 1998.
Towella **Brönnimann and Whittaker, 1991**, type species *Globigerina clarkei* Rögl and Bolli, 1973
Junior synonym of *Turborotalita*, previously applied only for *T. clarkei*.
Trilobigerina **Popescu, 1987**, type species *Globigerina triloba* Reuss, 1850
This genus has been erected for similar reasons to those that lead Spezzaferri et al. (2015) to establish *Trilobatus*. Since both genera are based on the same type species, *Trilobigerina* must be considered a senior synonym of *Trilobatus.* The existence of *Trilobigerina* was unknown to the authors of *Trilobatus* and almost never used since its establishment, including by the genus author himself. Therefore, an application to suppress *Trilobigerina* and retain *Trilobatus* has been formally submitted to the ICZN (Case 3837, Notice of New Applications to the Commission (Case 3827–3838), 2020), and until a ruling on this case, the prevailing name *Trilobatus* must be used (Article 82 of the Code of Zoological Nomenclature).

Table 1. Continued.

***Truncorotalia* Cushman and Bermúdez, 1949**, type species *Globorotalia truncatulinoides* (d'Orbigny 1839) with basionym *Rotalina truncatulinoides* d'Orbigny, 1839
First proposed as a subgenus of *Globorotalia*, it was subsequently elevated to full genus by Bermudez (1960; nom. transl.). Whilst we here refrain from retaining *Truncorotalia* for the classification of living planktonic foraminifera, we note that the concept of the genus as a monophyletic clade is not wrong and it may have merit when classifying fossil and modern species of the lineage leading to the living *G. truncatulinoides*.
Turborotalia* Cushman and Bermúdez, 1949, type species *Globorotalia centralis* Cushman and Bermudez, 1937*
A genus of Eocene planktonic foraminifera occasionally used (erroneously) instead of *Globoconella* as a (sub)genus for living *Globorotalia inflata*.

* Refers to extinct taxa (nominotypes).

the *Atlas of Oligocene Planktonic Foraminifera* (Pearson et al., 2018), we retain *Candeina* among the microperforate clade. This is consistent with its microperforate wall structure (Steineck and Fleisher, 1978) and early ontogeny (Brummer, 1988a), as well as with genetic evidence for its close link with *Globigerinita* (Ujiié and Lipps, 2009; Morard et al., 2019b). As a result, adhering to the principle of priority, we must classify the microperforate clade following Cushman (1927) as Candeinidae rather than using the name Globigerinitidae after Bermúdez (1961), which was adopted by Pearson et al. (2018). By retaining the Candeinidae, whilst separating the microperforate clade from the macroperforate foraminifera, Cushman's (1927) taxon must be raised to superfamily level as Candeinoidea n. transl., with Cushman (1927) remaining the author.

Overall, the classification of genera follows the scheme as implemented in Hemleben et al. (1989) and Schiebel and Hemleben (2017), with the exception of *Orcadia*, which is here returned to the family Hastigerinidae, following its original assignment by Rögl and Bolli (1973). The phylogenetic position of this genus has always been enigmatic, and in the absence of independent (genetic) evidence, we must continue to consider its classification as provisional. Finally, we note that Fordham (1986) erected a host of apparently suprageneric clade names, which are not reproduced here, because they are considered taxonomically invalid, as the work in which they appear did not follow the principles of binomial nomenclature. Loeblich and Tappan (1988, pp. 717–718) give a list of those names, noting "The following names were proposed as "cladegroups", a category not recognized under the International Code on Zoological Nomenclature (henceforth abbreviated as "Code"), hence not available.".

3.4 Status of types

For all accepted species, we provide information on the status of the type material as the primary reference fixing the taxonomy to a physical specimen (Table 2, Fig. 3). The existence of suitable types for the vast majority of the extant species is due to the monumental effort of Banner and Blow (1960a and subsequent work), who revised many of the species that had been described at times when types were not designated (Table 2). Our review shows that only six of the existing types originate from the living plankton and are thus unambiguously referable to living species. The majority of the types are derived from sediments, mainly from seafloor deposits of Holocene (surface sediment) or Pleistocene age (down-core). Two types of d'Orbigny (*G. bulloides* and *G. elongatus*) are from beach sediments from Rimini in Italy, with uncertain age, because the sediments contain reworked Miocene fauna (Lamb and Beard, 1972). The types are by most authors considered Quaternary (e.g. Spezzaferri et al., 2018b), and in both cases the concept of the taxa is not contested. In two cases, the types are derived from Neogene sediments, requiring a careful evaluation to prove that the fossil types refer to the same taxon as the living species. Indeed, the designation of types based on fossil material caused instability in nomenclature, as shown by the unfortunate case of *G. menardii*, which led to decades of confusing and inconsistent usage. We fear that, having fossil types of uncertain status, *Globigerina falconensis* and *Globoquadrina conglomerata* are likely to follow suit.

Six species were found to have no designated types. Among these, we succeeded in locating the original type material for *G. uvula* and pertinent material for *G. rubescens*, allowing us to designate types for these species (Figs. 4, 5). No types exist for *C. nitida*, *G. glutinata* and *G. radians*. The original material on which the species descriptions were based is in all cases considered lost. However, the localities of the original material can be narrowed down to specific regions, and all species were said to originate from recent sediments. In all three cases, the species concepts are not in doubt, and we therefore leave the designation of neotypes to future revisions. Finally, no type appears to have been designated for *B. variabilis*. Whilst suitable topotypic (or even syntypic) material is likely available, we refrain from pursuing the typification of this species at this time, since we believe that it should be done in association with a comprehen-

Table 2. Status of types of all species of living planktonic foraminifera recognized in this study. Species are listed in the same order as in the annotated list in the text, and the localities are shown in Fig. 3.

No.	Genus	Species	Author	Type	Age	Origin	Type locality	Latitude	Longitude	Note	Repository	Designated by
1	*Beella*	*digitata*	Brady (1879)	Lectotype	Recent	Seafloor sediment	South Atlantic, Globigerina ooze dredged on 21 March 1876 at Challenger Station 338, 1990 fathoms	21°15′ S	14°02′ W		London, BMNH 1958.8.18.3	Banner and Blow (1959)
2	*Berggrenia*	*pumilio*	Parker (1962)	Holotype	Recent	Seafloor sediment	Pacific Ocean, surface sediment (0–1 cm) in core HG 41 collected 1951–1952 during the Capricorn expedition, 3394 m	15°55′30″ S	117°13′48″ W		Washington, DC, USNM MO 638792	Parker (1962)
3	*Bolivina*	*variabilis*	Williamson (1858)	None designated	Recent	Seafloor sediment	Northwestern Atlantic, recent marine sands dredged off various locations around the British Isles	NN	NN	b, c		
4	*Candeina*	*nitida*	d'Orbigny (1839b)	None designated	Recent	Seafloor sediment	Caribbean, Cuba, recent marine sands collected probably by d'Orbigny in an unknown manner	NN	NN	b, c	? Paris, MNHN	
5	*Dentigloborotalia*	*anfracta*	Parker (1967)	Holotype	Recent	Seafloor sediment	Eastern Pacific, Gulf of Tehuantepec, sediment from top 3 in. of core CHUB BIV taken at depth of 195 m	15°18′ N	93°51.9′ W		Washington DC, USNM MO 643076	Parker (1967)
6	*Globigerina*	*bulloides*	d'Orbigny (1826)	Lectotype	?Pleistocene	Marine sediment exposed on land	Mediterranean, Adriatic Sea, beach sand from Rimini, known to contain recent as well as reworked Neogene foraminifera	44.07° N	12.582° E	a	Paris, MNHN, No. 12309	Banner and Blow (1960a)
7	*Globigerina*	*falconensis*	Blow (1959)	Holotype	Miocene	Marine sediment exposed on land	Venezuela, from an auger line RM 19285 sampled by near the N to S section of the Pozón–El Mene Road between Caiman and Buena Vista, near Pozón, eastern Falcón, Venezuela, from the Miocene (Aquitanian) Husito marly-clay member dated to the *Globigerinatella insueta*/*Globigerinoides bisphericus* subzone	11.026° N	68.697° W	a	Washington, DC, USNM MO 625697	Blow (1959)
8	*Globigerinella*	*adamsi*	(Banner and Blow, 1959)	Holotype	Recent	Seafloor sediment	Indian Ocean, Banda Sea, Ki Island, *Globigerina* ooze trawled on 24 September 1874 at Challenger Station 191 A, 580 fathoms	5°41′ S	132°04′ E		London, BMNH 1958.8.18.1	Banner and Blow (1959)
9	*Globigerinella*	*calida*	Parker (1962)	Holotype	Recent	Seafloor sediment	South Pacific, surface sediment collected 1957–1958 from R/V Downwind Baird core BG130 (0–4 cm), 3120 m	14°44′ S	112°06′ W		Washington DC, USNM MO 638685	Parker (1962)
10	*Globigerinella*	*radians*	Egger (1893)	None designated	Recent	Seafloor sediment	South Indian Ocean and Pacific Ocean; the species description mentions three localities, of which the first is off West Australia, reddish-white consolidated mud with foraminifera preserved with spines sampled by Baillie's sounding tube from *Gazelle* station 87 on 25 April 1875 at 915 m	20°49′ S	113°46′ E	c	Eggers material from the *Gazelle* expedition (1874–1876) was stored at the "Bayerische Staatssammlung für Paläontologie und Geologie" but appears to have been destroyed during second world war; the original type material is thus considered to be lost.	
11	*Globigerinella*	*siphonifera*	d'Orbigny (1839a)	Lectotype	Recent	Seafloor sediment	Caribbean, Cuba, recent marine sands collected probably by d'Orbigny in an unknown manner	NN	NN	b	Paris, MNHN (d'Orbigny label IV/15-18)	Banner and Blow (1960a)
12	*Globigerinita*	*glutinata*	Egger 1893)	None designated	Recent	Seafloor sediment	South Indian Ocean and Pacific Ocean; the species description mentions four localities, of which the first is off West Africa, reddish-brown–grey soft Globigerina ooze with whitish foraminifera sampled by Baillie's sounding tube from *Gazelle* station 17 on 31 July 1874 at 677 m	10°12.9′ N	17°25.5′ W	c	Eggers material from the *Gazelle* expedition (1874–1876) was stored at the "Bayerische Staatssammlung für Paläontologie und Geologie" but appears to have been destroyed during second world war; the original type material is thus considered to be lost.	
13	*Globigerinita*	*minuta*	Natland (1938)	Holotype	Recent	Seafloor sediment	Pacific Ocean, off Long Beach, California, Locality 117, 122 m	32°22′16″ N	118°18′40″ W		Washington, DC, USNM PP 22561	Natland (1938)
14	*Globigerinita*	*uvula*	Ehrenberg (1862)	Lectotype	Recent	Seafloor sediment	North Atlantic, Irminger Sea, 1000 fathoms (6000 feet)	62°40′ N	29°00′ W		Berlin, Museum für Naturkunde, Ehrenberg Collection, 313-271506, mica 3, red ring	This study
15	*Globigerinoides*	*conglobatus*	Brady (1879)	Lectotype	Recent	Seafloor sediment	South Atlantic, globigerina ooze dredged on 21 March 1876 at Challenger Station 338, 1990 fathoms	21°15′ S	14°02′ W		London, BMNH 1959.4.13.7	Banner and Blow (1960a)
16	*Globigerinoides*	*elongatus*	d'Orbigny (1826)	Lectotype	?Pleistocene	Marine sediment exposed on land	Mediterranean, Adriatic Sea, beach sand from Rimini, known to contain recent as well as reworked Neogene foraminifera	44.07° N	12.582° E	a	Paris, MNHN, number not given	Banner and Blow (1960a)

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Table 2. Continued.

No.	Genus	Species	Author	Type	Age	Origin	Type locality	Latitude	Longitude	Note	Repository	Designated by
17	*Globigerinoides*	*ruber albus*	Morard et al. (2019a)	Holotype	Recent	Plankton haul	Pacific Ocean, FS SONNE station SO226/113, sampled on 12 March 2013 at 21:00 UTC between 0–20 m, Specimen labelled as voucher C319 from which a partial SSU rDNA sequence has been extracted and deposited on NCBI under the accession no. MN384115	7.409° S	165.274° E		Naturalis Biodiversity Center, Leiden, RGM 1332320	Morard et al. (2019a)
18	*Globigerinoides*	*ruber ruber*	d'Orbigny (1839a)	Lectotype	Recent	Seafloor sediment	Caribbean, Cuba, recent marine sands collected probably by d'Orbigny in an unknown manner	NN	NN	b	Paris, MNHN, No. IV.12.14	Banner and Blow (1960a)
19	*Globigerinoides*	*tenellus*	Parker (1958)	Holotype	Recent	Seafloor sediment	Mediterranean, Ionian Sea, surface sediment collected on R/V *Atlantis Station 4711*, 3309 m	34°58′ N	19°24′ E		Washington, DC, USNM PR 6129	Parker (1958)
20	*Globoquadrina*	*conglomerata*	Schwager (1866)	Neotype	Neogene	Marine sediment exposed on land	Indian Ocean, Kar Nikobar, upper and lower clays, sample collected by Ferdinand von Hochstetter during the landing there of the Austrian frigate Novara in 1858	9.16° S	92.77° E	a	London, BMNH P.44031	Banner and Blow (1960a)
21	*Globorotalia*	*cavernula*	Bé (1967b)	Holotype	Recent	Plankton haul	South Pacific, USNS Eltanin Station EL 15-23-843 sampled at 07:00 am on 14 November 1964, water depth 200 to 500 m	55°54′ S	139°56′ W		Washington DC, USNM MO 686929	Bé (1967b)
22	*Globorotalia*	*crassaformis*	Galloway and Wissler (1927)	Holotype	Pleistocene	Marine sediment exposed on land	USA, California, Lomita Quarry, 2 miles south of Lomita (now in Los Angeles), coquina limestone, middle bed, Lower San Pedro Formation	33.7769° N	118.34° W	a	New York, Columbia University paleontological collections no. 19816	Galloway and Wissler (1927)
23	*Globorotalia*	*cultrata*	d'Orbigny (1839a)	Neotype	Recent	Seafloor sediment	Caribbean, off Cape Cruz on Cuba, recent marine sand collected in an unknown manner by A. Earland, exact location not specified	19.84° N	77.74° W	a	London, BMNH 1959.7.27.4	Banner and Blow (1960a)
24	*Globorotalia*	*eastropacia*	Boltovskoy (1974)	Holotype	Recent	Plankton haul	Eastern Equatorial Pacific, north of the Galapagos Islands, R/V *Undaunted Station 163* sampled on 19 September 1967 between surface and 228 m	2°59′ N	92°00′ W		Museo Argentino de Ciencias Naturales "B. Rivadavia" foraminifera collection (FMACN) No. 7468	Boltovskoy (1974)
25	*Globorotalia*	*hirsuta*	d'Orbigny (1839b)	Neotype	Recent	Seafloor sediment	North Atlantic, Canary Islands, Gomera, volcanic sandy mud dredged on 12 February 1873 at Challenger Station VIII, 620 fathoms	28°8′15″ N	17°27′ W		London, BMNH 1968.3.27.1	Blow (1969)
26	*Globorotalia*	*inflata*	d'Orbigny (1839b)	Neotype	Recent	Seafloor sediment	North Atlantic, Canary Islands, Gomera, volcanic sandy mud dredged on 12 February 1873 at Challenger Station VIII, 620 fathoms	28°08′15″ N	17°27′ W		London, BMNH 1966.2.3.23	Banner and Blow (1967)
27	*Globorotalia*	*scitula*	Brady (1882)	Lectotype	Recent	Seafloor sediment	North Atlantic, Faroe Channel, grey mud dredged overnight from 11. to 12 August 1880 at Knight Errant dredging station 7 (ship station 32), 530 fathoms	59°37′ N	7°19′ W		London, BMNH 1959.6.25.1	Banner and Blow (1960a)
28	*Globorotalia*	*truncatulinoides*	d'Orbigny (1839b)	Neotype	Recent	Seafloor sediment	North Atlantic, Canary Islands, Gomera, volcanic sandy mud dredged on 12 February 1873 at Challenger Station VIII, 620 fathoms	28°08′15″ N	17°27′ W		London, BMNH 1968.3.27.2	Blow (1969)
29	*Globorotalia*	*tumida*	Brady (1877)	Lectotype	?Pleistocene	Marine sediment transported by tsunami on land	Pacific Ocean, east side of New Ireland, white chalk collected from the beach and used by the natives to carve "grotesque figures of men and animals", some of which were presented by Rev. G. Brown to Prof. Liversidge in Sydney, who removed small fragments and presented those to Brady. According to Brown such rocks were found on the beach only after an earthquake and the rocks have been interpreted by Liversidge and Brady as deep-sea sediments of probably Pliocene age transported on the beach by a tsunami.	3.5° S	151.5° E	a	London, BMNH P.44034	Banner and Blow (1960a)
30	*Globorotalia*	*ungulata*	Bermúdez (1961)	Holotype	Recent	Seafloor sediment	Caribbean, south of Bahia de Corrientes, Cuba, R/V *Atlantis Station 2953*, 615 fathoms	21°47′ N	84°32′30″ W		Washington, DC, USNM MO 639053	Bermúdez (1961)
31	*Globorotaloides*	*hexagonus*	Natland (1938)	Holotype	Recent	Seafloor sediment	Pacific Ocean, off Long Beach, California, 884 m	33°27′20″ N	118°19′00″ W		Washington, DC, USNM PP 22560 (initially deposited under no. 496185)	Natland (1938)
32	*Globorotaloides*	*oveyi*	Buckley (1973)	Holotype	Recent	Plankton haul	Indian Ocean, Bay of Bengal, R/V *Anton Bruun*, Cruise I, Station 93, Smithsonian Oceanographic Sorting Center no. 479, sampled on 1 May 1963 between 0–250 m	13°08′ N	86°12′ E		London, BMNH 1972.5.5.1	Buckley (1973)

Table 2. Continued.

