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An updated suprageneric classification of planktic foraminifera after growing evidence of multiple benthic-planktic transitions

Una clasificación supragenérica actualizada de foraminíferos planctónicos tras la evidencia creciente de múltiples transiciones bentónico-planctónicas

Ignacio ARENILLAS, J. Antonio ARZ & Vicente GILABERT

Abstract: Planktic foraminifera have traditionally been classified within a single order: Globigerinida. However, recent phylogenetic studies, both molecular and stratophenetic, are evidencing the polyphyletic origin of planktic foraminifera from several benthic ancestors. At least four independent events of benthic-planktic transition have been identified. One of them occurred after the Cretaceous–Paleogene boundary mass extinction, originating the first Cenozoic globigerinids. Another three occurred in the Mesozoic, originating three groups of planktic foraminifera (globotruncanids, heterohelicids and guembelitriids) not related phylogenetically to each other or to current globigerinids. These findings make it necessary to carry out an exhaustive review of their suprageneric systematics, mainly at the order level. Here we propose a new, more natural classification, grouping them into four orders: Globigerinida, Heterohelicida, Globotruncanida n. ord., and Guembelitriida n. ord. To better reflect the diversity and phylogeny of planktic foraminifera, we have also defined two new superfamilies: Abathomphaloidea n. superfam. and Parvularugoglobigerinoidea n. superfam., and one new family: Parvularuglobigerinidae n. fam.

Resumen: Los foraminíferos planctónicos han sido tradicionalmente clasificados en un solo orden: Globigerinida. Sin embargo, estudios filogenéticos recientes, tanto moleculares como estratofenéticos, están evidenciando el origen polifilético de los foraminíferos planctónicos desde varios ancestros bentónicos. Se han identificado al menos cuatro eventos independientes de transición bentónico-planctónica. Uno de ellos ocurrió tras la extinción en masa del límite Cretácico–Paleógeno, originando los primeros globigerínidos cenozoicos. Otros tres ocurrieron en el Mesozoico, originando tres grupos de foraminíferos planctónicos (globotruncánidos, heterohelícidos y guembelítridos), los cuales no están filogenéticamente relacionados entre sí ni con los actuales globigerínidos. Estos hallazgos hacen necesario realizar una revisión exhaustiva de su sistemática supragenérica, principalmente a nivel de orden. Nosotros proponemos aquí una nueva clasificación más natural que los agrupa en cuatro órdenes: Globigerinida, Heterohelicida, Globotruncanida n. ord. y Guembelitriida n. ord. Para reflejar mejor la diversidad y la filogenia de los foraminíferos planctónicos, hemos definido también dos nuevas superfamilias: Abathomphaloidea n. superfam. y Parvularugoglobigerinoidea n. superfam., y una nueva familia: Parvularuglobigerinidae n. fam.

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Corresponding author:
Ignacio Arenillas
ias@unizar.es

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INTRODUCTION

In the last two decades, the systematics of planktic foraminifera have been subjected to continuous revisions. Multiple taxonomic studies are evidencing that their diversity is much greater than previously believed, and not only at the species level but also at generic and suprageneric levels (*e.g.*, Olsson *et al.*, 1999; Korchagin, 2003; Pearson *et al.*, 2006; Huber & Leckie, 2011; BouDagher-Fadel, 2012, 2015; Georgescu, 2013a, 2013b, 2015; Georgescu & Henderson, 2014; Georgescu *et al.*, 2014; Arenillas & Arz, 2017; Wade *et al.*, 2018). Planktic foraminifera have been traditionally classified according to the characteristics of their external calcareous test, both general morphology and microstructural features (Loeblich & Tappan, 1964, 1987; Hemleben *et al.*, 1989). However, a classification of planktic foraminifera exclusively based on morphologic characters may fail not only to determine their real diversity but also to know their origin and the true phylogenetic relationships between them. For example, after generating a pyrosequencing dataset of *ca.* 100,000 partial 18S rRNA foraminiferal sequences, Morard *et al.* (2018) recently discovered that, although their diversity is finite (probably a few hundred species of which just over 60 are known through morphological studies), a considerable part of current planktic foraminiferal species has its origin in unknown lineages. Nevertheless, deeper phylogenetic studies, both molecular in recent species (ribosomal DNA) and stratophenetic in fossil species (morphology-ontogeny and biostratigraphy), are allowing little by little to generate a more natural classification. The discovery of new phylogenetic lineages, which arose on many occasions through processes of iterative evolution, makes it necessary to carry out an exhaustive review of the suprageneric systematics of planktic foraminifera, even at the order level.

Planktic foraminifera have traditionally been clustered into the suborder Globigerinina Lankester, 1885 (see Loeblich & Tappan, 1964, 1987), which was elevated to order Globigerinida by Loeblich and Tappan (1992). However, the monophyletic character of the planktic foraminifera has gradually lost ground in the light of several molecular phylogenetic studies, which suggests several events of benthic-planktic transitions in their evolutionary history. For example, Darling *et al.* (1997, 2009), de Vargas *et al.* (1997) and Aurahs *et al.* (2009) provided new evidence after testing different hypotheses on the phylogenetic relationships of recent planktic foraminifera using ribosomal DNA sequences (**SSU-rDNA**). This implies that grouping all them in the order Globigerinida could be artificial. The molecular evidence is not yet conclusive, but high-resolution stratophenetic studies seem to corroborate the hypothesis that, except for the guembelitriids, the Cenozoic planktic foraminifera are unrelated with those of the Mesozoic (Arenillas & Arz, 2017). Similarly, BouDagher-Fadel (2012, 2015) proposed that the heterohelicids are not phylogenetically related with the order Globigerinida, and should be placed within the order Heterohelicida, which Fursenko (1958) defined to represent Cretaceous planktic foraminiferal taxa with serial arrangement (mainly biserial and multiserial, but also triserial).

In light of recent findings on polyphyletic origin of planktic foraminifera from benthic taxa, our objective is to update the classification of planktic foraminifera. For it, we propose a new order (Globotruncanida Arz, Arenillas & Gilabert n. ord.) that groups the spiral forms of the Mesozoic, which seem to have a monophyletic origin in the Middle Jurassic. In addition, we propose another new order (Guembelitriida Arenillas, Arz & Gilabert n. ord.), two new superfamilies (Parvularuglobigerinoidea Arenillas, Arz & Gilabert n. superfam., and Abathomphaloidea Arz, Arenillas & Gilabert n. superfam.) and one new family (Parvularuglobigerinidae Arenillas, Arz & Gilabert n. fam.), and review the suprageneric categories to better reflect the diversity and phylogeny of planktic foraminifera.

BACKGROUND ON PLANKTIC FORAMINIFERAL TAXONOMY AND PHYLOGENY

The suprageneric classification of planktic foraminifera at family and superfamily levels is based on significant characters such as the wall structure and surface or the mode of chamber addition (arrangement), although some also put emphasis upon the aperture position, the external apertural modifications or some significant test features, as the presence of tegilla, bullae, carinae or tubulospines (Loeblich & Tappan, 1987; BouDagher-Fadel, 2012, 2015). Many planktic foraminiferal families have been proposed depending on whether the wall surface is smooth, pitted, cancellate, reticulate (favusellid), spinose, hispid (finely pustulate), pustulate, muricate (densely pustulate), pore-mounded (papillate, papillose), rugose, costate or striate. Based mainly on these morphological criteria, Loeblich and Tappan (1987; see supplementary text S1) systematically described benthic and planktic foraminifera at generic and suprageneric levels. These authors drew on almost all previous studies on planktic foraminiferal taxonomy, such as Subbotina (1953, 1971), Loeblich (1957), Luterbacher (1964), Banner and Blow (1965), Loeblich and Tappan (1964), Postuma (1971), Jenkins (1971), Smith and Pessagno (1973), Stainforth *et al.* (1975), Berggren (1977), Robaszynski and Caron (1979), Blow (1979), Saito *et al.* (1981), Banner (1982), Korchagin (1982), Kennett and Srinivasan (1983), and Robaszynski *et al.* (1984).

Around the same time that Loeblich and Tappan (1987) finished their foraminiferal compilation, Bolli *et al.* (1985) edited an extensive review of planktic foraminiferal taxonomy in various chapters, highlighting Caron (1985) for Cretaceous, Toumarkine and Luterbacher (1985) for Paleocene and Eocene, and Bolli and Saunders (1985) for Oligocene to Holocene. During the four decades following the publication of these magnificent taxonomic monographs, the planktic foraminiferal systematics has been revised and updated, at least at genus and species levels. Among the most relevant, we could highlight the following: Banner and Desai (1988), Nederbragt (1991), Berggren and Norris (1997), BouDagher-Fadel *et al.* (1997), Olsson *et al.* (1999), Moullade *et al.* (2002), Korchagin (2003), Pearson *et al.* (2006, with 16 chapters), Huber and Leckie (2011), Arenillas and Arz (2017) and Wade *et al.* (2018, with 20 chapters), as well as the numerous works led by M. D. Georgescu (see citations throughout the text).

The most active planktic foraminiferal taxonomists are currently BouDagher-Fadel (2012, 2015) and authors of pforams@mikrotax website (Young *et al.*, 2017). They have reported the most recent compilations of described planktic foraminiferal species. The spiral planktic foraminiferal systematic of BouDagher-Fadel (2012, 2015) is based mainly on previous phylogenetic proposals by Banner and Blow (1965), Blow (1979), Banner (1982), Banner and Desai (1988) and BouDagher-Fadel *et al.* (1997), which are updated in light of more recent studies. The planktic foraminiferal systematics of the pforams@mikrotax website (Young *et al.*, 2017) is based on the work and publications of various planktic foraminiferal taxonomic working groups (*e.g.*, Kennet & Srinivasan, 1983; Olsson *et al.*, 1999; Pearson *et al.*, 2006; Georgescu & Huber, 2009; Huber & Leckie, 2011; Aze *et al.*, 2011; Wade *et al.*, 2018).