No.	Genus	Species	Author	Type	Age	Origin	Type locality	Latitude	Longitude	Note	Repository	Designated by
33	*Globoturborotalita*	*rubescens*	(Hofker, 1956)	Neotype	Recent	Seafloor sediment	Indian Ocean, Banda Sea, Gulf of Boni off Sulawesi, sediment recovered with an Ekman–Pratje sampler during the Siboga Expedition on 15 February 1930 at 18.15–20.30, 1407 m	4°43′ S	120°22′ E		Naturalis Biodiversity Center, Leiden, RGM 1333481	This study
34	*Hastigerina*	*pelagica*	d'Orbigny (1839c)	Neotype	Recent	Seafloor sediment	Locality not stated, from Challenger material	NN	NN	b	London, BMNH ZF.1562	Banner and Blow (1960b)
35	*Hastigerinella*	*digitata*	Rhumbler (1911)	Neotype	Recent	Seafloor sediment	North Atlantic, Beebe Station 1200, depth 600 fathoms	NN	NN	b	London, BMNH 1959.5.11.744	Banner (1965) based on a hypotype designated by Banner and Blow (1960b)
36	*Neogallitellia*	*vivans*	Cushman (1934)	Holotype	Recent	Seafloor sediment	Indian Ocean, Banda Sea, Little Ki Island, *Globigerina* ooze trawled on 26 September 1874 at Challenger Station 192 A, 129 fathoms	5°49′15″ S	132°14′15″ E		Washington, DC, USNM CC 21515	Cushman (1934)
37	*Neogloboquadrina*	*dutertrei*	d'Orbigny (1839a)	Lectotype	Recent	Seafloor sediment	Caribbean, Cuba, recent marine sands collected probably by d'Orbigny in an unknown manner	NN	NN	b	Paris, MNHN, No. 84.IV.19.21	Banner and Blow (1960a)
38	*Neogloboquadrina*	*incompta*	Cifelli (1961)	Holotype	Recent	Plankton haul	North Atlantic, New Jersey Slope, R/V *Crawford Station 3* sampled in August 1960 between surface and 200 m	38°39′ N	69°33′ W		Washington, DC, USNM MO 628588	Cifelli (1961)
39	*Neogloboquadrina*	*pachyderma*	Ehrenberg (1862)	Lectotype	Recent	Seafloor sediment	North Atlantic, Irminger Sea, 1000 fathoms (6000 feet)	62°40′ N	29°00′ W		Berlin, Museum für Naturkunde, 313-271506, mica 1, blue ring	Darling et al. (2006)
40	*Orbulina*	*universa*	d'Orbigny (1839b)	Lectotype	Recent	Seafloor sediment	Caribbean, Cuba, recent marine sands collected probably by d'Orbigny in an unknown manner	NN	NN	b	Paris, MNHN, d'Orbigny collection no. 252	Le Calvez (1974)
41	*Orcadia*	*riedeli*	Rögl and Bolli (1973)	Holotype	Pleistocene	Seafloor sediment	Caribbean, Cariaco Basin, DSDP Site 147, Core 6, core catcher, 51 m below sea floor, Upper Pleistocene, Zone X of Ericson and Wolin (1968)	10°42.48″ N	65°10.48′ W		Basel, NHM, C-27164	Rögl and Bolli (1973)
42	*Pulleniatina*	*obliquiloculata*	Parker and Jones (1865)	Neotype	Recent	Seafloor sediment	South Atlantic, Abrolhos Bank, 260 fathoms	22°54′ S	40°37′ W		London, BMNH ZF.3583	Bolli et al. (1957)
43	*Sphaeroidinella*	*dehiscens*	Parker and Jones (1865)	Lectotype	Recent	Seafloor sediment	Atlantic Ocean, 1080 fathoms	2°20′ N	28°44′ W		London, BMNH ZF.3580 (ex 94.4.3.368)	Bolli et al. (1957)
44	*Tenuitellita*	*fleisheri*	Li, 1987	Holotype	Pleistocene	Seafloor sediment	Mediterranean, Aegean Sea, Zante (Zakythos) Channel, Sample IS/82/8	37.807° N	21.038° E	a	London, BMNH P52030	Li (1987)
45	*Tenuitellita*	*iota*	Parker (1962)	Holotype	Recent	Seafloor sediment	South Pacific, surface sediment collected 1957–1958 from R/V *Downwind Baird core BG73* (0–2 cm), 3080 m	43°48′ S	108°09′ W		Washington, DC, USNM MO 638893	Parker (1962)
46	*Tenuitellita*	*parkerae*	Brönnimann and Resig (1971)	Holotype	Recent	Seafloor sediment	South Pacific, surface sediment (0–1 cm) in core HG 41 collected 1951–1952 during the Capricorn expedition, 3394 m	15°55′30″ S	117°13′48″ W		Washington, DC, USNM PAL 219445	Brönnimann and Resig (1971)
47	*Trilobatus*	*sacculifer*	Brady (1877)	Lectotype	?Pleistocene	Marine sediment transported by tsunami on land	Pacific Ocean, east side of New Ireland, white chalk collected from the beach and used by the natives to carve "grotesque figures of men and animals", some of which were presented by Rev. G. Brown to Prof. Liversidge in Sydney, who removed small fragments and presented those to Brady. According to Brown such rocks were found on the beach only after an earthquake and the rocks have been interpreted by Liversidge and Brady as deep-sea sediments of probably Pliocene age transported on the beach by a tsunami.	3.5° S	151.5° E	a	London, BMNH P.44033	Banner and Blow (1960a)
48	*Turborotalita*	*clarkei*	Rögl and Bolli (1973)	Holotype	Pleistocene	Seafloor sediment	Caribbean, Cariaco Basin, DSDP Site 147, Core 4, core catcher, 32 m below sea floor, Upper Pleistocene, Zone Y of Ericson and Wolin (1968)	10°42.48″ N	65°10.48′ W		Basel, NHM, C-27173	Rögl and Bolli (1973)
49	*Turborotalita*	*humilis*	Brady (1884)	Lectotype	Recent	Seafloor sediment	North Atlantic, Canary Islands, red clay dredged on 21 February 1873 at Challenger Station 5, 2740 fathoms	24°20′ N	24°28′ W		London, BMNH 1959.10.2.1 (ex ZF 2530)	Banner and Blow (1960a)
50	*Turborotalita*	*quinqueloba*	Natland (1938)	Holotype	Recent	Seafloor sediment	Pacific Ocean, off Long Beach, California, Locality 118, 152 m	33°22′20″ N	118°18′31″ W		Washington DC, USNM PP 22559	Natland (1938)

[a] Type localities where coordinates are estimated from maps or descriptions, [b] type localities which cannot be traced to a specific location, [c] where no type has been designated, we list localities mentioned in the original descriptions of the species.

Phylum Foraminifera d'Orbigny, 1826
Class Globothalamea Pawlowski, Holzmann and Tyszka, 2013
Order Rotaliida Delage and Hérouard, 1896

Superfamily Globigerinoidea Carpenter, Parker and Jones, 1862
- Family Globigerinidae Carpenter, Parker and Jones, 1862
  - *Beella* Banner and Blow, 1960
    - type species *Globigerina digitata* Brady, 1879 (type by original designation)
  - *Globigerina* d'Orbigny, 1826
    - type species *Globigerina bulloides* d'Orbigny, 1826 (type by subsequent designation)
  - *Globigerinella* Cushman, 1927
    - type species *Globigerina aequilateralis* Brady, 1879 accepted as *Globigerinella siphonifera* (d'Orbigny, 1839a) (type by original designation)
  - *Globigerinoides* Cushman, 1927
    - type species *Globigerina rubra* d'Orbigny, 1839a species name amended to agree in gender by article 31.2 of the Code to *Globigerinoides ruber* (d'Orbigny, 1839a) (type by original designation)
  - *Globoturborotalita* Hofker, 1976
    - type species *Globigerina rubescens* Hofker, 1956 (type by original designation)
  - *Orbulina* d'Orbigny, 1826
    - type species *Orbulina universa* d'Orbigny, 1839a (type by monotypy at time of designation)
  - *Sphaeroidinella* Cushman, 1927
    - type species *Sphaeroidina bulloides* var. *dehiscens* Parker and Jones, 1865 (type by original designation)
  - *Trilobatus* Spezzaferri et al., 2015
    - type species *Globigerina triloba* Reuss, 1850 † species name amended to agree in gender by article 31.2 of the Code to *Trilobatus trilobus* (Reuss, 1850) † (type by original designation)
  - *Turborotalita* Blow and Banner, 1962, emend. Pearson and Kucera, 2018
    - type species *Truncatulina humilis* Brady, 1884 (type by original designation)
- Family Hastigerinidae Bolli, Loeblich and Tappan, 1957
  - *Hastigerina* Thomson in Murray, 1876
    - type species *Hastigerina murrayi* Thomson in Murray, 1876 accepted as *Hastigerina pelagica* (d'Orbigny, 1839c) (type by monotypy at time of designation)
  - *Hastigerinella* Cushman, 1927
    - type species *Hastigerina digitata* Rhumbler, 1911 (type by monotypy at time of designation)
  - *Orcadia* Boltovskoy and Watanabe, 1982
    - type species *Hastigerinella riedeli* Rögl and Bolli, 1973 (type by original designation)

Superfamily Globorotalioidea Cushman, 1927
- Family Globorotaliidae Cushman, 1927
  - *Globoquadrina* Finlay, 1947
    - type species *Globorotalia dehiscens* Chapman, Parr and Collins, 1934 † (type by original designation)
  - *Globorotalia* Cushman, 1927
    - type species *Pulvinulina menardii* var. *tumida* Brady, 1877 (type by original designation)
  - *Globorotaloides* Bolli, 1957
    - type species *Globorotaloides variabilis* Bolli, 1957 † (type by original designation)
  - *Neogloboquadrina* Bandy, Frerichs and Vincent, 1967
    - type species *Globigerina dutertrei* d'Orbigny, 1839a (type by original designation)
  - *Pulleniatina* Cushman, 1927
    - type species *Pullenia obliquiloculata* Parker and Jones, 1865 (type by original designation)

Superfamily Candeinoidea Cushman, 1927
- Family Candeinidae Cushman, 1927
  - *Candeina* d'Orbigny, 1839a
    - type species *Candeina nitida* d'Orbigny, 1839a (type by monotypy at time of designation)
  - *Globigerinita* Brönnimann, 1951
    - type species *Globigerinita naparimaensis* Brönnimann, 1951 accepted as *Globigerinita glutinata* (Egger, 1893) (type by original designation)
  - *Tenuitellita* Li, 1987
    - type species *Globigerinita iota* Parker, 1962 (type by original designation)

Superfamily & Family incertae sedis
- *Berggrenia* Parker, 1976
  - type species *Globanomalina praepumilio* Parker, 1967 † (type by original designation)
- *Dentigloborotalia* Brummer, 1988
  - type species *Globorotalia anfracta* Parker, 1967 (type by original designation)

Superfamily Cassidulinoidea d'Orbigny, 1839c
- Family Bolivinitidae Cushman, 1927
  - *Bolivina* d'Orbigny, 1839c *
    - type species *Bolivina plicata* d'Orbigny, 1839c (type by subsequent designation)

Superfamily Turrilinoidea Cushman, 1927
- Family ?Stainforthiidae Reiss, 1963
  - *Neogallitellia* Özdikmen, 2009 *
    - type species *Guembelitria vivans* Cushman, 1934 (type by original designation)

Figure 2. Generic and suprageneric classification of living planktonic foraminifera. The symbol † refers to taxa (nominotypes) which are extinct; the symbol * refers to genera which contain species that are planktonic at least during one stage in their life cycle.

sive revision of species concepts established for planktonic material whilst considering all allied benthic lineages.

3.5 Other foraminifera in the plankton

Next to the holoplanktonic taxa considered in this review, other species of foraminifera are found in the plankton. Most of these represent specimens passively entrained into the water column from the benthos during discrete events like storms, or attached to seaweed and other drifting substrates. Some species of benthic foraminifera ascend into the plankton during the final stage of their life, such as *Tretomphalus* and *Cymbaloporetta*, while others may do so during early ontogeny. However, there are two small forms with serially arranged chambers consistently found in the living plankton to such a degree that they have been commonly considered fully planktonic (De Klasz et al., 1989; Kroon and Nederbragt, 1990). One of these has been classified as *Streptochilus*, but based on molecular genetics, Darling et al. (2009) and Kucera et al. (2017) have shown that specimens from the living plankton bearing the *Streptochilus* morphology are conspecific with the benthic *Bolivina variabilis* (Williamson

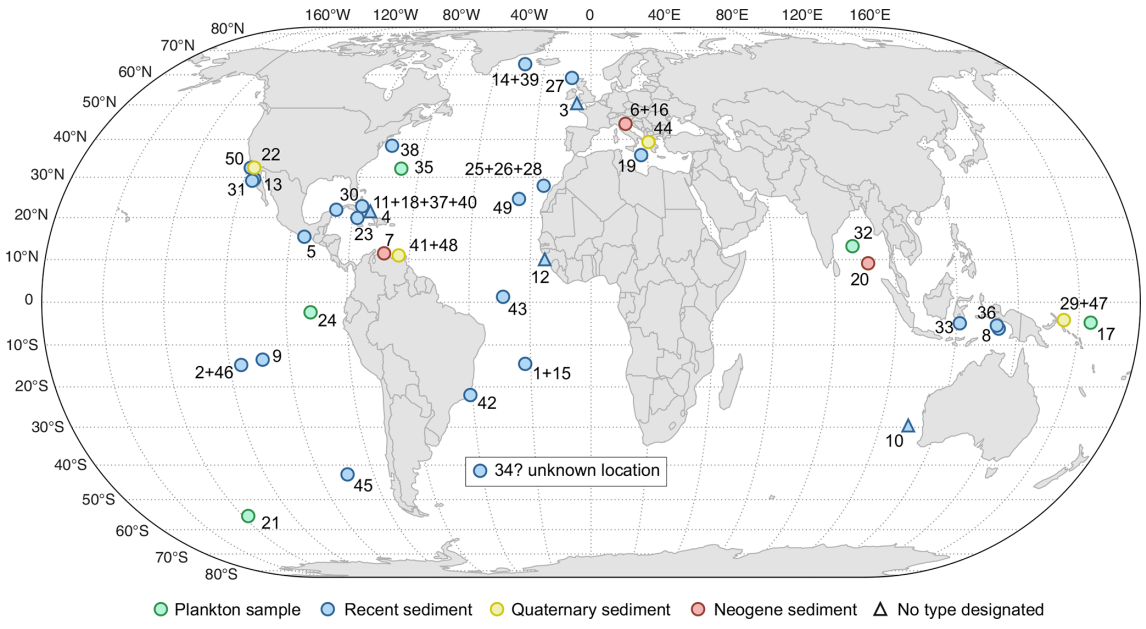

Figure 3. Location and nature of material from which types of extant species of planktonic foraminifera have been derived. Numbers refer to species as listed in Table 2. Triangles refer to the origin of type material in instances where no type has been formally designated. Question mark indicates an instance where the type locality could not be identified precisely.