The planktic foraminiferal phylogeny (Figs. 1–3) and classification postulated here is based mainly on those of BouDagher-Fadel (2012, 2015) and pforams@mikrotax website (Young *et al.*, 2017), with the incorporation of the new suprageneric taxa defined here and some old and recent taxa and phylogenetic proposals from other authors (Blow, 1979; Kennett & Srinivasan, 1983; Loeblich & Tappan, 1987; Nederbragt, 1991; Korchagin, 2003; Georgescu, 2009a, 2013a, 2013b, 2013c, 2015; Georgescu & Huber, 2009; Huber & Leckie, 2011; Georgescu *et al.*, 2011; Georgescu & Henderson, 2014). As the objective of this paper is not an exhaustive taxonomic study at the genus level, we have preserved a large part of the genera considered by all these taxonomists.

Some phylogenetic and taxonomic proposals illustrated in the Figures 1–3 are controversial. A summary of the main controversies is provided in the supplementary information. Among the globotruncanids, there are controversies regarding to the identification of the first appearance of truly planktic foraminifera, and to the number of genera and lineages of hedbergellids, rugoglobigerinids, globotruncanids, rotaliporids, globigerinelloids and planomalinoids (see supplementary text S2). Among the heterohelicids, controversies about the origin and evolution of the multiserial heterohelicids, spiroplectids and other heterohelicid lineages stand out (see supplementary text S3). Among the guembilitriids, the taxonomic positions of genera *Cassigerinella* Pokorný, 1955, and *Jenkinsina* Haynes, 1981, are the most problematic (see supplementary text S4). Taxonomic and phylogenetic controversies between globigerinids are more numerous (see supplementary text S5), highlighting the type of wall surface/texture of parvularuglobigerinoids, the validity of the families Globigerapsidae Blow, 1979, and Planorotalitidae BouDagher-Fadel, 2012, the taxonomic position of globanomalinoids, and the number of genera and lineages between globorotaloids and globigerinoids.

An example of controversy is the numerous evolutionary lineages of heterohelicids suggested by Georgescu (2013a, 2013b), Georgescu *et al.* (2013) and Georgescu and Henderson (2014), who have conducted the most extensive review of heterohelicids carried out to date. Some of these heterohelicid lineages contradict the traditional phylogenetic proposals of Nederbragt (1991). Nevertheless, their phylogenetic analyses demonstrate that the evolution of planktic foraminifera is much more complex than previously thought, with many examples of convergent, parallel and iterative evolution that cannot be unravelled without high-resolution stratophenetic studies.

POLYPHYLETIC ORIGIN OF THE PLANKTIC FORAMINIFERA

Evidence of a benthic origin for globotruncanids

The first benthic-planktic transition in the evolutionary history of foraminifera remains controversial. Many Triassic and Early Jurassic taxa have been suggested as planktic (Fuchs, 1967, 1973, 1975; see supplementary text S2), but later had to be reinterpreted as benthic (BouDagher-Fadel, 2012, 2015). According to most specialists (*e.g.*, Tappan & Loeblich, 1988; Wernli, 1988, 1995; Hart *et al.*, 2002, 2003; Wernli & Görög, 2007), the first planktic foraminiferal genus was *Conoglobigerina* Morozova, 1961, in Morozova and Moskalenko (1961), or alternatively *Globuligerina* Bignot & Guyader, 1971. The *Conoglobigerina*-*Globuligerina* group seems to have derived in the Middle Jurassic from the family Oberhauserellidae Fuchs, 1970 (Fig. 1), which includes benthic foraminifera with aragonitic tests (order Robertinida Mikhalevich, 1980). Gorbachik and Kuznetsova (1986) and BouDagher-Fadel *et al.* (1997) found evidence that the globuligerinids, as the oberhauserellids, have aragonitic tests. Furthermore, they suggested that, although most likely calcitic, the tests of conoglobigerinids could also be aragonitic, because the secondary nature of the calcite of their tests cannot be ruled out. The oberhauserellid genera *Praegubkinella* Fuchs, 1967, which is a descendent of *Oberhauserella* Fuchs, 1967, have been proposed as the direct ancestor of *Conoglobigerina* (Fuchs, 1975; Wernli, 1988, 1995; BouDagher-Fadel *et al.*, 1997). Nevertheless, von Hillebrandt (2012) and Clemence and von Hillebrandt (2013) have questioned the agaragonitic nature of *Conoglobigerina* and *Globuligerina*, so doubts persist as to which was the true benthic ancestor of the first planktic foraminifera.

Evidence of a benthic origin for heterohelicids

The phylogenetic origin of heterohelicids has traditionally been sought among conoglobigerinids. Fuchs (1975) proposed to the conoglobigerinid *Eoheterohelix* Fuchs, 1973, as their most direct ancestor, which descended from *Conoglobigerina* through *Woletzina* Fuchs, 1973. However, Loeblich and Tappan (1987) and BouDagher-Fadel (2012, 2015) warned that the Fuchs's material consists mainly of poorly preserved specimens, and probably belonged to recrystallized benthic specimens of the family Oberhauserellidae. On the other hand, Georgescu (2009a) ruled out the other two possible alternatives for a planktic origin of the heterohelicids: 1) heterohelicids come from a contemporary (Albian) genus, either trochospiral (*e.g.*, *Hedbergella* Brönnimann & Brown, 1958, or *Ticinella* Reichel, 1950) or planispiral (*e.g.*, *Globigerinelloides* Cushman

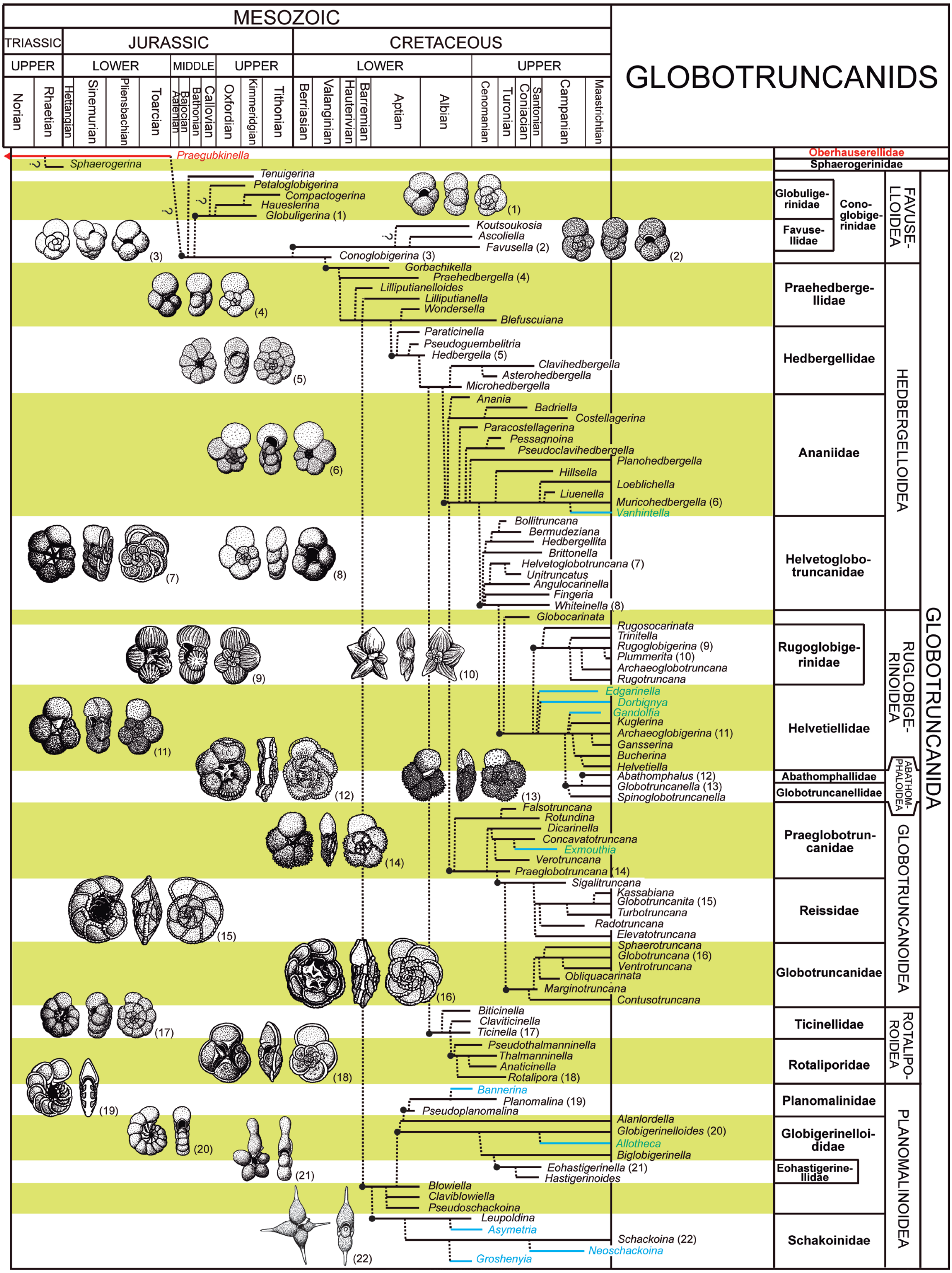

Figure 1. Benthic origin and evolutionary tree at the genus level of the order Globotruncanida n. ord. The phylogenetic relationships are based mainly on Caron (1985), Korchagin (2003), Huber and Leckie (2011), and BouDagher-Fadel (2012, 2015). In red, bio-chronostratigraphic ranges of benthic foraminiferal taxa. In blue, bio-chronostratigraphic ranges of evolutionary lineages proposed by Georgescu (see citations throughout the text, and supplementary text S2). Genus drawings are modified from or inspired by those of Banner (1982). Each node (black circle) represents the last common ancestor of each suggested phylogenetic group or suprageneric taxa.