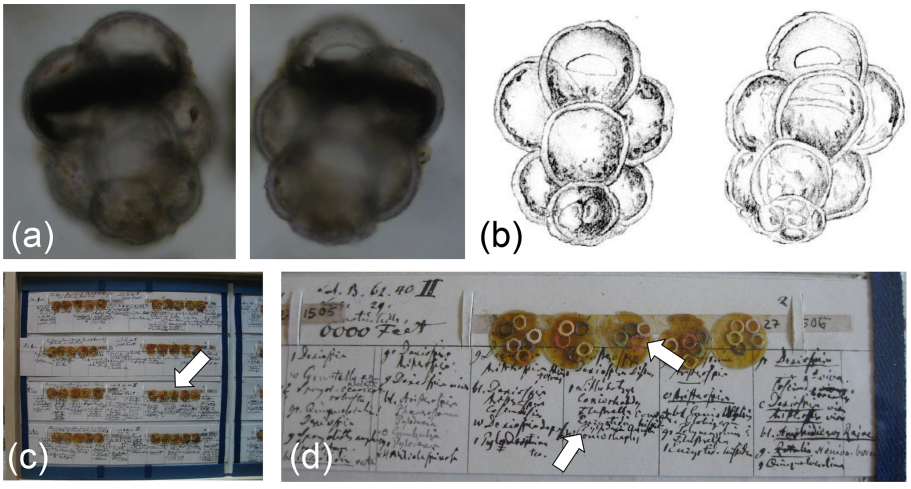

Figure 4. Lectotype of *Globigerinita uvula* (Ehrenberg, 1862), representing the specimen figured by Ehrenberg (1873) and labelled in his handwriting as *Pylodexia uvula*. Light microscope image of the lectotype specimen **(a)** imaged from both sides of the mica mount and compared with **(b)** the drawing in Ehrenberg (1873). The specimen, about 0.1 mm in length, is located in the Ehrenberg Collection at the Museum für Naturkunde in Berlin on Tray 27-15B **(c)** on mica set 27 1506 **(d)**, with the lectotype located on mica 3 within the red ring (white arrow) and labelled below (white arrow).

1858). Since *Streptochilus* has been typified by Brönniman and Resig (1971) using another Quaternary species, whose relationship to the extant taxa is not clear, it remains open whether the genus *Streptochilus* should be rejected as a junior synonym of *Bolivina* or retained as a suitable name for fossil taxa. The work by Kucera et al. (2017) indicates the existence of two distinct morphological types among the pelagic *Bolivina*, but their relationship to the two commonly recognized living species of *Streptochilus* (*S. globulosus* and *S. globigerum*) remains unclear and the entire group requires revision explicitly considering all relevant modern *Bolivina* species.

Similar to *Streptochilus*, Ujiié et al. (2008) have shown that the presumably planktonic triserial form "*Gallitellia" vivans* (Cushman, 1934) is genetically closely related (congeneric) with the benthic genera *Stainforthia* or *Virgulinella*,

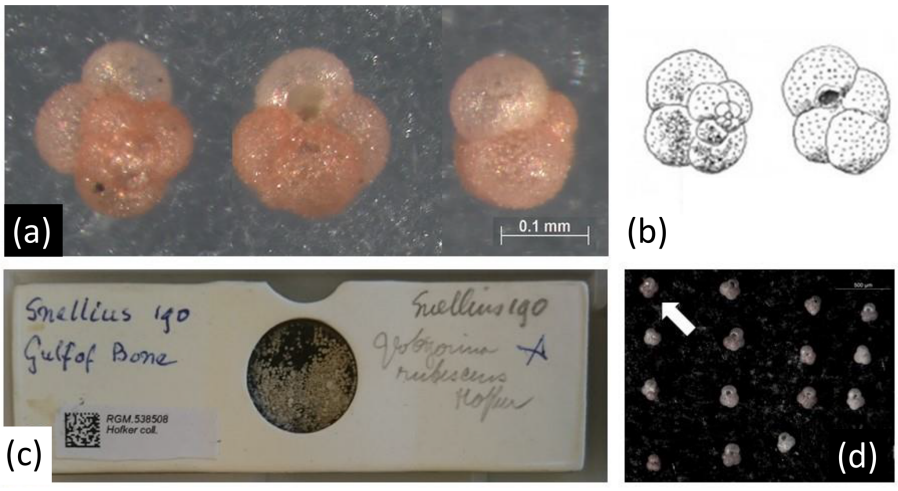

Figure 5. Lectotype **(a)** of *Globoturborotalita rubescens* (Hofker 1956) compared with original drawing **(b)** by Hofker (1956, his plate 35, figs. 18–19), selected from a slide marked originally by Hofker as containing "*Globigerina rubescens* Hofker" and deposited at the Zoological Museum in Amsterdam, transferred in 2011 to the Naturalis Biodiversity Center, Leiden, the Netherlands, and registered as RGM 538508. The slide **(c)** contains a sieved residue from a sediment collected during the Snellius expedition (Snellius station 190) from the Gulf of Boni off Sulawesi, Indian Ocean, at 4°43′ S, 120°22′ E, 1407 m water depth, taken on 15 February 1930 18.15–20.30 with an Ekman–Pratje sampler. The residue hosted 15 specimens of *G. rubescens* that were all extracted **(d)**, of which we here designate RGM 1333481 as the lectotype (**a**; white arrow in **d**), and specimens RGM 1333482–1333495 as paralectotypes.

indicating that this form could also represent a benthic species with the ability to remain active in the plankton for at least the early part of its life cycle. Since the name *Gallitellia* Loeblich and Tappan, 1986, is pre-occupied by the coral *Gallitellia* Cuif, 1977, and thus a junior homonym, Özdikmen (2009) proposed *Neogallitellia* as a replacement. Unlike *Streptochilus*, we cannot yet reject the possibility that *"Gallitellia" vivans* forms a distinct lineage justifying generic classification. Therefore we recommend provisionally retaining a separate generic name *Neogallitellia* for this lineage until further (genetic) work resolves the generic placement of *N. vivans* among known benthic genera.

3.6 Species concepts integrating genetic and morphological data

In order to make the taxonomy of living planktonic foraminifera consistent with and applicable to sedimentary material, we refrain from a formal treatment of genetically circumscribed lineages (cryptic species). In our view these should not enter the formal zoological nomenclature, unless accompanied with demonstrable differences in shell morphology or other visible traits, such that the resulting species could be traced in the fossil record at least to some extent. This is consistent with the species concept of Barraclough (2019), who argues that genetic distinction alone should not justify the distinction of new species and considers a species to be "an independently evolving group of organisms that is genetically and phenotypically distinct from other groups". It is important to note that "phenotype" refers to any realized traits, and theoretically, for the extant species, one could also make use of traits that are not manifested on the shell, such as differences in cellular structure, physiology, or habitat and seasonality (e.g. Faber et al., 1988). At present we refrain from using such characters, but note that in some instances, these differences could be resolved in the fossil record by elemental and isotopic signatures in the shell (e.g. Brummer et al., 2020). For a comprehensive discussion on a possible method to establish for genetically circumscribed taxa a stable nomenclature that exists outside of the Code, the reader is referred to the work by Morard et al. (2016).

Another situation arises when genetic distinction is found "post hoc" to be associated with morphological distinction (pseudocryptic species). In this case, we recommend that when a genetic type is being associated with a species name, it should be demonstrated that the observed differences are applicable throughout the distributional range of the classified species and do not represent ecophenotypic variation. Finally, we recommend abstaining from the establishment of new species names, without a thorough revision of the concepts of existing (but abandoned) species names. Indeed, previous taxonomic revisions based on genetic evidence could make use of existing species concepts, in some cases confirming rarely used taxonomic subdivisions (Weiner et al., 2015) or resuscitating species concepts that were abandoned in the past (Aurahs et al., 2011).

A special case arises when the otherwise morphologically "cryptic" species may be separated but only based on characters that can be observed on living (or recent) material. So far, traits that can only be observed among living taxa, such

Table 3. Species-level names and informal names associated with living planktonic foraminifera but recognized here as (eco)phenotypic variants, synonyms, invalid or informal names, or names referring to extinct species.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
acerosa *Globigerina (Orbulina)*	Owen (1868)	synonym	*O. universa*	
acostaensis *Globorotalia Neogloboquadrina*	Blow (1959)	extinct	*N. dutertrei*	Extinct since early Pleistocene (Aze et al., 2011)
aequilateralis *Globigerinella*	Brady (1879)	synonym	*G. siphonifera*	Synonymized by Banner and Blow (1960a)
akersi *Globorotalia*	Snyder (1975)	variant	*G. cultrata*	Distinguished by aberrant last chamber
amesbayensis *Globorotalia menardii*	McCulloch (1977)	variant	*G. cultrata*	
ambitacrena *Tinophodella*	Loeblich and Tappan (1957)	variant	*G. glutinata*	Overemphasizing the presence of bulla
antilliensis *Globigerina Pulleniatina*	Bermudez (1960)	variant	*P. obliquiloculata*	Lowered to a subspecies by Bermúdez and Bolli (1969)
antarctica *Globorotalia menardii*	McCulloch (1977)	variant	*G. cultrata*	
apertura *Globigerina Globoturborotalita*	Cushman (1918)	extinct	*G. bulloides*	Extinct since early Pleistocene (Aze et al., 2011)
atlantis *Globigerina*	Bermúdez (1961)	variant	*P. obliquiloculata*	
atlantisae *Globigerina Turborotalia*	Cifelli and Smith (1970)	variant	*T. iota*	Described from living plankton, without bulla
bermudezi *Globorotalia Hirsutella*	Rögl and Bolli (1973)	variant	*G. scitula*	Distinguished by open umbilicus
bermudezi *Globigerina*	Seiglie (1963)	variant	*G. bulloides*	Distinguished by aberrant last chamber

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Table 3. Continued.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
bikiniensis *Globigerinita*	McCulloch (1977)	synonym	*T. humilis*	
bikiniensis *Globigerinoides elongata*	McCulloch (1977)	variant	*G. elongatus*	High-spired form
bilobata *Globigerina* *Biorbulina*	d'Orbigny (1846)	variant	*O. universa*	Distinguished by aberrant last chamber
blowi *Neoacarinina* *Globorotalia*	Thompson (1973)	variant	*G. inflata*	Type species of *Neoacarinina* Thompson, 1973
borealis *Globigerina bulloides*	Brady (1881)	synonym	*N. pachyderma*	Asano (1957) considered it a variety of *G. bulloides*, but its synonymy with *N. pachyderma* is given by the nature of the lectotype designated by Banner and Blow (1960a).
bradyi *Globigerina* *Globigerinita*	Wiesner (1931)	synonym	*G. uvula*	
canariensis *Globigerina*	d'Orbigny (1839b)	synonym	*G. elongatus*	
canimarensis *Globigerinoides*	Bermúdez (1961)	synonym	*G. conglobatus*	
cariacoensis *Globigerina*	Rögl and Bolli (1973)	variant	*G. bulloides*	Distinguished by aberrant last chamber
cedrosensis *Globigerinoides elongata*	McCulloch (1977)	variant	*G. elongatus*	Referring to the high-spired form
chathamensis *Beella*	McCulloch (1977)	synonym	*B. digitata*	
clippertonensis *Globigerina*	McCulloch (1977)	synonym	*G. hexagonus*	
compressa *Toddella grata* *Toddina*	Fordham (1986)	invalid	*T. fleisheri*	Described as a phenon/subspecies under non-Linnean taxonomy
continens *Globigerina* (*Orbulina*)	Owen (1868)	synonym	*O. universa*	

Table 3. Continued.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
crassacrotonensis *Globorotalia*	Conato and Follador (1967)	extinct	*G. crassaformis*	Described from the Middle Pliocene
crassula *Globorotalia*	Cushman and Stewart (1930)	extinct	*G. hirsuta*	Extinct since the mid-Pleistocene (Aze et al., 2011)
cristata *Globigerina* *Turborotalita*	Heron-Allen and Earland (1929)	variant	*T. humilis*	Common growth stage in the living plankton; lectotype designated by Banner and Blow (1960a)
cristatiformis *Globigerina?*	McCulloch (1977)	synonym	*T. humilis*	
crotonensis *Globorotalia*	Conato and Follador (1967)	extinct	*G. crassaformis*	Described from the Middle Pliocene, considered a synonym of *G. crassula*
crozetensis *Globorotalia*	Thompson (1973)	variant	*G. cavernula*	
cryophila *Globigerina*	Herman (1980)	synonym	*N. pachyderma*	Replacement name for *Globigerina occlusa* Herman, 1974, non Blow and Banner (1962)
cyclostomus *Globigerina* *Globigerinoides*	Galloway and Wissler (1927)	synonym	*G. elongatus*	
diplostoma *Globigerina*	Reuss (1850)	extinct	*G. bulloides*	Described from Miocene sediments
dextralis *Neogloboquadrina pachyderma*	Setty (1977)	synonym	*N. incompta*	
digitiformans *Hastigerinopsis*	Saito and Thompson (1976)	invalid	*H. digitata*	Invalid replacement name (see Coxall, 2003)
discors *Beella*	McCulloch (1977)	synonym	*G. adamsi*	
dubia *Globigerina*	Egger (1857)	synonym	*N. dutertrei*	
dubiata *Globigerina*	McCulloch (1977)	variant	*? G. elongatus*	Distinguished by aberrant last chambers
egelida *Globigerina quinqueloba*	Cifelli and Smith (1970)	variant	*T. quinqueloba*	Described from living plankton; growth stage of *T. quinqueloba* (re-examination of holotype)

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Table 3. Continued.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
eggeri *Globigerina* *Neogloboquadrina*	Rhumbler (1901)	variant	*N. dutertrei*	Lacking apertural teeth
eggeri *Globigerina* *cretacea*	Heron-Allen and Earland (1922)	synonym	*T. humilis*	
eggeriformis *Globigerina*	McCulloch (1977)	variant	*N. dutertrei*	
eoconglobatus *Globigerinoides*	Stainbank et al. (2018)	extinct or variant	*G. conglobatus*	Described from Pleistocene sediments and mentioned as extant, here considered to represent either an extinct form or a variant within the morphologically plastic *G. conglobatus*, because there is no evidence for the existence of more than one extant species of this lineage, as confirmed by genetic data of Morard et al. (2019a).
excavata *Sphaeroidinella* *dehiscens*	Banner and Blow (1965)	variant	*S. dehiscens*	Form with wide and deep apertural slits in cortex
excelsa *Globorotalia* *truncatulinoides*	Sprovieri (1980)	synonym	*G. truncatulinoides*	
exumbilicata *Globigerina*	Herman (1974)	variant	*T. quinqueloba*	Common growth stage in the living plankton
fimbriata *Globorotalia* *Menardella*	Brady (1884)	variant	*G. cultrata*	With pustulate keel
finalis *Pulleniatina*	Banner and Blow (1967)	variant	*P. obliquiloculata*	
fistulosus *Globigerina* *Globigerinoides* *Globigerinoidesella*	Schubert (1910)	extinct	*T. sacculifer*	Extinct since the early Pleistocene (Wade et al., 2011); type species of *Globigerinoidesella* El-Naggar, 1971
flexuosa *Globorotalia* *tumida* *Globorotalia* *menardii*	Koch (1923)	variant	*G. tumida* *G. cultrata*	Proposed as a variant of *G. tumida*, raised to subspecies by Kennett and Srinivasan (1983); also used as subspecies for *G. cultrata*