& ten Dam, 1948); and 2) heterohelicids come from a species of *Archaeoguembelitria* Georgescu, 2009a. The first hypothesis was rejected because the earliest heterohelicids lack an early trochospiral or planispiral stage. The second hypothesis was disproved due to the relatively narrow variability of the *Archaeoguembelitria* species, which presents only triserial tests without any trend to develop biserial chamber arrangement. Consequently, Georgescu (2009a) concluded that the most likely alternative is a benthic origin.

The earliest heterohelicid, *Protoheterohelix* Georgescu & Huber, 2009, may have derived from the benthic genus *Praeplanctonia* Georgescu, 2009a, a direct descendent of the buliminid genus *Pleurostomella* Reuss, 1860 (Fig. 2). According to Georgescu (2009a) and Georgescu and Huber (2009), the microperforate smooth wall, the asymmetry of its test and the periapertural structures of *Protoheterohelix* are a vestige of its benthic ancestor, *i.e.*, *Praeplanctonia*. *Protoheterohelix* gave rise to several lineages and, later, these to the rest of heterohelicid members. BouDagher-Fadel (2012, 2015) instead suggested the buliminid genus *Brizalina* Costa, 1856, as ancestor of heterohelicids, adducing that it evolved in the late Albian changing their mode of life from being infaunal benthic dwellers of continental shelves to being planktic inhabitants of the surface waters of the open ocean.

Evidence of a benthic origin for guembelitriids

It is well known that *Guembelitria* Cushman, 1933, was probably the sole survivor of the Cretaceous–Paleogene boundary (**KPB**) mass extinction (Smit, 1982; Arenillas & Arz, 2017), but its origin is uncertain. Fuchs (1975) proposed *Conoglobigerina* as the ancestor of guembelitriids. However, since *Guembelitria* did not appear until the Santonian (or until Cenomanian in the case that the species of *Archaeoguembelitria* were considered guembelitriids), this group of triserial planktic foraminifera cannot belong to the same phylogenetic group as *Conoglobigerina*, which became extinct at the Valanginian (Figs. 1–2). Again, the most plausible alternative is a benthic origin. Georgescu (2009a), Georgescu *et al.* (2011) and BouDagher-Fadel (2012, 2015) suggested *Praebulimina* Hofker, 1953, *Pyramidina* Brotzen, 1948, or most likely *Neobulimina* Cushman & Wickenden, 1928, which belong to the family Turrilinidae Cushman, 1927, as possible benthic ancestors of the guembelitriids (Fig. 2).

There is stronger evidence that the guembelitriids are the ancestor of two incoming Danian lineages (Olsson *et al.*, 1999; BouDagher-Fadel, 2012, 2015): the biserial chiloguembelinids, whose main member is *Chiloguembelina* Loeblich & Tappan, 1956, and trochospiral globoconusids, whose main member is *Globoconusa* Khalilov, 1956 (Figs. 2–4). The early Danian genus *Chiloguembelitria* Hofker, 1978, played an important evolutionary role because it is the common ancestor of chiloguembelinids and globoconusids (Arenillas *et al.*, 2017). The first representative of the chiloguembelinids was the genus *Woodringina* Loeblich & Tappan, 1957, which exhibits a mixed triserial-biserial test, and that of the globoconusids was the genus *Trochoguembelitria* Arenillas, Arz & Náñez, 2012, which exhibits a mixed triserial-trochospiral test, at least in its early forms (see Arenillas *et al.*, 2012, 2016, 2017). We should note that the *Trochoguembelitria* species were attributed to *Parvularugoglobigerina* Hofker, 1978, by Olsson *et al.* (1999; see discussion above), or to *Postrugoglobigerina* Salaj, 1986, by Loeblich and Tappan (1987) and BouDagher-Fadel (2012, 2015; see supplementary text S5).

Evidence of a benthic origin for globigerinids

The evolutionary origin of cenozoic globigerinids is controversial because both benthic and planktic ancestors have been proposed (see discussion in Arenillas & Arz, 2017). Most experts take for granted that they descended from muricate hedbergellids (*Muricohedbergella* Huber & Leckie, 2011), which includes generalist species that, according to them, survived the KPB catastrophic mass extinction event. Both BouDagher-Fadel (2012, 2015) and authors of pforams@mikrotax website (Young *et al.*, 2017), the latter based on phylogenies of Olsson *et al.* (1999) and Aze *et al.* (2011), take for granted that the globigerinids evolved from muricate hedbergellids, and therefore keep the globotruncanids within the order Globigerinida. By contrast, Brinkhuis and Zachariasse (1988) and Arenillas and Arz (2017) postulated that the first cenozoic globigerinids evolved in the earliest Danian from the buliminid genus *Caucasina* Khalilov, 1951 (Figs. 3–4). They noted that muricate hedbergellids remained morphologically and texturally well separated from the earliest Cenozoic species. The latter were tiny globigeriniform species of microperforate, smooth wall (later called parvularugoglobigerinids), which rapidly evolved after the KPB extinction (Luterbacher & Premoli-Silva, 1964; Smit, 1982; Brinkhuis & Zachariasse, 1988; Arenillas & Arz, 2000). The first member of the parvularugoglobigerinids was *Pseudocaucasina* Arenillas & Arz, 2016 in Arenillas and Arz (2017), which is morphologically very similar to some Jurassic species of *Conoglobigerina*.

Muricohedbergella is commonly considered the ancestor of two lineages that appeared in the early Danian: globanomalinids and eoglobigerinids (*e.g.*, Berggren, 1962; Bandy, 1967; Olsson, 1970; Fordham, 1986; Olsson *et al.*, 1992, 1999; Liu & Olsson, 1994; Berggren & Norris, 1997; Apellániz *et al.*, 2002; Aze *et al.*, 2011; BouDagher-Fadel, 2012, 2015; Koutsoukos, 2014). However, after ascertaining that their stratigraphic ranges do not overlap in the lower Danian, Arenillas and Arz (2000) disproved *Muricohedbergella* as the ancestor of both lineages. In addition, Arenillas *et al.* (2018) raised doubts that *Muricohedbergella* was a real survivor of the KPB extinction event. According

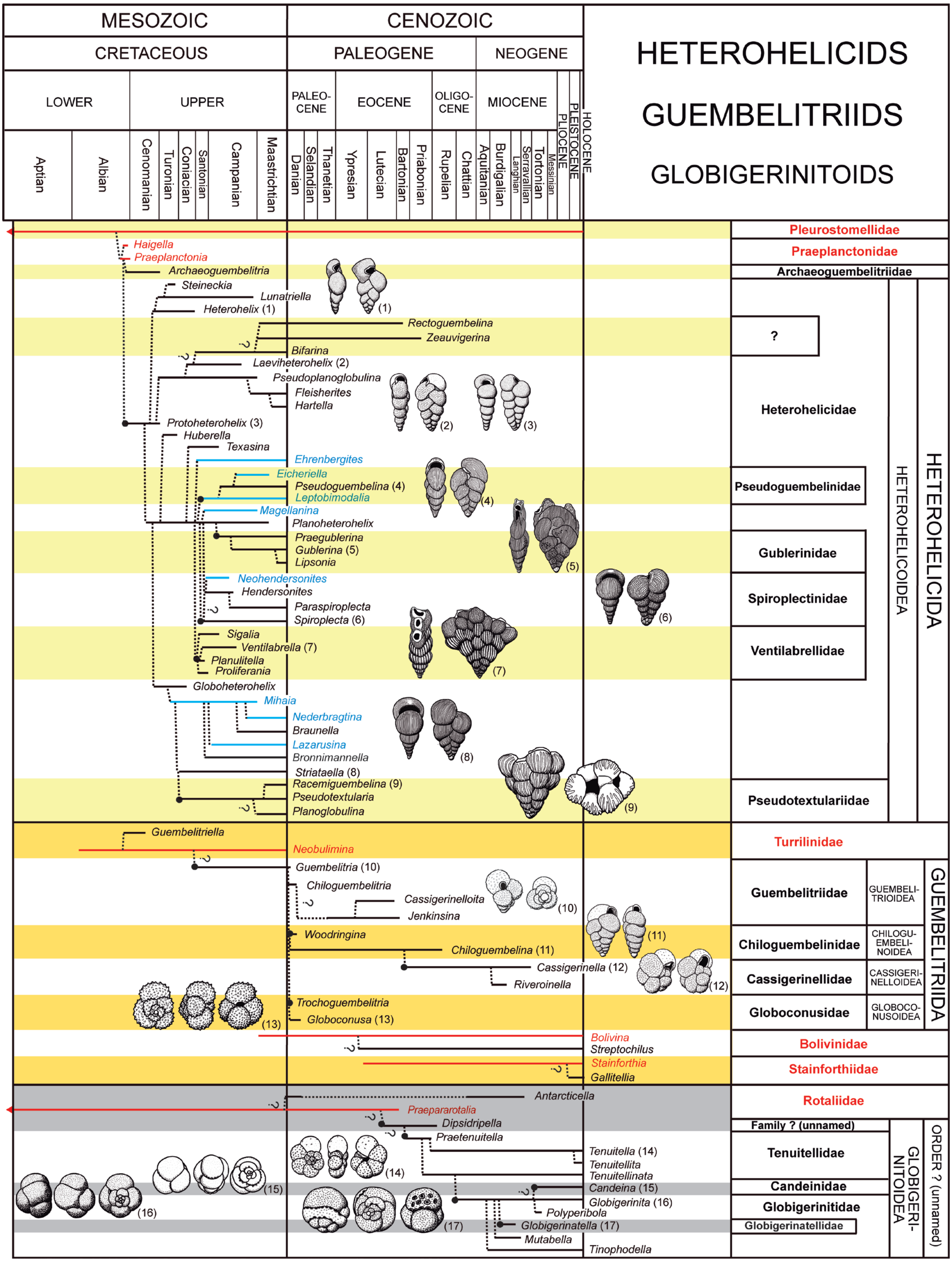

Figure 2. Benthic origin and evolutionary tree at the genus level of the orders Heterohelicida and Guembelitriida n. ord. The phylogenetic relationships are based mainly on Nederbragt (1991), Georgescu and Huber (2009), Georgescu *et al.* (2011), BouDagher-Fadel (2012, 2015), Georgescu (2013a, 2013b), and Arenillas *et al.* (2012, 2016, 2018). In red, bio-chronostratigraphic ranges of benthic foraminiferal taxa. In blue, bio-chronostratigraphic ranges of evolutionary lineages proposed by Georgescu (see citations throughout the text, and supplementary text S3). Genus drawings are inspired by those of Banner (1982). Each node (black circle) represents the last common ancestor of each suggested phylogenetic group or suprageneric taxa.

to Arenillas *et al.* (2018), the most plausible alternative is a benthic origin for the parvularugoglobigerinids, which would be more consistent with the molecular phylogenetic studies suggesting the order Globigerinida could have originated after the KPB (*e.g.*, Aurahs *et al.*, 2009).

Huber *et al.* (2020) have recently rejected this hypothesis, under the assumption that, unlike *Caucasina*, *Parvularugoglobigerina* exhibits pore-mounded wall (see supplementary text S5), as claimed by Liu and Olsson (1992) and Olsson *et al.* (1992, 1999). However, Arenillas and Arz (2000) could not confirm this surmise after reviewing the holotypes of the main parvularugoglobigerinid species defined by Luterbacher and Premoli-Silva (1964) at Gubbio (Italy), as well as the type sample of the *Parvularugoglobigerina eugubina* Zone at Ceselli (Italy), which is characterized by this assemblage of tiny globigerinids. Conversely, several high-resolution stratophenetic studies verify that parvularugoglobigirenids exhibits smooth wall texture in well-preserved specimens (Fig. 4) from the most complete and continuous lower Danian sections worldwide (*e.g.*, Smit, 1982; Brinkhuis & Zachariasse, 1988; Li & Radford, 1991; Li *et al.*, 1995; Arenillas & Arz, 2000, 2017). The assumption of Huber *et al.* (2020) lies probably in attributing to *Parvularugoglobigerina* the diagnostic characters of the more modern and larger globoconusid genus *Trochoguembelitria*, whose first appearance occurred almost at the same time as eoglobigerinids and globanomalinids (Fig. 4), acquiring gross morphologies very similar to real parvularugoglobigerinids (Arenillas *et al.*, 2016).

The enigmatic origin of the globigerinitoids

Candeinids, globigerinitids, globigerinatellids and tenuitellids appear to form a phylogenetic unit of enigmatic origin, which have been grouped in the superfamily Globigerinitoidea BouDagher-Fadel, 2012. The phylogenetic relationships between them still remain ambiguous. There is both stratophenetic and molecular evidence (Blow, 1979; Ujiié & Lipps, 2009) of a close relationship between *Candeina* d'Orbigny, 1839, and *Globigerinita* Brönnimann, 1951. The tenuitellids also appear to be closely related to globigerinitids, but there is no genetic evidence yet. Blow (1979), Kennett and Srinivasan (1983) and Li (1986), among others, suggested that the extinct genus *Globigerinatella* Cushman & Stainforth, 1945, and consequently the globigerinatellids, are also closely related to globigerinitids and candeinids. All of them may belong to the same phylogenetic group originated from the benthic ancestor conjectured by Ujiié *et al.* (2008) for the candeinids (see discussion below).

Pearson *et al.* (2018) have recently suggested that the microperforate, trochospiral genus *Dipsidripella* Brotea, 1995 (see supplementary text S6), was the first globigerinitoid to evolve (in the middle Eocene), giving rise to tenuitellids and, later, the latter to the rest of globigerinitoid members. Although initially considered uncertain (Huber *et al.*, 2006), the evolutionary origin of *Dipsidripella* may be related to the rotaliid genus *Praepararotalia* Liu, Olsson & Huber, 1998. Since a benthic ancestor has been proposed as the origin of this group (de Vargas *et al.*, 1997; Ujiié *et al.*, 2008; Ujiié & Lipps, 2009; Pearson *et al.*, 2018), and thus disconnecting them from the other planktic foraminiferal lineages, a new order should be erected to separate them from the order Globigerinida (Fig. 2). However, until their phylogenetic relationships are clarified, it is advisable for now not to define it. If it is confirmed that they form an independent phylogenetic group of planktic foraminifera, the simplest solution would be to elevate the superfamily Globigerinitoidea to order Globigerinitida.

Do candeinids and globorotaloids have independent benthic origins?

Testing different hypotheses on the phylogenetic relationships between and within the major groups of current planktic foraminifera using SSU-rDNA sequences, de Vargas *et al.* (1997) concluded that there have been at least three independent events of benthic-planktic transition in the history of modern planktic foraminiferal families: Globigerinidae (and Hastigerinidae Bolli, Loeblich & Tappan, 1957), Globorotaliidae Cushman, 1927, and Candeinidae Cushman, 1927. After new SSU-rDNA molecular studies, Aurahs *et al.* (2009) reached very similar conclusions, evidencing the phylogenetic relationships of the cenozoic planktic foraminifera remained ambiguous. Morphologically, these families are differentiated by the wall structure and surface (Saito *et al.*, 1981; Kennett & Srinivasan, 1983; Hemleben *et al.*, 1989). The genera of the first two families are usually characterized by having more globular tests and a spinose wall, either cancellate (Globigerinidae) or pitted (Hastigerinidae). The Globorotaliidae genera are usually characterized by having more flattened tests and a nonspinose, pitted to smooth wall. Finally, the Candeinidae genera exhibit tiny tests and microperforate, smooth wall. According to de Vargas *et al.* (1997) and Aurahs *et al.* (2009), Globigerinidae could originate after the KPB mass extinction, and the other two after the minor extinction event of the Eocene–Oligocene transition (**EOT**).

De Vargas *et al.* (1997) indicated that the assumption of the divergence of globorotaliids and candeinids in the Neogene from globigerinoid ancestors was not supported by molecular phylogeny. They suggested that the candeinids, which appeared in the fossil record during the EOT crisis, exhibit closer molecular relationships with benthic rotaliids and/or textulariids than with globigerinids. The relationships between globorotaliids and rotaliids-textulariids also are strongly suggested by ribosomal DNA sequence similarities. In

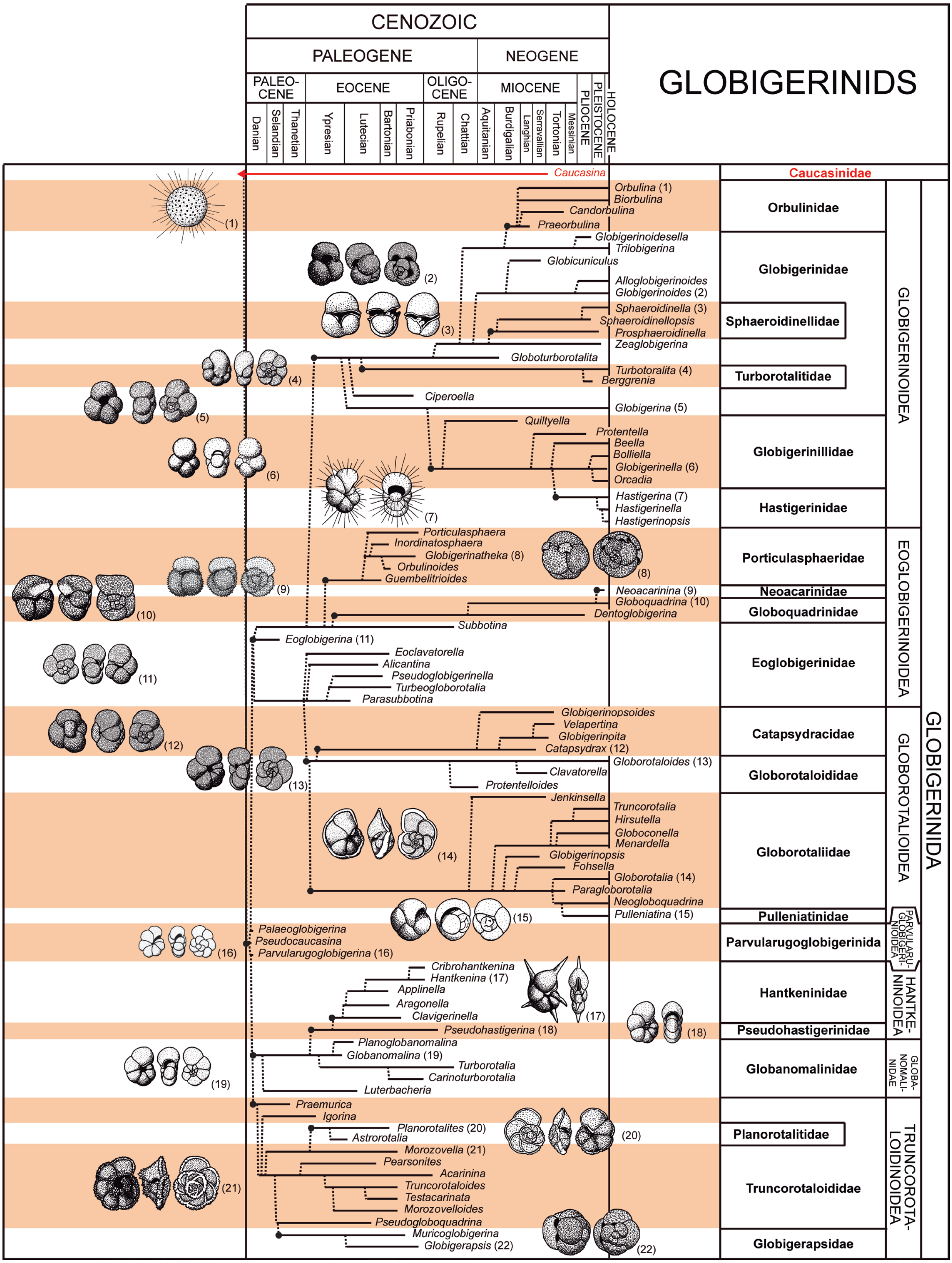

Figure 3. Benthic origin and evolutionary tree at the genus level of the order Globigerinida. The phylogenetic relationships are based mainly on Olsson *et al.* (1999), Pearson *et al.* (2006), Aze *et al.* (2011), BouDagher-Fadel (2012, 2015), Arenillas and Arz (2017), Wade *et al.* (2018) and Arenillas *et al.* (2018). In red, bio-chronostratigraphic ranges of benthic foraminiferal taxa. Genus drawings are modified from or inspired by those of Banner (1982). Each node (black circle) represents the last common ancestor of each suggested phylogenetic group or suprageneric taxa.

addition, it has even been observed that globorotaliids show benthic behaviour in culture (Hemleben *et al.*, 1989).