Table 3. Continued.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
flparkerae *Globigerinita glutinata*	Brönnimann and Resig (1971)	synonym	*G. glutinata*	Replacement name for *Globigerinoides parkerae* Bermudez, 1960
forma alba *Globigerinoides ruber*	Boltovskoy (1968)	invalid informal category	*G. ruber albus*	Described by Boltovskoy (1968) as "forma", thus not an available name in the sense of the Code
forma rosea *Globigerinoides ruber*	Boltovskoy (1968)	invalid informal category	*G. ruber ruber*	Described by Boltovskoy (1968) as "forma", thus not an available name in the sense of the Code
frailensis *Hastigerinella* (?)	McCulloch (1977)	synonym	*B. digitata*	
galapagosensis *Globigerina*	McCulloch (1977)	synonym	*N. dutertrei*	
gibberula *Globorotalia menardii*	Bé (1977)	variant	*G. cultrata*	Referring to unusually spiroconvex forms
gilberti *Pulvinulina*	Bagg (1908)	synonym	*G. cultrata*	Saito et al. (1981) incorrectly synonymized with *G. ungulata* (examination of types)
globigerus *Textilaria* *Textularia* *Streptochilus*	Schwager (1866)	?synonym	*B. variabilis*	The morphological and genetic variability of the tychopelagic *Bolivina variabilis* may justify the existence of more than one species, pending future revision.
globulosum *Bolivina* *Streptochilus*	Cushman (1933)	?synonym	*B. variabilis*	The morphological and genetic variability of the tychopelagic *Bolivina variabilis* may justify the existence of more than one species, pending future revision.
gomitulus *Globigerina*	Seguenza (1880)	synonym	*G. elongatus*	
groenlandica *Globigerina*	Stschedrina (1946)	synonym	*T. quinqueloba*	
guadalupensis *Beella*	McCulloch (1977)	synonym	*B. digitata*	
guadalupensis *Globigerina (?)*	McCulloch (1977)	synonym	*T. humilis*	
hancocki *Globigerina*	McCulloch (1977)	synonym	*N. dutertrei*	

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Table 3. Continued.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
helicina *Globigerina*	d'Orbigny (1826)	synonym confused	*G. ruber*	Initially considered by d'Orbigny's reference to an older illustration to represent abnormal *G. ruber*, but lectotype selected by Banner and Blow (1960a) depicts *N. dutertrei.*
hessi *Globorotalia*	Bolli and Premoli Silva (1973)	extinct	*G. crassaformis*	Likely synonymous, a variant with small final chamber
humerosa *Globorotalia* *Neogloboquadrina*	Takayanagi and Saito (1962)	extinct	*N. dutertrei*	Extinct since early Pleistocene (Aze et al., 2011)
hybrida *Globigerina*	McCulloch (1977)	synonym	*N. dutertrei*	
hystricosus *Globigerinoides quadrilobatus* *Globigerinoidesella*	Belford (1962)	variant	*T. sacculifer*	Proposed as subspecific variant; with aberrant last chamber also observed in laboratory cultures of *T. sacculifer*
immaturus *Globigerinoides sacculifer*	LeRoy (1939)	extinct or variant	*T. sacculifer*	Retained by Spezzaferri et al. (2015), not recognized in living plankton
imperfecta *Orbulina*	Rhumbler (1911)	variant	*O. universa*	Described from the living plankton, akin to *O. suturalis*
incisa *Globorotalia (Turborotalia)*	Brönnimann and Resig (1971)	extinct	*N. incompta*	A Pliocene to early Pleistocene small *Neogloboquadrina*
involuta *Globigerina aequilaterallis* *Hastigerina* *Globigerinella*	Cushman (1917)	variant	*G. siphonifera*	Strongly involute phenotype, originally proposed as a variety of *G. aequilateralis*
jamesbayensis *Globorotalia menardii*	McCulloch (1977)	variant	*G. cultrata*	Distinguished by aberrant (diminutive) last chamber
juvenilis *Globigerina*	Bolli (1957)	synonym	*G. glutinata*	A small form described from the Miocene distinguished by not possessing a bulla
lata *Globorotalia tumida*	Brönnimann and Resig (1971)	variant	*G. tumida*	Distinguished by different last chamber

Table 3. Continued.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
megastoma *Beella* *Globigerinella*	Earland (1934)	variant	*B. digitata*	Lacking digitate chambers
menardii *Globorotalia* *Menardella*	Parker et al. (1865)	extinct	*G. cultrata*	A Miocene Mediterranean form, previously incorrectly considered as living
milletti *Candeina*	Dollfus (1905)	variant	*C. nitida*	Aberrant form
murrayi *Hastigerina*	Thompson (1876)	synonym	*H. pelagica*	Type species of *Hastigerina* Thompson, 1876
naparimaensis *Globigerinita*	Brönnimann (1951)	synonym	*G. glutinata*	With complex bulla
neoflexuosa *Globorotalia* *menardii*	Srinivasan et al. (1974)	variant	*G. cultrata*	Proposed as a subspecies of *G. cultrata* with twisted last chamber
neominutissima *Globorotalia*	Bermudez and Bolli (1969)	synonym	*T. quinqueloba*	A small warm water form of *T. quinqueloba*
nipponica *Globigerina*	Asano (1957)	variant	*G. inflata*	With diminutive last chamber
obesa *Globorotalia* *Globigerinella*	Bolli et al. (1969)	extinct	*G. siphonifera*	Used for small, possibly pre-adult specimens, extinct since the Miocene (Aze et al., 2011)
obliquus *Globigerinoides*	Bolli (1957)	extinct	*G. elongatus*	Extinct since the mid-Pleistocene (Aze et al., 2011)
occlusa *Globigerina*	Herman (1974)	invalid	*N. pachyderma*	Junior objective homonym of *Globigerina occlusa* Blow and Banner, 1962, replaced by *G. cryophyla* Herman, 1980
oceanica *Globorotalia*	Cushman and Bermudez (1949)	synonym	*G. crassaformis*	Considered extant by Aze et al. (2011)
okinawaensis *Pulleniatina*	Natori (1976)	extinct variant	*P. obliquiloculata*	Referring to forms without streptospiral final chamber from Pleistocene sediments, either an extinct form or referring to small specimens of *P. obliquiloculata*
oscitans *Globorotalia*	Todd (1958)	variant	*G. inflata*	Small compact form restricted to the Mediterranean

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Table 3. Continued.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
pachytheca *Globorotalia truncatulinoides*	Blow (1969)	variant	*G. truncatulinoides*	Heavily encrusted compact phenotype, considered extant by Aze et al. (2011)
palpebra *Globorotalia (Turborotalia) Globigerina*	Brönnimann and Resig (1971)	synonym	*G. falconensis*	
paraobesa *Globigerina*	Herman (1974)	variant	*N. pachyderma*	With aberrant last chamber
parapelagica *Hastigerina Hastigerinella*	Saito and Thompson (1976)	variant	*H. digitata*	Likely a growth stage of *H. digitata*
parkerae *Globigerinoides Globigerinita*	Bermúdez (1961)	synonym	*G. glutinata*	Once transferred to *Globigerinita*, the name became a junior homonym of *G. parkerae* Brönnimann and Resig, 1971 and was replaced by *G. flparkerae* Brönnimann and Resig, 1971.
partidiana *Globigerina*	McCulloch (1977)	synonym	*N. dutertrei*	
parva *Orbulina*	Rhumbler (1949)	invalid	*O. universa*	The name appeared in the captions to plates that were meant to accompany the initial publication of Rhumbler (1911) but were first printed by Wetzel (1949).
patriciae *Globoquadrina*	McCulloch (1977)	synonym	*G. hirsuta*	
PD intergrade pachyderma-dutertrei intergrade *Neogloboquadrina*	Kipp (1976)	informal name	*N. dutertreiN. incompta*	Morphological intermediates between *N. dutertrei* and *N. incompta*, introduced for practical reasons by Kipp (1976)
pink *Globigerinoides ruber*	various authors	informal name	*G. ruber ruber*	As opposed to *G. ruber* "white"
planispira *Globorotalia (Turborotalia)*	Brönnimann and Resig (1971)	synonym	*N. incompta*	
polusi *Globigerina Neogloboquadrina*	Androsova (1962)	variant	*N. pachyderma*	With aberrant last chamber

Table 3. Continued.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
praecalida *Globigerina* *calida*	Blow (1969)	extinct	*G. calida*	Described from Pliocene likely referring to early populations leading to *G. calida*
primalis *Pulleniatina*	Banner and Blow (1967)	extinct	*P. obliquiloculata*	Extinct since the mid-Pleistocene (Aze et al., 2011)
puncticulata *Globigerina* *Globorotalia*	d'Orbigny (1826)	extinct	*G. inflata*	Initially nomen nudum, re-instated (lectotypified) by Banner and Blow (1960a), the species is extinct since the Pliocene (Aze et al., 2011)
pyramidalis *Globigerina* *Globigerinoides*	van den Broek (1876)	variant	*G. ruber* or *G. elongatus*	High spired form proposed as (sub)variety, occurs both in *G. ruber ruber* and *G. ruber albus* as well as in *G. elongatus*
pyriporosa *Globigerina*	Rhumbler (1911)	synonym	*N. dutertrei*	
quadrilatera *Globigerina*	Galloway and Wissler (1927)	synonym	*G. bulloides*	
quadrilobatus *Globigerina* *Globigerinoides* *Trilobatus*	d'Orbigny (1846)	extinct	*T. sacculifer*	Used for an (eco)phenotype of living *T. sacculifer* but recognized as separate fossil species by Spezzaferri et al. (2015).
recumbens *Globigerina* *bulloides*	Rhumbler (1901)	synonym	*T. sacculifer*	Described from the plankton with sac-like terminal chamber
rhumbleri *Hastigerina* *Hastigerinella*	Galloway (1933)	synonym	*H. digitata*	
rosacea *Globigerina*	Bermudez and Seiglie (1963)	synonym	*G. rubesecens*	
rotundata *Globigerina*	d'Orbigny in Fornasini (1898)	synonym	*N. dutertrei*	Nomen nudum until illustrated by Fornasini, lectotype designated by Banner and Blow (1960a), junior synonym of *N. dutertrei*, because in 1839 when *N. dutertrei* was described, the name was a nomen nudum and thus unavailable
santamariensis *Globigerina*	McCulloch (1977)	synonym	*P. obliquiloculata*	
seigliei *Globorotalia*	Bermudez and Bolli (1969)	synonym	*T. iota*	Saito et al. (1981) picture two specimens, of which the second is macroperforate

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Table 3. Continued.

(Sub)species name Genus name	Described by	Reason for rejection	Most likely referring to	Comments
sinistralis *Neogloboquadrina pachyderma*	various authors	informal name	*N. pachyderma*	
subcretacea *Globigerina*	Lomnicki (1901)	extinct	*N. dutertrei*	The name refers to a Miocene species but was later introduced into the synonymy of *N. dutertrei* by Parker (1962), who even considered it a distinct type within *N. dutertrei.*
suleki *Globigerinoides*	Bermúdez (1961)	synonym	*T. sacculifer*	Described from recent sediments, referring to a form without sac-like final chamber
suturalis *Orbulina*	Brönnimann (1951)	extinct	*O. universa*	Used to refer to aberrant forms in living *O. universa*
theyeri *Globorotalia*	Fleischer (1974)	synonym	*G. eastropacia*	Name published three months later than *G. eastropacia*
tosaensis *Globorotalia*	Takayanagi and Saito (1962)	extinct	*G. crassaformis*	Extinct since late Pleistocene (Aze et al., 2011)
trilobus *Globigerina* *Globigerinoides* *Trilobatus*	Reuss (1850)	extinct	*T. sacculifer*	Type species of *Trilobatus*. Living *T. sacculifer* first appears during the mid-Miocene, while *T. trilobus* appears in the earliest Miocene (Spezzaferri et al., 2015; Wade et al., 2011).
umbilicata *Globigerina*	Orr and Zaitzeff (1971)	variant	*G. bulloides*	Referring to forms with open umbilicus and up to five chambers in the last whorl
viola *Globorotalia* *crassula*	Blow (1969)	extinct	*G. crassaformis*	Considered extinct since early Pleistocene (Aze et al., 2011)
white *Globigerinoides* *ruber*	various authors	informal name	*G. ruber albus*	As opposed to *G. ruber* "pink"
wilesi *Globorotalia*	Thompson (1980)	variant	*G. scitula*	Form with compact outline

as cytoplasm characteristics or symbiont type (Faber et al., 1988), have never been used to differentiate species. In this way, the classification of extant planktonic foraminifera is kept congruent with that of fossil material. However, this is at the cost of the numerous genetically distinct types with distinct ecologies and biogeographies remaining taxonomically nameless (Morard et al., 2016). In some of these cases, the situation in our opinion could be treated by using subspecies to designate the distinct taxa in the recent material. As a formal species-level taxon, a subspecies requires the designation of a physical type specimen assuring it agrees with the nominate morphological species. This would have the advantage of the fossil specimens retaining the same species name as the extant ones. Such use of a subspecies would signal that the studied material is suitable to distinguish and identify them and that the subspecies which are not listed were not found. Conversely, the subspecies name left out would signal a situation where the character cannot be determined. Indeed, the first such case arose in the classification of *G. ruber*, where genetic evidence supports the separation of the "pink-pigmented" type, long recognized as an ecologically distinct taxon but referred to by various informal names. The case was initially left without taxonomic resolution because the key character disappears with age in fossil material (Aurahs et al., 2011), but Morard et al. (2019a) argued for the need to name the two genetically distinct lineages, identifiable in Quaternary material by shell pigmentation, and erected *G. ruber albus* for the type lacking pigmentation.

3.7 Recommendations for applications in operational taxonomy

With the increasing role of data syntheses in science, including in micropaleontology, it is becoming obvious that a major barrier to the replicability and interoperability (as key aspects of the FAIR principles) of census data is the lack of standardization of vocabularies (e.g. Jonkers et al., 2020), which then translates into the problem of inconsistent taxonomies. This not only refers to the trivial case of authors using idiosyncratic names or categories with an unclear relationship to named taxa. An example of a common practice that is not conducive to interoperability arises when authors present incomplete lists of species. When presented by such an incomplete list of taxa that were encountered and/or enumerated in a given sample, it is often not immediately obvious why a certain taxon is missing. This could be either because it was not found, or it was found but synonymized by the authors with another taxon, or it was not considered by the authors and the specimens belonging to a particular taxon were assigned to various taxa or left unidentified. We believe that the value of the present taxonomic scheme (Supplement 1), as well as the annotated opinion on the nature of various synonyms and other names, is that it could contribute towards more replicable and interoperable taxonomic lists and census counts. To this end, we propose that operational taxonomy proceeds following these recommendations:

1. The authors should explicitly state and cite the work(s) on which their taxonomy is based and provide a full list of species and categories that they considered (even if no specimens belonging to some of the considered taxa were found), indicating any deviations from the cited works and spelling out the full genus and species names in the tables presenting the counts or occurrences. This is essential to make the data machine-readable and to unambiguously interpret the absence of certain species in the data. To aid authors in this respect, we provide as an electronic appendix a list of all species recognized as extant in this work (Supplement 2).

   Example: "This work is based on the taxonomy in Schiebel and Hemleben (2017), recognizing all of their 47 species except for *T. compressa*, which is here considered a synonym of *T. fleisheri*."

   Example: "We considered all 50 species that are recognized as extant by Brummer and Kucera (2022), reporting abundances of all, including the seven species that were not encountered in any of the analysed samples."

2. If the authors did not or could not differentiate any particular taxon, they should provide explicit reference to this in the paper and in the dataset they generated.

   Example: "In the census counts, we did not differentiate *G. elongatus*, which is counted together with *G. ruber albus*."

3. We strongly recommend always including a category for unidentified specimens. Such a category is required for specimens lacking distinguishing features, such as damaged or abnormal specimens or for pre-adult specimens from the plankton. Where it was not possible to identify at the species level, but an assignment to a higher-level category is possible, the authors are encouraged to record such specimens separately and apply open nomenclature, stating which taxa are being subsumed.

   Example: "Specimens that could not be identified because of damage or abnormalities are reported in the category *unidentified*."

   Example: "Individuals smaller than 0.1 mm, which appear spinose but lack further distinguishing features are here reported as *unidentified spinose juveniles*. This category potentially includes representatives of all the encountered spinose species."

   Example: "Small specimens of spinose foraminifera with extraumbilical aperture and a tendency towards planispiral coiling could not be consistently differentiated at the species level and are reported here in the category *Globigerinella* spp., likely subsuming all four extant species of the genus."

4. Authors who decide to separate taxa or count separately certain morphological variants (such as pre-adult specimens, coiling varieties, or any of the known morphological aberrations and forms with peculiar terminal features) should indicate how these categories map onto the parent taxonomy and next to the separate counts also provide the total for the parent category.

   Example: "Specimens of *T. sacculifer* with the distinctive sac-like final chamber are reported in a category labelled *T. sacculifer* with sac, remaining specimens of the species are reported as *T. sacculifer* without sac."

   Example: "Pre-adult specimens of *P. obliquiloculata* without a cortex are here reported separately as *P. obliquiloculata* uncrusted."

   Example: "We consistently separated small specimens with deep umbilicus within what is commonly considered as *G. scitula* and report these here as *G. bermudezi*."

   Example: "Dextral and sinistral specimens of *G. truncatulinoides* have been counted separately."

5. We recommend always reporting the actual number of counted specimens rather than percentages or concentrations, alongside the total number of specimens counted, and provide information on the portion (split) of the sample that was counted and the size fraction (sieve or mesh size) that was used.

   Example: "All specimens of planktonic foraminifera were counted in the fraction > 0.1 mm. Where the total number of specimens in a sample exceeded 500, the sample was split and the portion analysed is recorded alongside the actual counts in Table 3 and in the electronic supplement."

6. Authors are asked to provide the information on all of the above and on all metadata associated with the counted assemblage and the material from which it derives together with the counts in a digital repository, so future users can interpret the taxonomy and the counts without searching for this information in the literature in which it may or may not be mentioned.

7. At any time when the taxonomy is revised, the authors are asked to avoid changes, as far as possible, which result in a name being assigned a new meaning which conflicts with previous usage.

4 Conclusions and outlook

Despite half a century of their extensive applications in the field of paleoceanography, the taxonomy of extant and late Quaternary planktonic foraminifera is not yet entirely stable. Some of the recent amendments reflect only the necessity to change a name or transfer a species, without questioning the underlying morphospecies concepts (such as the establishment of *Trilobatus* by Spezzaferri et al., 2015), but others attest to the incomplete understanding of the nature of morphological variability within species (such as the reinstatement of *Globigerinoides elongatus* by Aurahs et al., 2011). Both aspects combined contribute to the ongoing lack of consistency in taxonomic identifications (e.g. Al-Sabouni et al., 2018; Fenton et al., 2018), hampering biodiversity and paleoecology studies as well as efforts to generate community resources to automate species identification to achieve high throughput (Hsiang et al., 2019; Mitra et al., 2019). We hope the taxonomic benchmark provided in this study will help contribute to the development of a more effective and robust taxonomy of extant, and indirectly also fossil, species of this important group of marine microfossils.

We realize that this contribution is not the last word on the taxonomy of modern planktonic foraminifera. Indeed, in many instances, we anticipate revisions resulting from new molecular evidence as well as from ontogenetic morphology (by 3D microtomography) or revision of fossil taxa and types, and we highlight these instances explicitly in the annotations. In parallel with the classical approach of taxonomic revisions being presented in formal publications, the last decade has seen the rise of internet-based resources, allowing simultaneous access to species descriptions, taxonomic opinions, images and stratigraphic data. Prime examples for planktonic foraminifera are the Mikrotax system for web delivery of taxonomy (Huber et al., 2016; Young et al., 2020) and the World foraminifera database (Hayward et al., 2020) maintained as a part of the World Register of Marine Species (WoRMS Editorial Board, 2020), linked with the GBIF biodiversity information facility (GBIF.org, 2020). These resources are complemented by providers of specific information such as the images database Foraminifera.eu (Hesemann, 2015) or the PFR2 database of SSU rDNA barcode sequences of extant planktonic foraminifera (Morard et al., 2015). Whilst there will always be space for classical taxonomic revisions, especially for the purpose of formal documentation of taxonomic acts, internet-based taxonomic resources will likely become the main reference for everyday taxonomic work, including for biostratigraphical species identification or paleoecological census counts. We highly endorse these efforts and call the community to contribute by sharing images and data and by citing these resources whenever appropriate.

5 Annotated inventory of genera and species of extant planktonic foraminifera

In the following, we provide a complete annotated list of all 24 genera and 50 species and subspecies of modern planktonic foraminifera, which we consider to be found among the living plankton. We highlight important taxonomic observations for selected taxa and discuss key synonyms and other

names with reference to the taxonomies presented previously (e.g. Schiebel and Hemleben, 2017; Hemleben et al., 1989; Saito et al., 1981) when of added value. Genera are sorted alphabetically as are the species within them. The taxonomic relationships among the genera are shown in Fig. 2.

Beella Banner and Blow, 1960

Initially considered a subgenus of *Globorotalia* by Banner and Blow (1960b), because of its distinct apertural shape, but a relationship to *Globigerina* was firmly established by Parker (1962). Kennett and Srinivasan (1983) also derived the genus from *Globigerina*, but genetic evidence indicates that it diverged from *Globigerinella* (Weiner et al., 2015). The genus is retained here because it has well resolved fossil history and allows clear demarcation of its type species *Beella digitata* (Brady, 1879) from the homonymous *Hastigerinella digitata* (Rhumbler, 1911). One extant and several fossil species.

Beella digitata (Brady, 1879)

A rare but distinct extant species typified by a specimen from recent sediments. As shown already by Parker (1962), the characteristic chamber elongation is less well developed in small specimens. This has led some authors (e.g. Aze et al., 2011) to separate these forms as *Beella megastoma* (Earland, 1934) or consider the extinct ancestral *Beella praedigitata* (Parker, 1967) to persist to the present. The existence of the homonymous *Hastigerinella digitata* (Rhumbler, 1911) has created some confusion in the past, with both species being occasionally assigned to the same genera (*Globigerinella*, *Hastigerina*).

Berggrenia Parker, 1976

Typified by the extinct *Berggrenia praepumilio* (Parker, 1967), the phylogenetic position of this genus remains enigmatic. It features an adumbilically displaced ampullate final chamber, like the spinose *Turborotalita*, but its wall is non-spinose with the umbilical side ornamented by radial striae and pores concentrated along the sutures on the spiral side. For example, Saito et al. (1981) emphasized the ampullate final chamber to assign to *Berggrenia* the minute *Turborotalita clarkei*, a decision which we here reject. We consider it likely that *Berggrenia* represents a lineage of foraminifera that invaded the plankton from an independent benthic ancestor, and the genus must be retained until its phylogenetic position is resolved by genetic data. One extant and one fossil species.

Berggrenia pumilio (Parker, 1962)

Small and rarely recorded species with distinct morphology and ornament, initially assigned by Parker (1962) to *Globorotalia*. This species has always been elusive, but it has been reported from the plankton (e.g. Rebotim et al., 2017) and when pictured always features the typical morphology and ornament (Saito et al., 1981; Schiebel and Hemleben, 2017).

Bolivina d'Orbigny, 1839

This genus comprises species with biserially arranged chambers, most of which are considered benthic, but one extant lineage appears to also live in the plankton during part of its life cycle (Darling et al., 2009). To what degree this also applies to fossil species of *Bolivina* and whether or not the abundant Neogene fossil biserial planktonic foraminifera should also be assigned to this genus remains unclear. One extant species in the plankton, many extant and fossil benthic species.

Bolivina variabilis (Williamson, 1858)

Abundant and ubiquitous species occurring in outer shelf and upper slope sediments and in the plankton of tropical to temperate oceans (Darling et al., 2009; Kucera et al., 2017). No type appears to have been designated, but the species was described from recent sediments off the British Isles, indicating that the name should be associated with an extant species, and the species concept has remained stable ever since. Designation of a type would require a thorough revision of species concepts invoked for material derived from the plankton, combined with the evaluation of other morphologically similar species described from the benthos.

Candeina d'Orbigny, 1839

One of the three still valid genera erected by d'Orbigny (1839a). Typified by the extant *Candeina nitida* d'Orbigny, 1839, the genus is distinct and it has been always easy to distinguish it, but it proved difficult to fit it into the phylogenetic system (see statements to this end in Parker, 1962, and Saito et al., 1981). Parker (1962) considered earlier classification attempts "illogical" and following Hofker (1954) suggested a link with *Globigerinita*. This classification of *Candeina* is indeed consistent with its microperforate wall and early ontogeny (Brummer, 1988a), as well as with genetic evidence indicating that this genus is related to *Globigerinita* (Ujiié and Lipps, 2009; Morard et al., 2019b). Following most recent works but unlike Pearson et al. (2018), we here retain *Candeina* among the microperforate clade. One extant and several extinct species.

Candeina nitida d'Orbigny, 1839

One of the three extant species lacking a type, with the original material considered lost. Morphologically distinct and its species concept undisputed, we feel it is not essential to designate a neotype at this stage.

Dentigloborotalia Brummer, 1988

Characterized by compressed reniform chambers and wall texture with shark-tooth like pustules, this monotypic genus has been established to accommodate the peculiar species *D. anfracta*. Supported by molecular genetic data (Morard et al., 2019b), we consider it likely that *Dentigloborotalia* represents a lineage of foraminifera that invaded the plankton from an independent benthic ancestor and the genus must be retained until the phylogenetic position of the species relative to its benthic ancestors is resolved.

Dentigloborotalia anfracta (Parker, 1967)

A distinct species found abundantly in the plankton and in sediments, but recorded rarely because of its small size (Brummer, 1988b). When recognized, the species concept is mostly applied consistently (Saito et al., 1981). Holotype from recent sediments represents the typical morphology with reniform chambers.

Globigerina d'Orbigny, 1826

The most iconic and the earliest described genus of planktonic foraminifera, typified by the well-established *Globigerina bulloides* d'Orbigny, 1826. Originally used widely for almost all species considered planktonic, now limited to a lineage of spinose planktonic foraminifera with a finely spinose wall and single umbilical aperture (Spezzaferri et al., 2018a). Two extant and a number of fossil species.

Globigerina bulloides d'Orbigny, 1826

The concept of the species was initially applied more broadly but with the description of new species it progressively converged towards the current understanding of the taxon and remained stable since. d'Orbigny erected *G. bulloides* and *G. elongata* formally as replacement names for species illustrated by Soldani (1791) in a non-Linnean and thus unavailable work. Although d'Orbigny provided no description, he validated the species by referring to Soldani's (1791) illustrations. Guided by plaster models made by d'Orbigny, *G. bulloides* was typified by a lectotype selected by Banner and Blow (1960a). The species is abundant in productive waters along the Equator, in temperate regions and in all upwelling regions, often showing strong seasonality. It harbours substantial genetic diversity (Darling et al., 2017), and it is possible that some of the constituent genetic types will prove pseudocryptic, vindicating the use of some of the numerous names considered here as morphological variants within the species (such as *G. umbilicata* or *G. cariacoensis*).

Globigerina falconensis Blow, 1959

Although the species resembles *G. bulloides*, causing frequent confusion (Al-Sabouni et al., 2018), the two species are distinct morphologically (Malmgren and Kennett, 1977) and ecologically, and when applied to modern plankton, the concept of *G. falconensis* is used consistently. Unfortunately, the species is typified by a specimen from Miocene deposits in Venezuela. The overall morphology of the holotype is consistent with the present concept of *G. falconensis*, but a recent investigation revealed consistent morphological differences between the Miocene and Recent populations of the lineage (Bridget Wade and Alessio Fabbrini, personal communication, 2021), indicating that the species name may require revision.

Globigerinella Cushman, 1927

Synonymized with *Hastigerina* by Bolli et al. (1957) and Banner and Blow (1960b), the two genera were separated again because of differences in wall texture (Saito et al., 1981; Kennett and Srinivasan, 1983). In its present concept, the genus refers to a lineage descending from *Globigerina* with extraumbilical to equatorial apertures and a tendency towards planispiral coiling (Spezzaferri et al., 2018a). Typified by the extant *Globigerinella siphonifera* (d'Orbigny, 1839), the genus is paraphyletic, giving rise to several genera characterized by the development of radially elongated chambers, including the here accepted *Beella*, the here rejected *Bolliella* and the fossil *Protentella*, rejected by Spezzaferri et al. (2018a). Four extant and many fossil species.

Globigerinella adamsi (Banner and Blow, 1959)

Classified as *Bolliella adamsi* by Schiebel and Hemleben (2017), but the rarely used, strictly monotypic and phylogenetically unnecessary genus *Bolliella* is here rejected. A rare element of Indo-Pacific tropical plankton, possessing distinct adult morphology, but pre-adult specimens may be difficult to distinguish from other species of *Globigerinella*.

Globigerinella calida (Parker, 1962)

Erected by Parker (1962) to differentiate smaller, less planispiral forms with radially elongated chambers from the more planispiral and larger *Globigerinella siphonifera*. The two species have a distinct ecology, and the *G. calida* morphology is associated with a specific genetic lineage within the genetically diverse *Globigerinella* (Weiner et al., 2015), justifying the retention of this species. However, the morphological separation from *G. siphonifera* is often gradual and the identification is confounded by the existence of *Globigerinella radians*, making it difficult to apply the species concept consistently (Al-Sabouni et al., 2018).

Globigerinella radians (Egger, 1893)

Resurrected by Weiner et al. (2015) to resolve a taxonomic confusion resulting from the apparently parallel evolution of radially elongated chambers in this species and *G. calida* (and for that matter in *G. adamsi*). Banner and Blow (1960b)

were the first to indicate affinity of this obscure Ehrenberg's species to the *Globigerinella* clade by assigning it to their newly erected subgenus *Beella*. No type has been designated and Egger's material from the German *Gazelle* expedition, initially deposited at the Bayerische Staatssammlung in München, appears to have been destroyed during the Second World War and is thus considered lost. It is possible that further genetic work on *Globigerinella* will provide new evidence requiring further revisions within the genus.

Globigerinella siphonifera (d'Orbigny, 1839)

Frequently referred to as *Globigerinella aequilateralis* (Brady, 1879). The synonymy of the two species has been established already by Banner and Blow (1960a), who also selected suitable lectotypes based on original material of d'Orbigny and Brady. Their decision to exhume the name "*siphonifera*" was grudgingly accepted by Parker (1962), who resented that d'Orbigny's name had been disinterred by Banner and Blow (1960a) but conceded the need to now reject the popular *G. aequilateralis*. Unfortunately, other authors such as Saito et al. (1981, p. 28) maintained that *G. siphonifera* was a *nomen oblitum* (which was clearly incorrect at that time, considering the usage by Parker, 1962) and retained *G. aequilateralis*, and this decision was followed by key works such as by Kennett and Srinivasan (1983), explaining the long history of parallel names. The apparent phylogenetic placement of *G. calida*, the establishment of *G. radians*, and likely the existence of *G. adamsi* all appear to make this genetically hyperdiverse species (Weiner et al., 2014) in its present concept paraphyletic (Weiner et al., 2015).

Globigerinita Brönnimann, 1951

Typified by *Globigerinita naparimaensis* Brönnimann, 1951, which was later accepted as a synonym of the extant *Globigerinita glutinata* (Egger, 1893). For a discussion on the synonymy, the reader is referred to the study by Parker (1962). This microperforate genus was initially applied to various species possessing a bulla, irrespective of wall texture (Bolli et al., 1957), but was refocused on the microperforate species by Parker (1962), although she at that time also included in *Globigerinita* the macroperforate and spinose *T. humilis*. In its current concept, the genus refers to Oligocene to extant microperforate taxa with an umbilical aperture (Pearson et al., 2018). The genus is paraphyletic, giving rise to *Candeina*. Three extant species.

Globigerinita glutinata (Egger, 1893)

The original description of the species by Egger (1893) is sufficiently detailed to confirm that the name refers to a microperforate species (Egger specifically highlighted the felt-like surface of the shell) with a morphology consistent with its modern representatives. A type has never been designated and our own enquiries at the Bayerische Staatssammlung in München failed to locate Egger's material, derived from the German *Gazelle* expedition, which must therefore be considered lost. Since the concept of the species is not contested and has been used consistently on modern material, we leave the designation of a type for future work. The considerable morphological variability in the species, especially in terms of the different development of the bulla, has led to a proliferation of names. Following the practice initiated by Parker (1962) and followed by Pearson et al. (2018), these forms are here all considered as synonyms. However, we note that the species is genetically diverse (Morard et al., 2019b), and it is at present not clear if the genetic types are associated with morphological differences.