There is evidence that Candeinidae, as belonging to globigerinitids (see discussion above, and Fig. 2), could evolved from a benthic taxon after the EOT crisis (Pearson *et al.*, 2018). On the contrary, it seems to be well established by stratophenetic evidence that globorotaloids evolved from a planktic ancestor in lower Eocene, being its first members *Globorotaloides* Bolli, 1957, and *Paragloborotalia* Cifelli, 1982 (Olsson *et al.*, 2006a, 2006b; Aze *et al.*, 2011). If the stratophenetic data are correct (Aze *et al.*, 2011), globigerinoids and globorotaloids evolved from eoglobigerinoids, the first from *Subbotina* Brotzen & Pożaryska, 1961, and the second from *Parasubbotina* Olsson, Hemleben, Berggren & Liu, 1992 (Fig. 3). The common ancestor of these two genera was *Eoglobigerina* Morozova, 1959, and their divergence occurred shortly after the KPB mass extinction event (Arenillas & Arz, 2013a, 2013b). This account for the apparent phylogenetic disconnection between both groups (globigerinoids and globorotaloids) according to the SSU-rDNA molecular studies. In any case, if an independent benthic origin for globorotaloids is demonstrated, the superfamily Globorotalioidea Cushman, 1927, would have to be elevated to the order category.

MORE EXAMPLES OF MULTIPLE INVASIONS OF BENTHIC FORAMINIFERA TO THE PELAGIC DOMAIN

Leckie (2009) noted that the ancestry of a number of planktic foraminiferal lineages remains a mystery. The iterative origin of planktic taxa with a microperforate wall, either smooth, pore-mounded or finely pustulate (hispid), during the Mesozoic and Cenozoic is poorly known: *Sphaerogerina* Korchagin & Kuznetsova, 2003, in the Rhaetian (Late Triassic), *Conoglobigerina* in the Bajocian (Middle Jurassic), *Archaeoguembelitria* and *Protoheterohelix* in latest Albian, *Guembelitria* and *Bifarina* Parker & Jones, 1872, in the Santonian, *Zeauvigerina* Finlay, 1939, and *Rectoguembelina* Cushman, 1932, in the Maastrichtian, *Pseudocaucasina* in the earliest Danian, *Cassigerinella* in the Bartonian, *Dipsidripella* in the Lutecian, *Tenuitella* Fleisher, 1974, in the Rupelian, *Antarcticella* Loeblich & Tappan, 1987, in the Chattian (or in the earliest Danian according to Liu *et al.*, 1998), *Candeina* in the Tortonian, and *Gallitellia* Loeblich & Tappan, 1986, in the Pleistocene. All may have had benthic ancestors and being the result of multiple invasions of benthic foraminifera to the pelagic domain.

Benthic origins of other globotruncanid-type taxa

Korchagin *et al.* (2003) described a globigeriniform planktic genus in the Triassic: *Sphaerogerina*, which first appeared in the Rhaetian, and did not survive the End-Triassic mass extinction event. They phylogenetically related *Sphaerogerina* to favuselloids, specifically to a *Globuligerina* species that according to them lived in the Rhaetian. However, BouDagher-Fadel (2012, 2015) warned that this species is probably an agglutinated benthic foraminifer. In addition, since *Sphaerogerina* went extinct at the end of the Triassic, they cannot belong to the same phylogenetic group as the true favuselloids, which did not appear until the Middle Jurassic. On phylogenetic grounds, BouDagher-Fadel (2012) placed *Sphaerogerina* in a new family: Sphaerogerinidae. BouDagher-Fadel (2012, 2015) suggested that, like *Conoglobigerina*, *Sphaerogerina* emerged from oberhauserellids in an independent benthic-planktic transition (Fig. 1).

Benthic origins of other heterohelicid-type taxa

Some cretaceous heterohelicid-type genera are also considered descendants of benthic ancestors. The most notable are the biserial genera, with a tendency to become uniserial, such as *Bifarina*, *Zeauvigerina*, and *Rectoguembelina*. They have been related to heterohelicids (Fig. 2), as descendants of *Heterohelix* Ehrenberg, 1843, or more likely of *Laeviheterohelix* Nederbragt, 1991 (see, for example, Huber & Boersma, 1994; Olsson *et al.*, 1999; Huber *et al.*, 2006; BouDagher-Fadel, 2012, 2015). Stable isotopic evidence that some of their species are planktic have been reported by Huber and Boersma (1994) and D'Haenens *et al.* (2012). However, there are still doubts that all their species have a planktic mode of life. Loeblich and Tappan (1987) included *Zeauvigerina* in the buliminid family Loxostomatidae Loeblich & Tappan, 1962. Olsson and Leckie (1994) considered *Bifarina* as a benthic foraminifer inhabiting of inner and middle sublittoral environments in epicontinental seas. *Rectoguembelina*, which was synonymized with *Bifarina* and *Tubitextularia* Šulc, 1929, by Loeblich and Tappan (1964, 1987), was originally considered benthic (see Stainforth *et al.*, 1975). There is also the possibility that at any stage of their life and under stressful conditions they swapped their mode of life from benthic to planktic or *vice versa* (BouDagher-Fadel, 2012, 2015).

Benthic origins of other guembelitriid-type taxa

Examples of guembelitriid-type genera with an independent benthic origin are *Archaeoguembelitria*, *Streptochilus* Brönnimann & Resig, 1971, and current *Gallitellia* (Fig. 2). Georgescu (2009a) erected the genus *Archaeoguembelitria* to include the latest Albian–earliest Turonian triserial planktic foraminifera, regarded as phylogenetically unrelated to the Late Cretaceous genus *Guembelitria*. *Archaeoguembelitria* included both benthic and planktic species, and may have derived from another, different ancestral benthic lineage (Georgescu, 2009a): the buliminid *Praeplanctonia*,

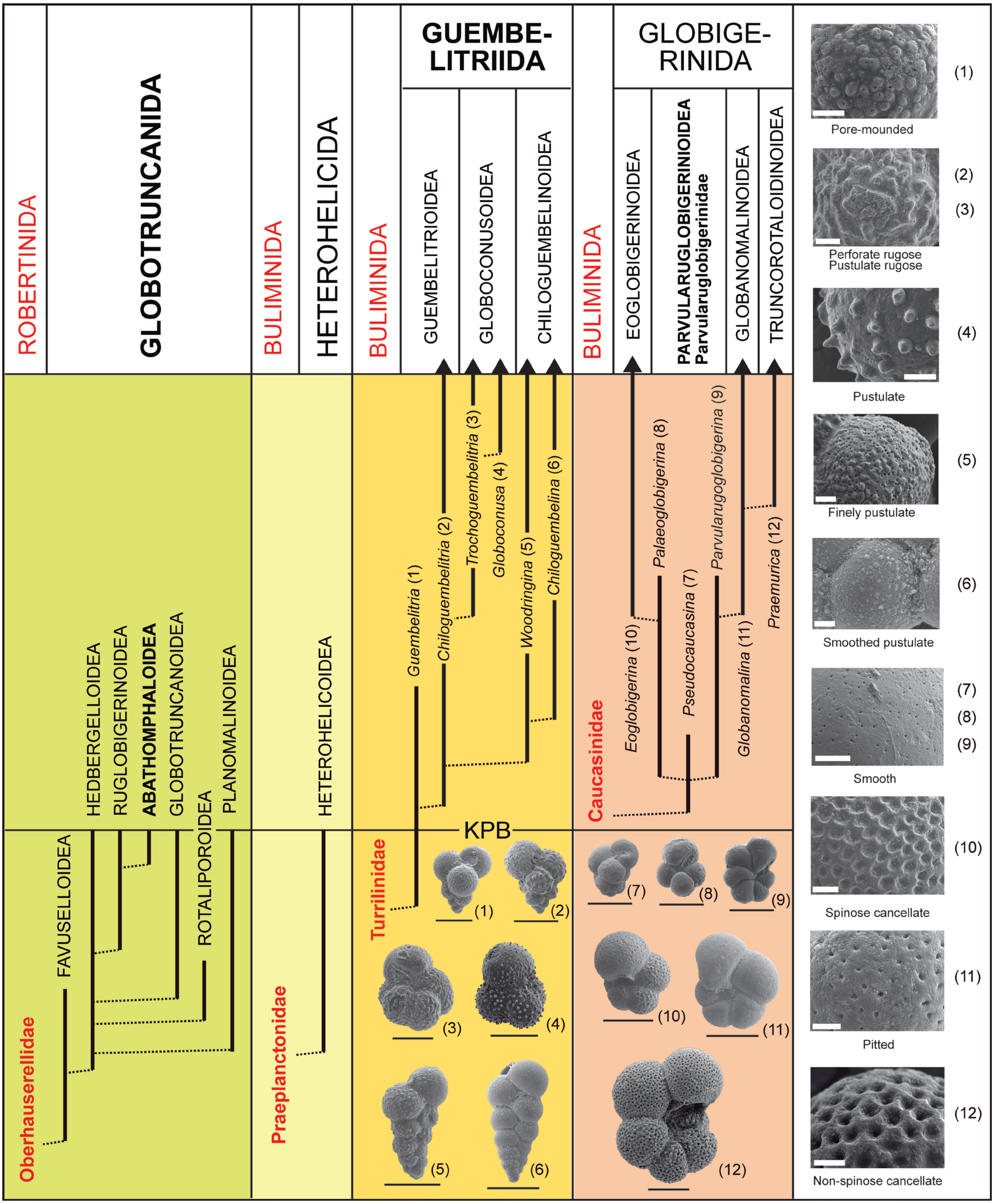

Figure 4. Benthic origins and evolutionary trees of the orders Globotruncanida, Heterohelicida, Guembelitriida and Globigerinida, based on the most up-to-date phylogenetic proposals (see discussion in main text and supplementary information), the first two at the superfamily level, and the last two at the genus level and only for the early Danian. This figure includes wall textures/surfaces of early Danian genera of Guembelitriida and Globigerinida. Note that the wall surface of parvularuglobigerinids is smooth, and microperforate to finely perforate. Note also that the wall surface of *Trochoguembelitria* is microperforate, pore-mounded to rugose (see discussion in main text and supplementary information). Defined taxa are in bold font; scale bar = 100 μm; scale bar of wall details = 5 μm.