Globigerinita minuta (Natland, 1938)

Like in many other species referable to *Globigerinita*, the species was originally misinterpreted with the multiple infralaminar apertures leading Natland (1938) to assign his new species to *Globigerinoides*. An SEM rendering of the holotype published by the National Museum of Natural History (Smithsonian, Washington DC, United States) confirms that it is microperforate and less trochospiral than in the illustration by Natland (1938). This is consistent with the observations by Parker (1962), who synonymized *G. minuta* with *G. uvula* but noted the lower spire in the holotype of *G. minuta*, referring to specimens on her plate 8, figs. 24–26, which we indeed consider consistent with *G. minuta*. Despite the overall similarity with *G. uvula*, the species is genetically distinct and this distinction appears to be associated with moderately high-spired specimens bearing a characteristic highly arched aperture and showing a different ontogenetic trajectory (Brummer, 1988a; Morard et al., 2019b), consistent with the concept by Saito et al. (1981) and Schiebel and Hemleben (2017).

Globigerinita uvula (Ehrenberg, 1862)

The specimen of *G. uvula*, which was illustrated by Ehrenberg (1873), is preserved at the Museum für Naturkunde in Berlin. The sheet with the original drawing contains information that facilitated the identification of the drawn specimen in one of Ehrenberg's mica mounts (Ehrenberg mounted samples of deep-sea sediment akin to smear slides in Canada Balsam on thin mica sheets and indicated the position of pictured specimens by small coloured paper rings stuck on the mount). Following recommendations by the Code, this specimen (Fig. 4) can be considered syntypic and is here designated as the type (lectotype), analogous to the designation of the lectotype of *N. pachyderma* by Darling et al. (2006). The species has been often referred to as *Globigerinita bradyi* (Wiesner, 1931), which is a junior synonym (Parker, 1962; Saito et al., 1981). Like for *N. pachyderma*, the year of description has been often erroneously stated as 1861.

Globigerinoides Cushman, 1927

Typified by the extant *Globigerinoides ruber* (d'Orbigny, 1839), the genus refers to a diverse and abundant warm-water clade of spinose species with supplementary apertures (Morard et al., 2019a). To assure the monophyly of *Globigerinoides*, Spezafferri et al. (2015) transferred the extant *sacculifer*-plexus to their newly erected genus *Trilobatus*. The genus name *Globigerinoides* is grammatically masculine, and after quite some discussion decades ago, the grammatical gender of the constituent species has been adjusted accordingly and stabilized (e.g. *Globigerinoides rubra* becoming *Globigerinoides ruber*). However, the fourth edition of the Code contains an amendment to article 30, which deals with gender-group words of this type, in a way that could be interpreted as implying that the name should be feminine. This is because it opens up the possibility for names created with the ending -oides, which are grammatically masculine, to be considered of different gender, if the original author stated so, for example by combining it with a species name in another gender form. In the interest of nomenclatural stability, we refrain from applying this amendment to *Globigerinoides*. Five extant and many fossil species and subspecies.

Globigerinoides conglobatus (Brady, 1879)

A well-established species, with adequate type from recent sediments. Morphologically variable, with large changes in chamber shape through ontogeny, but appears genetically homogenous in the modern ocean (Morard et al., 2019a).

Globigerinoides elongatus (d'Orbigny, 1826)

Synonymized with *Globigerinoides ruber* by Parker (1962), causing a proliferation of informal names for morphotypes within the resulting broad concept of *G. ruber*, including the popular *G. ruber* sensu lato of Wang (2000). Reinstated in a combined morphological and genetic investigation by Aurahs et al. (2011), the species is distinguished by an asymmetrically flattened (compressed) final chamber and occasionally also the penultimate chamber. Type specimen with representative morphology was designated by Banner and Blow (1960a) from a region where the genetic type associated with this name and morphology has been found to occur (Aurahs et al., 2011). Numerous synonyms, or partial synonyms, highlighting different degrees of spire elongation (a character also occurring in *G. ruber*), chamber compression and aperture size. Specimens figured by Schiebel and Hemleben (2017) on plate 2.8, figs. 12–16 as *G. ruber* have to be considered *G. elongatus*.

Globigerinoides ruber albus Morard et al., 2019

Established to differentiate the extant lineage of *G. ruber* without the red pigmentation from the ecologically and genetically distinct lineage with pigmentation (Morard et al., 2019a). The only case in planktonic foraminifera where the type specimen (shell) is associated with a DNA barcode (a fragment of the SSU rDNA extracted from the cytoplasm within the shell). Possessing the typical *G. ruber* morphology with inflated chambers, *G. ruber albus* is consistent with *Globigerinoides ruber* sensu strictu of Wang (2000). The large morphological variability, long-term confusion with *Globigerinoides elongatus* (see Aurahs et al., 2011) and existence of aberrant morphologies has lead to the establishment of many synonyms. None of these appear justified at present, but we note that *G. ruber albus* harbours several apparently cryptic genetic types (Morard et al., 2019a), and a further revision may be justified if some of these prove pseudocryptic.

Globigerinoides ruber ruber (d'Orbigny, 1839)

Referring to the conspicuous reddish pigmentation of the shell, d'Orbigny's name must be the nominotype for the subspecies designating the genetic lineage of *G. ruber* where the pigmentation occurs (Morard et al., 2019a). Indeed, Banner and Blow (1960a) designated and figured a lectotype of *G. ruber*, noting that "the earlier part of the test is red coloured". The name is thus safely associated at the subspecies level with the red-pigmented form of the otherwise genetically and morphologically diverse species.

Globigerinoides tenellus Parker, 1958

An unusually small species of the genus *Globigerinoides*, despite possessing a supplementary aperture on the final chamber for decades considered to belong to *Globoturborotalita*. Identified genetically as a sister species to *G. elongatus* and thus transferred to *Globigerinoides* by Morard et al. (2019a).

Globoquadrina Finlay, 1947

Typified by the extinct species *Globoquadrina dehiscens* (Chapman et al., 1934), the assignment of the only modern representative, *G. conglomerata*, to this genus is problematic. Wade et al. (2018b) transferred the species to *Dentoglobigerina*, leaving the previously species-rich *Globoquadrina* monotypic. The extant species, endemic to the tropical Indo-Pacific, is genetically distinct from all other non-spinose taxa (Morard et al., 2019b), requiring classification in a distinct genus. Because *Dentoglobigerina* is spinose according to Wade et al. (2018b), we cannot assign the extant and ostensibly non-spinose species to this genus. Therefore, we here provisionally retain *Globoquadrina*, awaiting revision of the fossil species leading to the modern taxon. As applied here the genus contains one extant and at least one fossil species.

Globoquadrina conglomerata (Schwager, 1866)

A conspicuous modern species, which is commonly thought to have descended from the Neogene *Globoquadrina venezuelana* (Kennet and Srinivasan, 1983; Aze et al., 2011). Wade et al. (2018b) reexamined the types of *G. conglomerata* and found them to be conspecific with *G. venezuelana*, which is consistent with observations by Banner and

Blow (1960a) and Parker (1962) that the two species are similar and potentially synonymous. It remains to be established whether the topotypic material, presumably of Pliocene or upper Miocene age, including the neotype selected by Banner and Blow (1960a), is consistent with the modern species. If it is not, then the modern species needs a new name. If it is consistent, as it seems from the illustrations, then the name *G. conglomerata* would have priority over *G. venezuelana*. Either way, the taxonomic conundrum spills over to the generic assignment of the species, as Wade et al. (2018b) transferred *G. venezuelana* together with *G. conglomerata* to the genus *Dentoglobigerina*, which they consider spinose. Since there is no evidence for spines in living *G. conglomerata*, and molecular genetic data do not show any evidence for a relationship with the spinose clade (Morard et al., 2019b), we here choose to retain this modern non-spinose species in *Globoquadrina* but anticipate a need for revision of modern and fossil representatives of this lineage.

Globorotalia Cushman, 1927

Typified by the extant *Globorotalia tumida* (Brady, 1877), the genus was initially used for a range of extant and fossil taxa with compressed shells and/or an extraumbilical aperture. Once it became obvious that these features evolved independently several times, the genus concept was gradually narrowed to a single Neogene lineage leading to the nominotype species. The concept was still too broad at the time of the revision by Parker (1962) but assumed a similar form to modern usage by the revision in Kennett and Srinivasan (1983), albeit still including their *Jenkinsella*, which is now known to be unrelated (Leckie et al., 2018). With 10 extant and many fossil species, the genus is unusually diverse. It comprises several distinct lineages, which have been treated as subgenera, and the subgenus names were later sometimes raised to genera. We here retain a single genus, because the use of other generic names has little tradition among extant planktonic foraminifera and the subdivision of the genus is not necessary, as the genus in the broad concept remains monophyletic. We note that many of the erected subgenera may be useful, especially when tracing the phylogeny of the extant species (e.g. Kennett and Srinivasan, 1983; Aze et al., 2011). However, we point out that the subgenera are riddled with synonyms and homonyms and their reinstatement would require a careful revision of the nomenclature (Table 1).

Globorotalia cavernula Bé, 1967

Since its original description by Bé (1967b), *G. cavernula* has been elusive. Nevertheless, this species is retained because of the extensive documentation of its distinct morphology and relatively high abundance in the plankton claimed by the original author. The holotype indicates that the species is related to *G. truncatulinoides*, and the lack of occurrence records elsewhere indicates that it may be restricted to cold waters of the South Pacific. It is possible that *G. cavernula* refers to one of the known cryptic species of *G. truncatulinoides* (Quillévéré et al., 2013).

Globorotalia crassaformis (Galloway and Wissler, 1927)

This species is typified by a specimen derived from Pleistocene sediments, from well within its commonly accepted stratigraphic range (Kennett and Srinivasan, 1983) and showing morphology entirely consistent with its living representatives. An important element of sub-thermocline faunas in tropical to temperate regions, the species is morphologically diverse and a host of names exists for various forms (see Saito et al., 1981). These are all here considered synonyms with respect to the extant *G. crassaformis*, but we note that for example Aze et al. (2011) considered *Globorotalia oceanica* Cushman and Bermúdez, 1949, as extant and lists five additional species allied to *G. crassaformis* as extinct. Genetic data are so far too scarce to decide whether pseudocryptic diversity exists within the species.

Globorotalia hirsuta (d'Orbigny, 1839)

A neotype was designated by Blow (1969) from recent sediments, and a second (later invalidated) neotype has been designated by Le Calvez (1974). The species is abundant in temperate waters and appears morphologically as well as genetically homogenous.

Globorotalia inflata (d'Orbigny, 1839)

A distinct and abundant extant species, typified by a specimen from recent sediments designated by Banner and Blow (1967). A second (later invalidated) neotype has been designated by Le Calvez (1974). Two distinct pseudocryptic species (Morard et al., 2011) indicate a potential for future revision.

Globorotalia cultrata (d'Orbigny, 1839)

Whereas the morphological concept of this conspicuous extant species remained relatively stable, the name has a turbulent history. The confusion arose from the inconsistent usage of d'Orbigny's (1826) name *Rotalia* (*Rotalie*) *menardii*, which was, like almost all other names in that work, initially a nomen nudum and thus invalid. However, a description was later provided by Parker et al. (1865), which, unfortunately, separated the name from the original concept by d'Orbigny such that it became synonymous with d'Orbigny's (1839a) *G. cultrata*. This created the impression that both names refer to the same entity, with *G. menardii* having priority by ascribing its authorship incorrectly to d'Orbigny (1826). This view has been cemented by Banner and Blow (1960a) designating a neotype for *G. menardii* from recent sediments, which is representative of the extant species and thus conspecific with *G. cultrata*. The controversy over the nomenclatural priority of *G. menardii* is covered in detail by Banner

and Blow (1960a), Parker (1962) and Stainforth et al. (1975). Stainforth et al. (1975) decided to resolve the situation by insisting that *G. menardii* should be used for Miocene biconvex forms, because the material that d'Orbigny (1826) studied could have only referred to that form. The discussion resulted in a formal ICZN case and ruling (Stainforth et al., 1978: ICZN Case 2145; ICZN Opinion 1234, 1982), which re-attached the name *G. menardii* to the original concept of d'Orbigny, referring to an extinct Neogene Mediterranean form, and the authorship has been fixed to d'Orbigny in Parker et al. (1865). Unfortunately, this ruling has been misunderstood as a complete suppression of the name *G. cultrata*, and the name *G. menardii* continued to be used for the extant species as well, which is clearly at variance with the intention of Stainforth et al. (1975, 1978). Upon review of the relevant literature, we must conclude that the validly described and available name *Rotalina cultrata* d'Orbigny 1839, fixed by a highly representative type specimen derived from recent sediments (Fig. 6) and conspecific with what is commonly considered as the extant *G. menardii*, must be reinstated for the extant species.

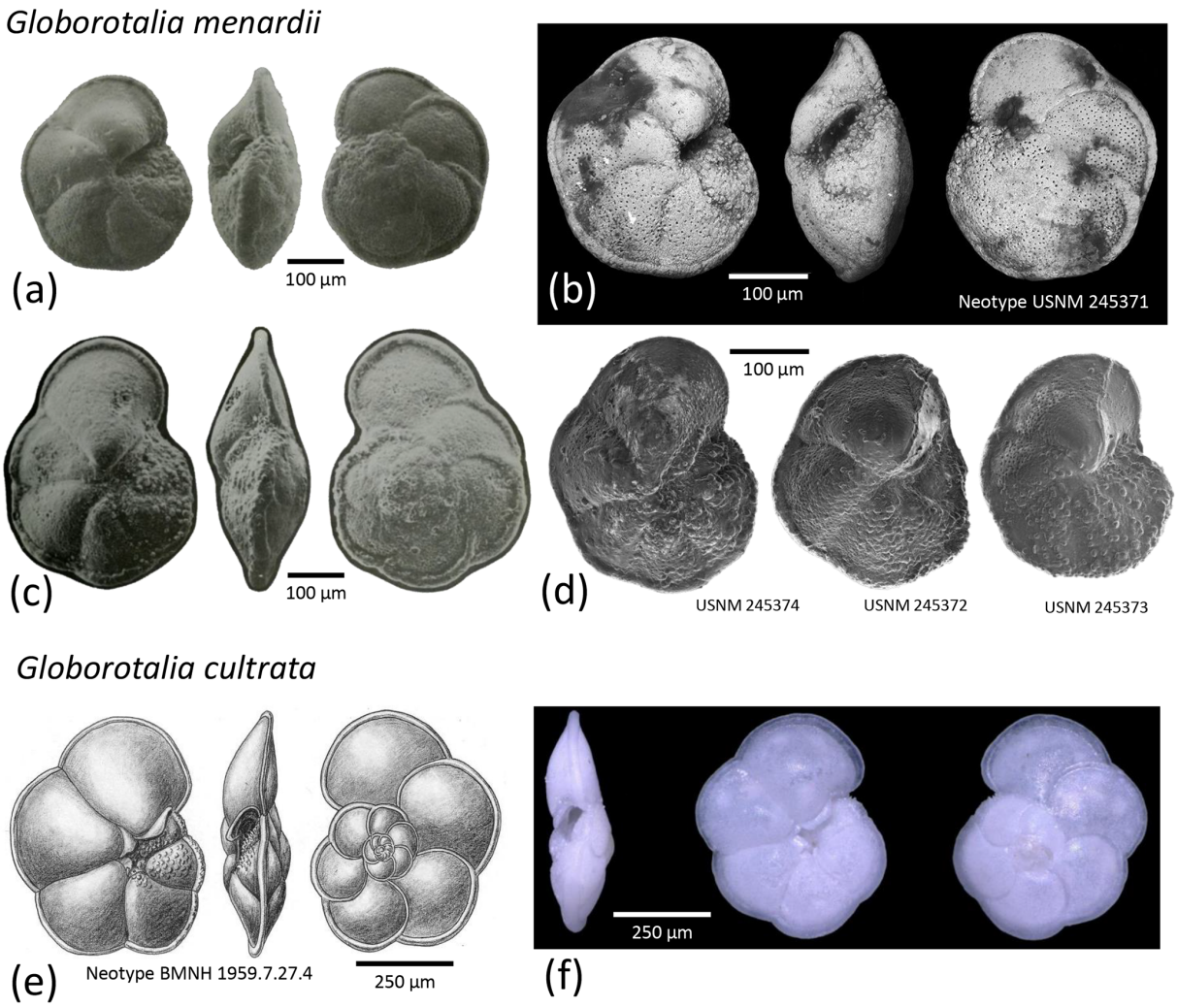
The initial concept of d'Orbigny, where *G. menardii* was based on material that is now considered Neogene, made Stainforth et al. (1975) designate a Miocene neotype (Fig. 6), which was upheld by ICZN ruling (ICZN Opinion 1234, 1982) over the Quaternary lectotype selected for *G. menardii* by Banner and Blow (1960a). Remarkably, on examination of the type material in the Smithsonian Institution, the specimen designated by Stainforth as neotype and deposited in the collections as USNM245371 is quite obviously not the same specimen as the neotype designated by Stainforth et al. (1978; their plate 1, fig. 1) and upheld by the ICZN ruling. Instead, this specimen is identical to that which Stainforth et al. (1978) depict on their plate 2, fig. 1 (Fig. 6). Next to the specimen labelled as neotype, Stainforth deposited three further specimens at the Smithsonian Institution, which have been imaged courtesy of the curator Brian Huber and are depicted here in Fig. 6. None of these correspond to the neotype of Stainforth et al. (1978), and two show damage to the last chamber as commonly occurs when specimens are being removed from an SEM mount. There are no other specimens deposited in the USNM collections on the occasion of the type designation for *G. menardii*. In the opinion of the curator, which we share, the formally designated neotype was damaged during handling and replaced by Stainforth. Therefore, we conclude that the neotype designated by the ICZN Opinion 1234 (1982) ruling must be considered lost and we here designate the specimen deposited under USNM245371 as a replacement neotype. The specimen clearly originates from the same type series as the ICZN type and was labelled as type by the author. It possesses representative morphology and is undamaged.