which is also the ancestor suggested for the first heterohelicid genus (*Protoheterohelix*). The typical pore-mounded wall of triserial planktic foraminifera, such as *Guembelitria* and *Archaeoguembelitria*, could be an adaptation that improved the ability to float (Dubicka & Wierzbowski, 2019).

The biserial genus *Streptochilus* was originally considered a descendant of *Chiloguembelina* (see, for example, Stainforth *et al*., 1975; Kennett & Srinivasan, 1983; Huber *et al*., 2006). However, Darling *et al.* (2009) demonstrated that the extant planktic *Streptochilus globigerus* (Schwager, 1866) and the benthic *Bolivina variabilis* (Williamson, 1858) are the same biological species. Therefore, *Streptochilus* seems to include ecologically flexible species actively grow within the open-ocean waters, occupying both pelagic and benthic domains (Smart & Thomas, 2018). When they are planktic, they inhabit surface and thermocline of the open ocean and, when they are benthic, they live as shallow to intermediate infaunal dwellers. Smart and Thomas (2007) even suggested that the *Streptochilus* species may have evolved polyphyletically.

Based on molecular evidence, Ujiié *et al.* (2008) indicated that the modern triserial genus *Gallitellia*, of microperforate, smooth wall, may have evolved in the Miocene from the buliminid genera *Stainforthia* Hofker, 1956, or alternatively *Virgulinella* Cushman, 1932. They also noted that the sporadic occurrence of triserial planktic foraminifera in the fossil record may reflect multiple transitions from a benthic to a planktic mode of life.

Benthic origins of other globigerinid-type taxa

A globigerinid-type taxon of uncertain origin is *Antarcticella*, which was endemic to high southern latitudes (Loeblich & Tappan, 1987; BouDagher-Fadel, 2012, 2015). This genus inhabited shallower environments of marginal basins, and probably includes both benthic and planktic species (Liu *et al*., 1998; Malumián & Náñez, 2011; Huber *et al*., 2020). It was initially considered late Oligocene–middle Miocene in age and included among the globigerinitids (Loeblich & Tappan, 1987). However, Liu *et al.* (1998) claimed that *Antarcticella* originated immediately after the KPB mass extinction event, evolving from the rotaliid *Praepararotalia* (Fig. 2). As previously suggested by Leckie and Webb (1985), Liu *et al.* (1998) surmised that *Antarcticella* was the direct ancestor of *Candeina*. However, the hypothesis that suggests *Dipsidripella* as the ancestor of the globigerinitoids, to which the candeinids belongs, is gaining more acceptance among taxonomists (Pearson *et al*., 2018). Therefore, *Antarcticella* seems to belong to another different lineage descended from benthic foraminifera.

UNDERLYING CAUSES OF THE JUMP FROM BENTHOS TO PLANKTON IN FORAMINIFERA

Taxonomists have postulated benthic ancestry hypotheses for all planktic foraminiferal taxa and lineages described above, but the causes that have induced the jump from benthic to planktic mode of life are still unclear. A first clue can be found in the habitat and ecological niche that they or their benthic ancestors occupied, including their depth habitat, ecological strategy (specialists, generalists, opportunists), and mode of life (holobenthic, meroplanktic, tychoplanktic or holoplanktic). Other clues may emerge after checking whether or not their first appearances coincide with environmental crises or ecological stress events. Additionally, identifying the taxonomic group to which their benthic ancestor belongs can also help to understand why the jump from benthos to plankton occurred.

Dwellers of near-surface ocean waters

Many of the taxa more closely related to their benthic ancestors inhabited exclusively neritic environments of epicontinental seas. Others became also successful in the oceanic realm, mainly in continental margins. The neritic environment, probably close to continental margins, was the preferred habitat for the first Jurassic favuselloids, *i.e.*, *Conoglobigerina* and *Globuligerina* (Gordon, 1970; Hart *et al*., 2002, 2003; Hudson *et al*., 2009; Gradstein *et al*., 2017; Kendall *et al*., 2020; Gajewska *et al*., 2021). *Protoheterohelix* and its closest descendants (*e.g.*, *Planoheterohelix* Georgescu & Huber, 2009) were inferred to be upper mixed layer dwellers (Nederbragt, 1991; Nederbragt *et al*., 1998). *Guembelitria* lived mainly on shelf areas (Smith & Pessagno, 1973; Leckie, 1987) but they were also abundant in paleo-upwelling areas of the continental margins (Kroon & Nederbragt, 1990). Biogeographic and oxygen isotopic data suggest that *Guembelitria* inhabited a near-surface planktic niche (Boersma *et al*., 1979; Boersma, 1984; D'Hondt & Zachos, 1993; Olsson *et al*., 1999). Similar niche and habitat are occupied by the current *Gallitellia*, which lives mainly over shelf areas, in semi-enclosed basins, and in upwelling areas, being rare in the open ocean (Kroon & Nederbragt, 1990). Regarding *Pseudocaucasina* and the rest of the smooth-walled parvularugoglobigerinids, there are no stable isotope evidence available on their habitat. Nevertheless, paleobiogeographic data indicate that they inhabited in the open ocean, occupying the surface waters of external neritic and oceanic environments (Arenillas & Arz, 2017).

Other examples include *Antarcticella*, which inhabited shallow environments of marginal basins (Liu *et al.,* 1998; Malumián & Náñez, 2011; Huber *et al*., 2020), *Bifarina* and *Zeauvigerina*, which preferably inhabited inner and middle neritic environments with a restricted geographic distribution (Leckie, 2009), and *Rectoguembelina*, which seems to have also inhabited upper surface waters in open sea (Huber & Boersma, 1994). Doubts persist as to whether all species of *Bifarina* and *Zeauvigerina* are planktic (see Huber *et al.*, 2006). For example, *Bifarina* has been reported occurring in nearshore sediments (Olsson & Leckie, 1994). Something similar happens with *Dipsidripella* because there are doubts as to whether it was benthic for part of its life cycle or it was planktic occupying a much deeper habitat than co-occurring planktic foraminifera (Huber *et al.*, 2006). Current *Streptochilus* and *Tenuitella* are, on the contrary, from deeper habitat, the former inhabiting the thermocline (Resig & Kroopnick, 1983), and the latter preferably living within the oxygen minimum zone (Huber *et al.*, 2006; Pearson *et al.*, 2018).

Opportunists in episodes of global environmental stress

Several of the evolutionarily basal genera mentioned above have been described as opportunistic forms, which allowed them to acquire ecological advantage in times of environmental stress for the microplankton communities. For example, some environmental crisis could favour the evolution of the conoglobigerinids from the oberhauserellids in the Middle Jurassic. Fuchs (1975) suggested that the change in the test mineralogy from aragonite to calcite in the conoglobigerinids was likely due to the climate cooling that occurred in the Early Jurassic, as well as the reduction in the magnesium content in the oceans. However, Hart *et al.* (2002, 2003) suggested that the origin of conoglobigerinids was one of the probable results of the early Toarcian oceanic anoxic event. An alternative explanation was provided by BouDagher-Fadel (2012, 2015), who suggested that the sudden appearance of many of the *Conoglobigerina* species could be related to the rise in sea level of the Bajocian, which could open up new niches. According to Leckie (2009), fluctuating sea level and changing conditions of the oxygen minimum zone and the phytoplankton community structure were three of many factors that may have provided opportunities for benthic foraminifers to make the leap into the pelagic environment.

Among the opportunistic planktic foraminifera, *Guembelitria* is a paradigmatic example, since it has been described as small-sized disaster triserials, common to abundant in less stable palaeo-environments, and tolerant to disturbed environments and under eutrophic conditions (Nederbragt, 1989; Kroon & Nederbragt, 1990; Keller & Pardo, 2004; Abramovich *et al.*, 2010). Triserial guembelitriids have the potential to persist during times of drastically changing marine conditions, as recorded just after the KPB, when other species became extinct (Kroon & Nederbragt, 1990). Other guembelitriid-type taxa, as *Archaeoguembelitria* (Eicher & Worstell, 1970b, referred to as *Guembelitria*) and *Gallitellia* (Kroon & Nederbragt, 1990), are also opportunists, being relatively abundant where environmental conditions are adverse for other species. Between the heterohelicids, *Protoheterohelix, Planoheterohelix* and *Zeauvigerina* are also considered opportunistic taxa (Nederbragt, 1991; Nederbragt *et al.*, 1998; D'Haenens *et al.*, 2012).