In the concept of Stainforth et al. (1975, 1978), as also evidenced by their selection of type, *G. menardii* is distinct from the extant species, and in their revision, Stainforth et al. (1975) clearly state that their *G. menardii* refers to a Miocene form from the Mediterranean, distinct from modern representatives of the lineages, which they considered as *G. cultrata*. The Miocene form is commonly found in Neogene Mediterranean sediments, with a well recorded and stratigraphically useful last occurrence in the late Miocene throughout the Mediterranean (Lirer et al., 2019). Unfortunately, the confusion between *G. menardii* and *G. cultrata* has not been resolved as intended by the ICZN ruling, and both names continued to be in use for extant material, either as synonyms or as names for morphological variants (e.g. Regenberg et al., 2010), with *G. menardii* being the more common designation, adopted by authoritative works (Kennett and Srinivasan, 1983; Hemleben et al., 1989) and perpetrated by almost all users, including us. With *G. menardii* in the concept of Stainforth et al. (1975, 1978) being placed on the Official List of Species Names by the ICZN (Name Number 2832), the name cannot be applied to extant taxa without a new ruling by the ICZN, which would have to overrule its own earlier decision. This causes a situation where the stability of the nomenclature requires a change, which is in conflict with prevailing usage. Unfortunately, we feel compelled to implement this change, and we here urge the community to adopt the name *G. cultrata* for the distinct and abundant extant form and abandon the erroneous usage of *G. menardii*, which clearly refers to an extinct form, with a distinct morphology (Fig. 6).

With respect to the proposed change in usage, we believe that it is safe to assume that all references to *G. cultrata* to date refer to our *G. cultrata*, as do all references to *G. menardii* applied on extant or Quaternary material. References to *G. menardii* in material older than Quaternary may refer either to our *G. cultrata* or to the extinct *G. menardii* of Stainforth et al. (1975, 1978). Although we have not ventured to clarify the phylogenetic relationship of the two taxa in the fossil record, we note a number of distinct morphological features allowing in our opinion unambiguous diagnosis of the extant *G. cultrata* against the Mediterranean Miocene *G. menardii* (Fig. 6). The extant *Globorotalia cultrata* has been confirmed by molecular genetic data to be distinct from other globorotaliids, with no evidence for genetic diversity among its extant populations (Morard et al., 2015) to support the commonly used subspecies such as *G. menardii flexuosa* (the type of this subspecies indicates that it originally referred to *G. tumida*) and *G. menardii fimbriata*, which in our opinion both refer to extinct taxa, morphological variants or aberrations without taxonomical significance.

Globorotalia scitula (Brady, 1882)

Lectotype selected by Banner and Blow (1960a) based on the original surface sediment material from Brady (1982). Small forms with an open umbilicus, occurring in modern plankton, have been described as *Globorotalia bermudezi* Rögl and Bolli, 1973, and this species was considered as



Character	*Globorotalia cultrata*	*Globorotalia menardii*
Test outline in side view	Flat, ultimate chamber highest point in the middle of the chamber	Biconvex, ultimate chamber highest point close to the umbilicus
Test outline in spiral view	Lobate	Compact to slightly lobate
Aperture position	Extending from the umbilicus towards the periphery	Not extending all the way towards the periphery
Apertural modifications	Broad lip sometimes extending into a flap	May have narrow lip
Umbilicus	Open, with relict apertures of all chambers in the final whorl opening into the umbilicus	Closed, or narrow pit, no relict apertures
Umbilical sutures	Straight to slightly sinuous	Straight towards the periphery, curved towards the umbilicus
Spiral sutures	Limbate, equally thickened throughout	More thickened towards the periphery

Figure 6. Neotype of *Globorotalia menardii* (Parker, Jones and Brady, 1865) as designated here with **(a)** being the specimen imaged by Stainforth et al. (1978) on their plate 2, fig. 1, and **(b)** the specimen labelled as type and deposited as such by Stainforth in the USNM collections and here designated as neotype. The specimen initially designated by Stainforth et al. (1978) as the neotype **(c)** deviates from all other specimens deposited by Stainforth at the USNM **(a, d)** and must be considered lost. **(e)** Neotype of *Globorotalia cultrata* (d'Orbigny, 1839) as designated and drawn by Banner and Blow (1960a), compared to **(f)** a light microscope image of a topotypical specimen extracted from Caribbean surface sediments (image by Adrian Baumeister). The table below the illustrations is listing key morphological characters differentiating the two species.

extant by Aze et al. (2011). There could well turn out to be (pseudo)cryptic species in *G. scitula*, in which case *G. bermudezi* may be reinstated, but at present there is no strong evidence for morphological discontinuity within the extant representatives of the species.

Globorotalia eastropacia Boltovskoy, 1974

Specimens of this distinct Indo-Pacific form have been initially assigned to other species, but many authors noted the differences to established taxa. Parker (1962) assigned this form to *G. hirsuta* but noted that these specimens belonged to a distinct group (Group 3, her plate 5, figs. 13 and 15) characterized by flat spiral side and poorly developed keel, occurring frequently in the Indo-Pacific. Saito et al. (1981) erroneously synonymized with this species the figured specimens of group 1 by Parker (1962, her plate 5, figs. 12 and 14), which Parker (1962) clearly considered "typical" of *G. hirsuta* as found around the Canary Islands. The same morphological distinction led Boltovskoy (1974) to describe *Globorotalia hirsuta eastropacia* from plankton tows in the Pacific. His description was published in January 1974, clearly referring to the same species described as *Globorotalia theyeri* by Fleisher in a work published in April 1974 (Fleisher, 1974). Hence the more commonly used name *G. theyeri* is a junior synonym, and in the absence of a strong case against *G. eastropacia*, which has been occasionally used (e.g. Saito et al., 1981), the name *G. eastropacia* should be adopted instead.

Globorotalia truncatulinoides (d'Orbigny, 1839)

Since the type specimen of *Rotalina truncatulinoides* from d'Orbigny (1839b) was lost, Blow (1969) designated a neotype from recent sediments. An invalid, since later, lectotype has been designated by Le Calvez (1974). The general concept of this distinct and abundant deep-dwelling species has remained stable, but the large intraspecific morphological variability (e.g. Lohmann and Malmgren, 1983) led to the proliferation of names referring to various subfossil and extant forms. Aze et al. (2011) recognize two extant and three extinct species with a morphology falling within the range of variability of extant *G. truncatulinoides*, whereas Kennett and Srinivasan (1983) followed a more conservative approach close to the current species concept. The species harbours at least five distinct genetic types, which appear to be associated with morphological differences (Quillévéré et al., 2013), heralding the potential for future revision.

Globorotalia tumida (Brady, 1877)

Type species of *Globorotalia*, itself typified by a lectotype selected by Banner and Blow (1960a) from presumably Quaternary or Pliocene rock fragments collected on a beach of New Ireland after a tsunami. The species has been often lumped with *G. cultrata* (then referred to as *G. menardii*) in studies based on quantitative census counts of Quaternary assemblages. This was due to a combination of the taxonomic confusion between the fossil *G. menardii* and modern *G. cultrata* (as lamented by Parker, 1962) and by ignoring at the same time also the distinct *G. ungulata*. The current species concept is consistent with Saito et al. (1981) and Kennett and Srinivasan (1983) and includes specimens referred to as *Globorotalia flexuosa* (Koch 1923), which we consider to represent a morphological aberration as long as the name is applied on extant species.

Globorotalia ungulata Bermúdez, 1961

Often ignored, but representing a necessary category to correctly assign specimens of the *G. tumida–G. cultrata* plexus. Applied consistently with current understanding by Saito et al. (1981) and Kennett and Srinivasan (1983). Specimen figured by Schiebel and Hemleben (2017) on plate 2.30 and figs. 1–3 represents *G. ungulata*, not *G. tumida*. Typified by a holotype from recent sediments and confirmed by molecular genetic data to be distinct, but related to *G. tumida* (Morard et al., 2015).

Globorotaloides Bolli, 1957

Typified by the extinct species *Globorotaloides variabilis* Bolli, 1957, which has been connected with some confidence to a lineage leading to the extant species (Coxall and Spezzaferri, 2018). A distinct dominantly Indo-Pacific form with two extant and many fossil species.

Globorotaloides hexagonus (Natland, 1938)

Distinct deep-water form found in the plankton only in the Indo-Pacific. The Quaternary holotype refers to a morphology with straight dorsal sutures, frequently observed in the sediments and consistent with the concept by Parker (1962).

Globorotaloides oveyi Buckley, 1973

A second form among the extant *Globorotaloides*, characterized by curved dorsal sutures and more compressed chambers was observed in plankton samples from the Indian Ocean by Buckley (1973), leading him to the establishment of a new species. Remarkably, Saito et al. (1981), otherwise consistent splitters, have considered *G. oveyi* synonymous with *G. hexagonus*. However, considering the distinct morphology of *G. oveyi*, its occurrence in the plankton and our own observations from the plankton (Fig. 7), we see no grounds on which to reject *G. oveyi* as a distinct species, but note that this decision requires confirmation by genetic data.

Globoturborotalita Hofker, 1976

Typified by the only extant species of the genus, *Globoturborotalita rubescens* (Hofker, 1956), *Globoturborotalita* comprises a large number of fossil species, all characterized

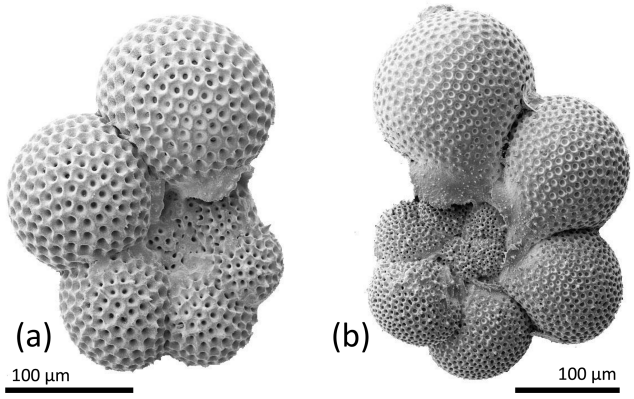


Figure 7. SEM images of *Globorotaloides* collected during the M74 1b expedition (Bohrmann et al., 2010) in the Arabian Sea, showing shell morphology consistent with the original description of **(a)** *Globorotaloides hexagonus* (Natland) and **(b)** *Globorotaloides oveyi* (Buckley). Both specimens appeared alive (with coloured cytoplasm) when collected. Specimen in **(a)** is from station 947, 300–500 m water depth; that in **(b)** is from station 945, 500–700 m water depth.

by small globular shells with inflated chambers and coarse, cancellate wall texture (Spezzaferri et al., 2018b). The extant species now classified as *Globigerinoides tenellus* has been assigned in the past to *Globoturborotalita* (e.g. Schiebel and Hemleben, 2017; Spezzaferri et al., 2015), being the only species of the genus with supplementary aperture. The species was authoritatively transferred to *Globigerinoides* based on genetic evidence by Morard et al. (2019a), allowing *Globoturborotalita* to be circumscribed as lacking supplementary apertures.

Globoturborotalita rubescens (Hofker, 1956)

Distinguished by the conspicuous reddish pigmentation of the shell, developed on most specimens and expressed in the species name. Hofker did not designate a holotype, neither in his original description of this species (Hofker, 1956), nor when describing the genus *Globoturborotalita* of which *G. rubescens* is the type species (Hofker, 1976). Hofker (1956) noted that the specimens that lead him to erect *G. rubescens* were derived from recent sediments from western Indonesia (Malay Archipelago) collected during the Dutch Siboga expedition (1899–1900). The location of this material is unclear, but we have located in the Hofker collection (originally deposited at the Zoological Museum in Amsterdam, and then transferred in 2011 to the Naturalis Biodiversity Center, Leiden, the Netherlands, and curated there) a slide registered as RGM 538508 with a written note on the slide apparently in Hofker's handwriting, stating that the sample contains "*Globigerina rubescens* Hofker" (Fig. 5c). The slide contains a sieved residue from a sediment collected during the Snellius expedition (Snellius station 190) off Sulawesi, i.e. from the same region as the Siboga material. It is impossible to establish when the labelling of the slide occurred, but because of the genus name it must have been before 1976. Since it appears likely that Hofker considered this material when he established *G. rubescens* in 1956 and because of the clear labelling by Hofker, the specimens in the sample can be considered syntypic, and the sample represents in our opinion the best available material to select a type. The residue contained a rich and well preserved assemblage of planktonic foraminifera from which we were able to extract 15 specimens of *G. rubescens*. From among those, we here designate specimen RGM 1333481 as the lectotype, and specimens RGM 1333482–1333495 as paralectotypes (Fig. 5).

Hastigerina Thomson in Murray, 1876

Monotypic genus without a notable fossil record, typified by *Hastigerina pelagica* (d'Orbigny, 1839c) representing a distinct lineage of spinose planktonic foraminifera with triradiate, barbed spines.

Hastigerina pelagica (d'Orbigny, 1839)

Banner and Blow (1960) selected a neotype, which is at the same time the lectotype of the junior synonym *Hastigerina murrayi* (Thompson, 1876). The species is genetically diverse (Weiner et al., 2012), and it may be that a closer examination of the three genetic lineages will justify taxonomic revision.

Hastigerinella Cushman, 1927

A substantial complexity arose due to the application of this genus on fossil taxa, which was clearly at variance with the intention of Cushman and the nature of the type species *Hastigerinella digitata* (Rhumbler, 1911). The genus was formally reinstated with *Hastigerinella digitata* as a type to stabilize the nomenclature of the Eocene *Clavigerinella*, by placing *Hastigerinella digitata* on the list of valid species by ICZN ruling (Coxall, 2003). In consequence, the replacement name *Hastigerinellopsis* Saito et al., 1976 had to be abandoned. To observe the ICZN ruling, this monotypic genus is retained, with the added advantage of providing a clear distinction between *Beella digitata* (Brady, 1879) and *Hastigerinella digitata* (Rhumbler, 1911).

Hastigerinella digitata (Rhumbler, 1911)

Following the opinion of Banner and Blow (1960b), who figured a number of specimens (hypotypes) and emended the species description in a way consistent with the current usage, the species has been formally placed on the list of valid taxa by ICZN ruling (Coxall, 2003). Banner and Blow (1960b) did not succeed in locating the type material, which is considered lost, but Banner (1965) later designated one of the hypotypes figured in Banner and Blow (1960b) as the neotype. *Hastigerina parapelagica* Saito and Thompson, 1976, is here considered a growth stage of *Hastigerinella digitata*, in a stage prior to the development of the branching chambers.

Neogallitellia Özdikmen, 2009

Monotypic genus established for the only extant species in the plankton with triserial chamber arrangement. A replacement name for *Gallitellia* Loeblich and Tappan, 1986, which is a junior homonym of the coral *Gallitellia* Cuif, 1977. One extant species.