On the other hand, the immediate benthic ancestor of globigerinid *Pseudocaucasina, i.e.*, *Caucasina*, has also been considered an opportunist, specifically a phytodetritivore tolerant to eutrophic, dysoxic environments (Poag, 1989, 2012; Koutsoukos & Hart, 1990). The pelagic niches emptied after the KPB mass extinction event may have favoured *Caucasina* to invade the pelagic environment, giving rise to the parvularugoglobigerinids only a few thousand years later (Arenillas & Arz, 2017). Something similar could have happened during the EOT crisis, as de Vargas *et al.* (1997) proposed. The climate cooling across the EOT (Priabonian and Rupelian) wiped out lineages that had dominated during the Paleogene (truncorotaloids, hantkeninoids, globanomalinoids, porticulasphaerids), allowing the evolutionary radiation of globigerinoids and globorotaloids, and the appearance of globigerinitoids (*Dipsidripella*-*Tenuitella*) from their benthic ancestor (Pearson *et al.*, 2018). In summary, mass extinctions events may strongly have favoured repopulation from benthic ancestors.

Meroplanktic and tychoplanktic modes of life

It has been suggested that conoglobigerinids were meroplanktic taxa, *i.e.*, planktic for only a part of their life cycle (Banner *et al.*, 1985; BouDagher-Fadel *et al.*, 1997; BouDagher-Fadel, 2012, 2015). The earliest known favuselloids (*Conoglobigerina*) have a discorbid-like early growth habit (Banner, 1982). They all have at least five to six chambers in the early whorls, while the last whorl has only four chambers. This discorbid-like morphology may indicate that they were benthic in the juvenile stage. However, the last whorls exhibit globular chambers, suggesting that they were planktic in the adult stage. The meroplanktic mode of life seems to have been associated with dimorphism by alternation of generations (*i.e.*, dimorphic life cycle with microspheric and megalospheric forms), a character unknown in any holoplanktic foraminifera (BouDagher-Fadel, 2012, 2015). Consequently, the evolution of conoglobigerinids could occur initially by adopting a meroplanktic mode of life.

Such transitions from the benthic to the planktic mode of life are well documented in many modern rotaliids inhabiting of shelf environments (Banner *et al.*, 1985; BouDagher-Fadel *et al.*, 1997), as for example among discorboids (*e.g.*, tretomphaloid-type rosalinids) and planorbulinoids (*e.g.*, cymbaloporids). Hart *et al.* (2003) suggested that the perturbation created by the early Toarcian gas hydrate surge, and the ensuing oceanic anoxic event, could be the cause of the transition to a meroplanktic mode of life. The holoplanktic mode of life did not emerge until the appearance of *Globuligerina* in the Bathonian.

A similar case may be that of early parvularugoglobigerinids (*Pseudocaucasina*), which exhibit a juvenile stage with fourth to five chambers and an adult stage with three chambers (Arenillas & Arz, 2017). Its benthic ancestor, *Caucasina*, which groups infaunal taxa that inhabit from inner sublittoral to bathyal (Poag, 1989, 2012; Koutsoukos & Hart, 1990), display a similar morphology, with five to six chambers in the early whorls, and only two to three chambers in the last whorls (see Arenillas & Arz, 2017). For comparison with conoglobigerinids, we can speculate that *Caucasina* and perhaps *Pseudocaucasina* were meroplanktic taxa.

Nonetheless, there is another possibility. Darling *et al.* (2009) claimed that the species surviving the KPB extinction, which have been described as inhabitants of shallow neritic environments (*e.g.*, *Guembelitria* or *Zeauvigerina*), may very well have been tychoplanktic. Darling *et al.* (2009) suggested that radiation and repopulation of the empty niche in the plankton after the KPB extinction may at least in part have occurred from tychoplanktic benthic species rather than from neritic planktic ones. The tychoplanktics are species capable of living both in the benthic and in the pelagic domain, as demonstrated for current *Bolivina variabilis*/*Streptochilus globigerus*. Such species are endowed with a great ecological advantage, enabling a rapid recolonization of the pelagic domain from the benthos (Leckie, 2009; Clemence & von Hillebrandt, 2013). After mass extinctions in the plankton, as caused by bolide impacts, climate cooling or oceanic anoxic events, tychoplanktic species may well be capable of repopulating the pelagic realm and evolve into fully planktic forms (Darling *et al.*, 2009).

Kucera *et al.* (2017) recently showed that the initial phase of the pelagic colonization by benthic taxa could even be achieved without external forcing, *i.e.*, without environmental stress, through the evolution of a tychoplanktic mode of life, which may have evolved as a strategy for dispersal of benthic foraminifera. They speculated that the final step to switch from the tychoplanktic to holoplanktic mode of life could be the adoption of obligate sexual reproduction or suppression of the asexual phase of the life cycle. The existence of such meroplanktic or tychoplanktic modes of life in foraminifera provides a possible mechanism through which planktic lineages may have evolved multiple times from benthic ancestor since the Jurassic times (Darling *et al.*, 2009; Clemence & von Hillebrandt, 2013).

Relevance of buliminids as ancestors of planktic foraminifera

Most of the putative benthic ancestors of planktic foraminiferal groups are buliminids. This is the case of *Praeplanctonia* (ancestor of *Protoheterohelix* and *Archaeoguembelitria*), *Neobulimina* (ancestor of *Guembelitria*), *Caucasina* (ancestor of *Pseudocaucasina*), and *Stainforthia* (ancestor of *Gallitellia*). *Streptochilus* and *Zeauvigerina* may in fact be buliminids. Therefore, the buliminids seem to have played a relevant role as ancestors of various microperforate planktic foraminifera, with triserial or high trochospiral test and with pore-mounded or smooth wall. Buliminids are commonly infaunals that inhabited environments with a high nutrient supply and low levels of oxygen (Sen-Gupta & Machain-Castillo, 1993; Bernhard *et al.*, 1997).

Alve (1999) and Dubicka and Wierzbowski (2019) showed that some bi- and triserial benthic foraminiferal species of Cretaceous buliminid genera, such as *Pseudouvigerina* Cushman, 1927, *Bolivinoides* Cushman, 1927, *Eouvigerina* Cushman, 1926, and *Loxostomum* Ehrenberg, 1854, seem to have a propagule dispersal mechanism and the ability to occupy both pelagic and benthic domains (tychoplanktic mode of life). They exhibit microperforate wall with pore-mounded –and/or finely pustulate– surface, which is relatively rare in benthic foraminifera and more common in planktic foraminifera. It suggests that the pore-mounded wall stood for an exceptional morphological advantage, which iteratively evolved in buliminid foraminifera during the Mesozoic and Cenozoic, and could become a bridge between a benthic and planktic mode of life (Dubicka & Wierzbowski, 2019).

The uvegirinid and bolivinid genera studied by Dubicka and Wierzbowski (2019) were grouped in the superfamily Serioidea by Holzmann and Pawlowski (2017) (see supplementary text S8). This superfamily also includes to the family Stainforthiidae Reiss 1963, which in turn probably comprises the current triserial planktic genus *Gallitellia*. The bimodal lifestyle, apparently linked to a pore-mounded wall, is likely characteristic of this superfamily, which can be interpreted as a link between benthic and planktic foraminifera, as already postulated by Georgescu *et al.* (2011).

The only exceptions may be *Praegubkinella* (ancestor of *Conoglobigerina*) and *Praepararotalia* (ancestor of *Dipsidripella*-*Tenuitella* and *Antarcticella*). As mentioned above, the former was a robertinid (oberhauserellid) and the latter a rotaliid. *Praegubkinella*, like *Oberhauserella*, was an opportunist tolerant to dysoxic conditions and stressed environments, and probably with a meroplanktic mode of life (BouDagher-Fadel, 2012, 2015; Clemence & von Hillebrandt, 2013). *Praepararotalia* was an outer sublittoral dweller, that lived in relatively oxygen-depleted or food-enriched waters, and probably with a tychoplanktic mode of life (Liu *et al.*, 1998; Huber *et al.*, 2020). Consequently, both taxa have an ecological niche similar to many buliminids, and may have shared the same role as bridge between benthic and planktic modes of life.

JUSTIFICATION FOR THE NEW DEFINED TAXA

New order Globotruncanida

If the hypothesis that Cenozoic globigerinids evolved after the KPB extinction from the benthic genus *Caucasina* is verified, as proposed by Brinkhuis and Zachariasse (1988) and Arenillas and Arz (2017), then Mesozoic planktic foraminifera are phylogenetically disconnected from those of the Cenozoic. Even excluding heterohelicids as already postulated by Fursenko (1958) and BouDagher-Fadel (2012, 2015), the order Globigerinida becomes polyphyletic if the spiral Mesozoic taxa are included. It is therefore necessary to separate the latter in a new order, which we have called Globotruncanida, because the genus *Globotruncana* Cushman, 1927, and the family Globotruncanidae Brotzen, 1942, are the ones that best characterize it. Consequently, it is also necessary to emend the order Globigerinida.

This new order includes *Conoglobigerina*, the first planktic foraminifera to appear (if *Sphaerogerina* is excluded), as well as all its descendants (Fig. 1). Consequently, the order Globotruncanida appeared in the Bajocian (Middle Jurassic), and includes 7 superfamilies and 20 families. The globotruncanids reached at the Maastrichtian the largest test size of all planktic foraminifera, up to 1 mm in diameter as in the case of *Contusotruncana* Korchagin, 1982. For comparison, Cenozoic and current species do not exceed 600 µm in diameter.

New order Guembelitriida

Fursenko (1958) joined all planktic foraminifera with bi- and triserial arrangement, at least in the early ontogenetic stage, in the order Heterohelicida, consequently clustering the families Heterohelicidae Cushman, 1927, Guembelitriidae Montanaro-Gallitelli, 1957, Chiloguembelinidae Loeblich & Tappan, 1956, Globoconusidae BouDagher-Fadel, 2012, and Cassigerinellidae Bolli, Loeblich & Tappan, 1957 (see BouDagher-Fadel, 2012, 2015). However, this order also becomes polyphyletic if the guembelitriids and their Cenozoic descendants (chiloguembelinids, globoconusids and cassigerinellids) are included. It is therefore necessary to separate these families in a new order, which we have called Guembelitriida, because the genus *Guembelitria*, and the family Guembelitriidae Montanaro-Gallitelli, 1957, are the ones that best characterize it. Consequently, it is also necessary to emend the order Heterohelicida. Guembelitriida n. ord. includes 4 families: Cassigerinellidae, Chiloguembelinidae, Globoconusidae and Guembelitriidae (Fig. 2), which we have also elevated to the category of superfamily.