Neogallitellia vivans (Cushman, 1934)

This small but distinct species, typified by a specimen from recent sediment, is frequently encountered in the plankton, especially along continental margins, and may be holoplanktonic, but its close genetic relationship with benthic taxa (Ujiié et al., 2008) implies that it could also represent a form that is planktonic only during one part of its life cycle, akin to the tychopelagic *Bolivina variabilis*.

Neogloboquadrina Bandy, Frerichs and Vincent, 1967

Typified by the extant *Neogloboquadrina dutertrei* (d'Orbigny, 1839a), this distinct and diverse genus has been established to separate the modern non-spinose lineage with "globoquadrinid" chambers from other fossil lineages possessing this character. The genus is paraphyletic, giving rise to *Pulleniatina*. Three extant and many fossil species.

Neogloboquadrina dutertrei (d'Orbigny, 1839)

A morphologically diverse tropical species, covering in its current concept specimens that have been in the past assigned to various taxa, most notably *Neogloboquadrina eggeri* (Rhumbler, 1901) or *Neogloboquadrina blowi* Rögl and Bolli, 1973, listed by Saito et al. (1981) despite the fact that Parker (1962) established a broad concept of the species, concluding that the different variants (four types described specifically) "all belong to the same species". McCulloch (1977) alone described five new species, all being obvious synonyms of *N. dutertrei*. A lectotype showing morphological characteristics consistent with extant populations of the species was designated from recent sediments in the Caribbean by Banner and Blow (1960a). Kipp (1976) established the long-used informal category pachyderma/dutertrei (P/D) intergrade. There appears to exist only a limited amount of genetic diversity within the genus (André et al., 2014), providing so far no evidence justifying this category as a taxon. Most specimens assigned to this category are now considered *N. incompta* (Kucera et al., 2005).

Neogloboquadrina incompta (Cifelli, 1961)

Synonymized with *N. pachyderma* by Parker (1962), but reinstated by some workers and finally confirmed by the discovery of genetic distinction between the two coiling variants of *Neogloboquadrina pachyderma* by Darling et al. (2006). This species refers to specimens previously recorded in Quaternary sediments and plankton as *N. pachyderma* dextral (variously abbreviated) or *N. pachyderma dextralis* Setty, 1977, and likely comprise most specimens assigned to the pachyderma/dutertrei (P/D) intergrade of Kipp (1976). One of the six extant species with a holotype derived from the plankton.

Neogloboquadrina pachyderma (Ehrenberg, 1862)

Contrary to common belief, Ehrenberg's report on his investigations in 1861 of various deep-sea sediment samples was published in 1862, which must be considered the correct publication date for the species. The original specimen, later figured by Ehrenberg (1873), has been located and illustrated by Darling et al. (2006) and designated as type (as it comes from material which must be considered syntypic, it represents a lectotype). With *N. incompta* being accepted, the name *N. pachyderma* is reserved for specimens previously recorded in Quaternary sediments and plankton as *N. pachyderma* sinistral (variously abbreviated or incorrectly labelled as "*sinistralis*", being a nomen nudum). Considerable morphological variability, noted already by Parker (1962), with numerous species names listed by Saito et al. (1981), is echoed by the existence of many distinct genetic types (Darling et al., 2017). In the absence of evidence for taxonomic significance of any of the alternative species concepts (or the many morphotypes in the species), all of the names previously applied to modern material are here considered synonyms. We note, however, that a future revision of the genetic variability and its link to shell morphology may lead to the reinstatement of some.

Orbulina d'Orbigny, 1826

Typified by the only extant species *Orbulina universa* d'Orbigny, 1839, *Orbulina* is together with *Globigerina* the earliest established genus of planktonic foraminifera. Several fossil species have been proposed but only *O. universa* and *O. suturalis* are currently recognized.

Orbulina universa d'Orbigny, 1839

Extant populations of *Orbulina universa* host specimens with shell morphologies that have been often identified as *Orbulina suturalis* and *Biorbulina bilobata* (e.g. Rossignol et al., 2011). However, despite earlier claims of the species surviving to the present (e.g. Kennett and Srinivasan, 1983; Aze et al., 2011), *Orbulina suturalis* is in our opinion to be understood as a short-lived species occurring in the middle Miocene (Wade et al. 2011) during a time when the diagnostic morphology of *O. universa* evolved (Pearson et al., 1997). Among living *O. universa*, forms similar to *O. suturalis* do occur but are rare and associated with an anomalously small spherical chamber relative to the enclosed "spiral" shell, or by the excentric envelopment of the sphere with respect to the spiral shell. *Biorbulina bilobata* is a rare form of *O. universa* referring to specimens that had formed a second terminal spherical chamber. This aberrant morphology is likely

associated with higher food availability (Robbins, 1988), and its development has been observed in the laboratory during the growth of specimens that otherwise do not differ from *Orbulina universa* (Caron, 1987; Bonnin, et al., 2019). Consequently, *O. suturalis* and *B. bilobata* are not recognized as species or any other taxonomic categories among the living plankton. On the other hand, there is evidence that the three cryptic species of extant *O. universa* (de Vargas et al., 1999) are associated with differences in the size and distribution of pores and areal apertures on the terminal chamber (Morard et al., 2009), heralding a potential for future refinement of the taxonomy.

Orcadia Boltovskoy and Watanabe, 1982

The phylogenetic position of this monotypic genus remains enigmatic, requiring retention of the genus name (Holmes, 1984; Brummer et al., 1988c). It is here provisionally placed among the Hastigerinidae, awaiting revision based on molecular data.

Orcadia riedeli (Rögl and Bolli, 1973)

A conspicuous small species, occurring in temperate to subpolar waters of both hemispheres. The species is distinct and cannot be confused when observed under the SEM, but specimens in the plankton could be confused with *T. quinqueloba* or juvenile *Hastigerina* or *Hastigerinella*.

Pulleniatina Cushman, 1927

Typified by the extant *Pulleniatina obliquiloculata* (Parker and Jones, 1865), the concept of this genus remained stable since its establishment by Cushman (1927), referring to a distinct lineage descendant from *Neogloboquadrina* in the late Miocene. One extant and several fossil species.

Pulleniatina obliquiloculata (Parker and Jones, 1865)

Unusual among the extant planktonic foraminifera because of the streptospiral coiling of its adult chambers. The first mention of the name by Carpenter (1862) is considered a nomen nudum, and the correct publication year must be 1865. A neotype was selected by Bolli et al. (1957) from material in slide 94.4.3.1045 and figured and described by Banner and Blow (1960a, 1967). The material was initially considered syntypic, but Hodkinson (1992) pointed out that the material is not from the original syntype series and the type specimens must be considered to represent a neotype. Although not optimally preserved, the specimen does show the typical adult morphology. Numerous synonyms or names were applied to specific morphologies within the species (see Saito et al., 1981), most notably *Pulleniatina finalis* Banner and Blow, 1967, considered extant by Aze et al. (2011), and a host of names (Table 3) was applied to presumably immature specimens of the species with hispid shell surface, lacking the thick cortex. The species comprises three genetic types that appear separated longitudinally (Ujiié and Ishitani, 2016), but it is not clear if any of these are associated with morphological distinction.

Sphaeroidinella Cushman, 1927

Typified by the extant *Sphaeroidinella dehiscens* (Parker and Jones, 1865), the monotypic genus is justified by preserving common usage and paying tribute to the significance of the development of supplementary apertures as a genus-level character among all other Neogene lineages of planktonic foraminifera.

Sphaeroidinella dehiscens (Parker and Jones, 1865)

A rare but conspicuous extant species, characterized by a glassy cortex deposited at the end of its life cycle, but in pre-terminal stages found in the plankton resembling *T. sacculifer* (Huang, 1981). There is no evidence for more than one extant species and forms described as *Sphaeroidinella excavata* Banner and Blow, 1965, are considered as morphological variants without taxonomic significance.

Tenuitellita Li, 1987

Typified by the extant *Globigerinita iota* Parker, 1962, we propose this validly described but previously dismissed name to be used for the extant representatives of the microperforate lineage containing the type species instead of *Tenuitella*. This is because molecular phylogenetic analysis of the living representatives of the genus shows that they belong to a single clade derived relatively recently from *Globigerinita* (Morard et al., 2019b), and since the continuity of the modern species with the last surviving Miocene *Tenuitella* has not been established (Kennett and Srinivasan, 1983; Li, 1987), it is likely that the extant clade is unrelated and requires a different name. The existing and validly described *Tenuitellita* represents the obvious choice for a name based on one of the extant species, and we here also assign *T. fleisheri* and *T. parkerae* to this genus. Three extant species.

Tenuitellita fleisheri (Li, 1987)

Despite its distinct form, characterized by compressed chambers, and common occurrence in the fine fraction in the plankton, this species has often been ignored. Previously considered to be a junior synonym of *T. compressa* (Fordham, 1986), but Fordham's species has not been described validly and the name is not available. Schiebel and Hemleben (2017) list *T. compressa* alongside *T. fleisheri*, implying that they are distinct species, an opinion for which there is no morphological or genetic evidence. Indeed, one of the specimens of *T. compressa* pictured in Schiebel and Hemleben (2017, plate 2.35, fig. 4) is identical with an illustration in Hemleben et al. (1989), where the specimen is labelled as

T. fleisheri. The earlier name by Fordham (1986) has to be rejected, because of the inconsistent use of binomial nomenclature in that work. The name "*compressa*" is labelled by Fordham (1986) as n.subsp. but also as n.ph. (ph. standing for phenon) of *Todella grata* (Todd, 1957), which, incidentally, Todd (1957) compared to *Globorotalia mayeri*, a distinct macroperforate taxon. Whereas a description as a subspecies may be valid even if the work where it is published does not follow binomial nomenclature (Article 11.4.2. of the Code), the concomitant designation of the taxon as n.ph. must be seen as a departure from the usage of Code categories or as an analogy to Article 15.2. of the Code and the name thus becomes unavailable.

Tenuitellita iota (Parker, 1962)

Described in detail by Parker (1962), the subsequent application of the species concept has been often hampered by the impression of the obligatory presence of a complex bulla, as seen on the type and two other specimens (plate 10, figs. 26–28 of Parker, 1962). This character refers to only one type within the species and Parker (1962) explicitly states that the species also contains a type where the bulla is rare, as exemplified by her specimen pictured on plate 20, fig. 29. In our experience, most specimens in the plankton have no terminal bulla but are easily distinguished from the superficially similar *G. glutinata* by their consistently umbilical–extraumbilical aperture and a distinctly smooth wall texture with few large pustules concentrated in the umbilical region, such as in the specimens figured as *T. iota* by Brummer (1988a) and Morard et al. (2019b).

Tenuitellita parkerae (Brönnimann and Resig, 1971)

Not to be confused with the homonymous *Globigerinita parkerae* (Bermúdez 1961). The latter refers to an extinct form (e.g. Kennett and Srinivasan, 1983), closely related to and perhaps even synonymous with *G. glutinata*. *Tenuitellita parkerae* is characterized by smooth wall texture and a tendency to grow radially elongated and slightly compressed chambers (Holmes, 1984; Brummer et al., 1988a), explaining why the species has been also assigned to the macroperforate *Globorotalia* (e.g. by Saito et al., 1981). Whilst the holotype represents the typical morphology, we note that the second specimen pictured by Brönniman and Resig (1971, their fig. 10) and designated as paratype is not microperforate and corresponds without doubt to the spinose *Turborotalita clarkei*.

Trilobatus Spezzaferri et al., 2015

Established by Spezzaferri et al. (2015), because both fossil and genetic evidence pointed to independent origin of this lineage from the clade including *Globigerinoides ruber* and allied species. The type species, *Trilobatus trilobus* (Reuss, 1850), is described from Miocene sediments, but its continuity with the extant species of the genus is well established (Spezzaferri et al., 2015). The genus is paraphyletic, giving rise to the Miocene *Orbulina* and Pliocene *Globigerinoidesella* (Poole and Wade, 2019). One extant and several fossil species and subspecies.

Trilobatus sacculifer (Brady, 1877)

The only extant representative of *Trilobatus*, shown to be genetically remarkably homogeneous (André et al., 2013), despite considerable morphological variability, leading to the proliferation of various names, which are all here rejected for the extant taxon (Table 3). In their concept of the species, Spezzaferri et al. (2015) distinguished late Oligocene and early Miocene populations of this lineage as *Trilobatus trilobus* (Reuss, 1850), lacking the typical sac-like final chamber, from late Neogene populations identified as *T. sacculifer* and consistently containing specimens with the sac-like final chamber. There is ample genetic (André et al., 2013) and fossil (Poole and Wade, 2019) evidence that the use of names other than *T. sacculifer* (such as *T. trilobus*, *T. quadrilobatus*, *T. immaturus* or any of the names describing particular forms of the final chamber such as *T. hystricosus* or *Globigerinoidesella fistulosa*) is inappropriate for the extant taxon, because there is no evidence for more than one species of *Trilobatus* at present. We note that some of those names may be valid for the description of fossil representatives of this lineage, with *G. fistulosa* representing a valid Pliocene form with distinct stratigraphic range (Poole and Wade, 2019). Since the sac-like final chamber is a facultative character, developed during the late ontogeny in some specimens (Bé et al., 1981), it cannot be used to distinguish taxa in the extant lineage even at the level of species. Therefore, we reject the usage of subspecies names in any combination, such as *T. sacculifer trilobus* or *T. trilobus sacculifer*, and advocate informal labelling of specimens with the sac-like final chamber, for example as *T. sacculifer* "with sac". Beyond this distinction, the broad concept of the species is undisputed and likely to be applied consistently. The species is typified by an adequate, albeit likely fossil, lectotype selected by Banner and Blow (1960a) and re-illustrated and discussed by Williams et al. (2006).

Turborotalita Blow and Banner, 1962, emended Pearson and Kucera (2018)

A conspicuous genus of living planktonic foraminifera, typified by the extant *Turborotalita humilis* (Brady, 1884). In their emended diagnosis, Pearson and Kucera (2018) characterized the genus as having an adumbilically displaced, ampullate terminal chamber, which has been in the past inappropriately labelled as bulla. Three extant and several fossil species.

Turborotalita clarkei (Rögl and Bolli, 1973)

Although rarely recorded, *T. clarkei* likely represents the smallest as well as numerically most abundant of all

modern species (Boltovskoy, 1991; Pearson et al., 2018; Chernikhovsky et al., 2020). Like *T. humilis*, *T. clarkei* is known in a lightly calcified lobate form commonly encountered in the living plankton as well as a heavily calcified compact (terminal) form often found in the sediment. The species was recognized by Saito et al. (1981) but erroneously assigned to *Berggrenia*. In Schiebel and Hemleben (2017), specimens of *T. clarkei* on plate 2.13, figs. 14–15 and plate 2.16, figs. 13–17 are erroneously labelled as *T. quinqueloba*.

Turborotalita humilis (Brady, 1884)

Like *T. clarkei*, *T. humilis* is known in a lightly calcified lobate form predominant in the living plankton as well as a heavily calcified and more compact (terminal) form commonly found in the sediment. Heavily calcified specimens with radially elongated chambers and lobate outline have also been referred to as *Turborotalita cristata* (Heron-Allen and Earland 1929), such as by Kennet and Srinivasan (1983) or Aze et al. (2011). Although the genetic diversity within *T. humilis* has not been sufficiently constrained yet, there is no evidence at present to consider *T. cristata* anything other than a calcification variant of *T. humilis*.

Turborotalita quinqueloba (Natland, 1938)

The morphological variability in this abundant species has led to the establishment of many names, proposed for terminal forms with differently developed ampullate final chambers (such as *T. exumbilicata*), including adult specimens from the living plankton without it (such as *T. egelida*), which we here subsume as ontogenetic variants under a single extant species. However, the species shows significant phenotypic variation (Kroon et al., 1988) and is genetically diverse (Darling et al., 2017) so that some of the names synonymized here may prove useful in future revisions considering pseudocryptic diversity, or when referring to extinct taxa.

Data availability. No data sets were used in this article.

Supplement. The supplement comprises an overview of all accepted species names with key distinguishing features (Supplement 1) and a list of species names (Supplement 2). The supplement related to this article is available online at: https://doi.org/10.5194/jm-41-29-2022-supplement.

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