New superfamily Abathomphaloidea

The superfamily Abathomphaloidea has been defined to accommodate the families Globotruncanellidae Maslakova, 1964, and Abathomphalidae Pessagno, 1967, that form a phylogenetic group already recognized by Robaszynski *et al.* (1984). Abathomphalidae and Globotruncanellidae have traditionally been included in the superfamily Globotruncanoidea. However, they have an independent origin, probably from rugoglobigerinoids as *Archaeoglobigerina* Pessagno, 1967 (see Caron, 1985).

New superfamily Parvularugoglobigerinoidea and new family Parvularuglobigerinidae

In addition to proposing that *Pseudocaucasina* was the first Cenozoic globigerinid genus to appear, Arenillas and Arz (2017) were in favour of including this genus in a new ancestral Cenozoic family of the order Globigerinida together with *Parvularugoglobigerina* and *Palaeoglobigerina* Arenillas, Arz & Náñez, 2007. Until now, these taxa have been informally termed parvularugoglobigerinids. They gather the tiny species with microperforate, smooth wall discovered by Luterbacher and Premoli-Silva (1964) immediately above the KPB (also see Arenillas & Arz, 2000). We here group these primitive Cenozoic taxa into the new family Parvularuglobigerinidae, because *Parvularugoglobigerina* is the genus that best characterizes it. The parvularugoglobigerinids cannot be included in the family Eoglobigerinidae Blow, 1979, or in the family Globanomalinidae Loeblich & Tappan, 1984, because they are the ancestral forms of both, and do not conform to the wall-texture characteristics of either of them (Figs. 3, 4). Consequently, it is also necessary to separate them into a new superfamily (Parvularuglobigerinoidea) to differentiate them from superfamilies Eoglobigerinoidea BouDagher-Fadel, 2012, and Globanomalinidoidea Loeblich & Tappan, 1984.

PLANKTIC FORAMINIFERAL SYSTEMATICS

We follow Lee (1990) who raised the order Foraminiferida to class Foraminifera, and consequently the previously recognized suborder Globigerinina to order Globigerinida (Loeblich & Tappan, 1992). A brief discussion on the higher-rank classification and phylogeny of foraminifera is presented in supplementary text S7. For each one of the taxa considered, we have added its type-taxon, its chronostratigraphic range, and lower rank taxa it includes. Only newly defined taxa and emended orders are described in their diagnosis section. We have also included the *derivatio nominis* of the defined taxa.

Class FORAMINIFERA Lankester, 1885
Order GLOBOTRUNCANIDA Arz, Arenillas & Gilabert n. ord.

Type-superfamily. Globotruncanidae Brotzen, 1942.

Derivatio nominis. As for the superfamily Globotruncanidae Brotzen, 1942.

Chronostratigraphic range. Bajocian–Maastrichtian.

Diagnosis. Test trochospiral or planispiral. Peripheral margin without keel, or with one or two keel. Aperture bordered by a lip or protected by a porticus or a tegillum, rarely by a bulla. Finely perforate to macroperforate. Wall surface smooth, pore-mounded, pitted, reticulate, hispid, pustulate, muricate, rugose, or costate. Wall hyaline calcitic, but early forms may be aragonitic.

Superfamilies included. Abathomphaloidea Arz, Arenillas & Gilabert n. superfam.; Favuselloidea Longoria, 1974; Hedbergelloidea Longoria & Gamper, 1975; Globotruncanoidea Brotzen, 1942; Planomalinoidea Bolli, Loeblich & Tappan, 1957; Rotaliporoidea Sigal, 1958; Rugoglobigerinoidea Subbotina, 1959.

Superfamily ABATHOMPHALOIDEA Arz, Arenillas & Gilabert n. superfam.

Type-family. Abathomphalidae Pessagno, 1967.

Derivatio nominis. As for the family Abathomphalidae Pessagno, 1967.

Chronostratigraphic range. Middle Campanian–Maastrichtian.

Diagnosis. Test trochospiral. Peripheral margin without keel, with pustulate pseudo-keel or one or two keels. Aperture protected by a porticus or a tegillum. Macroperforate. Wall surface pustulate (muricate), rugose or discontinuous costate.

Families included. Abathomphalidae Pessagno, 1967; Globotruncanellidae Maslakova, 1964.

Family ABATHOMPHALIDAE Pessagno, 1967

Type-genus. *Abathomphalus* Bolli, Loeblich & Tappan, 1957.

Chronostratigraphic range. Maastrichtian.

Genera included. *Abathomphalus* Bolli, Loeblich & Tappan, 1957.

Family GLOBOTRUNCANELLIDAE Maslakova, 1964

Type-genus. *Globotruncanella* Reiss, 1957.

Chronostratigraphic range. Middle Campanian–Maastrichtian.

Genera included. *Globotruncanella* Reiss, 1957; *Spinoglobotruncanella* Georgescu & Sawyer, 2014.

Superfamily FAVUSELLOIDEA Longoria, 1974

Type-superfamily. Favusellidae Longoria, 1974.

Chronostratigraphic range. Bajocian–lower Cenomanian.

Families included. Conoglobigerinidae BouDagher-Fadel, Banner & Whittaker, 1997; Favusellidae Longoria, 1974; Globuligerinidae Loeblich & Tappan, 1984.

Family CONOGLOBIGERINIDAE BouDagher-Fadel, Banner & Whittaker, 1997

Type-genus. *Conoglobigerina* Morozova, 1961, in Morozova and Moskalenko (1961).

Chronostratigraphic range. Bajocian–middle Valanginian.

Genera included. *Conoglobigerina* Morozova, 1961, in Morozova and Moskalenko (1961); *Tenuigerina* Gorbachik & Kuznetsova, 1998.

Problematic taxa (other benthic origins). *Sphaerogerina* Korchagin & Kuznetsova, 2003, in Korchagin *et al.* (2003) (Family Sphaerogerinidae BouDagher-Fadel, 2012).

Family FAVUSELLIDAE Longoria, 1974

Type-genus. *Favusella* Michael, 1973.

Chronostratigraphic range. Berriasian–lower Cenomanian.

Genera included. *Ascoliella* Banner & Desai, 1988; *Favusella* Michael, 1973; *Koutsoukosia* Georgescu, 2009a.

Family GLOBULIGERINIDAE Loeblich & Tappan, 1984

Type-genus. *Globuligerina* Bignot & Guyader, 1971.

Chronostratigraphic range. Bathonian–middle Tithonian.

Genera included. *Compactogerina* Simmons, BouDagher-Fadel, Banner & Whittaker, 1997, in BouDagher-Fadel *et al.* (1997); *Globuligerina* Bignot & Guyader, 1971; *Haeuslerina* BouDagher-Fadel, Banner & Whittaker, 1997; *Petaloglobigerina* Gradstein, 2021, in Gradstein and Waskowska (2021).

Superfamily HEDBERGELLOIDEA Longoria & Gamper, 1975

Type-family. Hedbergellidae Loeblich & Tappan, 1961.

Chronostratigraphic range. middle Valanginian–Maastrichtian.

Families included. Ananiidae El-Nakhal, 2010; Hedbergellidae Loeblich & Tappan, 1961; Helvetoglobotruncanidae Lamolda, 1976; Praehedbergellidae Banner & Desai 1988.

Family ANANIIDAE El-Nakhal, 2010

Type-genus. *Anania* El-Nakhal, 2010.

Chronostratigraphic range. Middle Albian–Maastrichtian.

Genera included. *Anania* El-Nakhal, 2010; *Badriella* El-Nakhal, 2002; *Costellagerina* Petters, El-Nakhal & Cifelli, 1983; *Hillsella* Georgescu, 2008a; *Liuenella* Georgescu, 2010c (new name for *Liuella* Georgescu, 2008b); *Loeblichella* Pessagno, 1967; *Muricohedbergella* Huber & Leckie, 2011; *Paracostellagerina* Georgescu & Huber, 2006; *Pessagnoina* Georgescu, 2009b; *Planohedbergella* BouDagher-Fadel, Banner, Whittaker & McCarthy, 1997, in BouDagher-Fadel *et al.* (1997); *Pseudoclavihedbergella* Georgescu, 2009b.

Genus-level taxa defined as evolutionary lineages (without type species). *Vanhintella* Georgescu, 2013b.

Family HEDBERGELLIDAE Loeblich & Tappan, 1961

Type-genus. *Hedbergella* Brönnimann & Brown, 1958.

Chronostratigraphic range. Middle Aptian–Coniacian.

Genera included. *Asterohedbergella* Hamaoui, 1964; *Clavihedbergella* Banner & Blow, 1959; *Hedbergella* Brönnimann & Brown, 1958; *Microhedbergella* Huber & Leckie, 2011; *Paraticinella* Premoli-Silva, Caron, Leckie, Petrizzo, Soldan & Verga, 2009; *Pseudoguembelitria* Huber & Leckie, 2011.

Family HELVETOGLOBOTRUNCANIDAE Lamolda, 1976

Type-genus. *Helvetoglobotruncana* Reiss, 1957.

Chronostratigraphic range. Lower Cenomanian–lower Campanian.

Genera included. *Angulocarinella* Korchagin, 2001; *Bermudeziana* Georgescu, 2011; *Bollitruncana* Korchagin, 2001; *Fingeria* Georgescu, 2010b; *Hedbergellita* Maslakova, 1983; *Brittonella* Korchagin, 1989; *Helvetoglobotruncana* Reiss, 1957; *Unitruncatus* Korchagin, 2001; *Whiteinella* Pessagno, 1967.

Family PRAEHEDBERGELLIDAE Banner & Desai 1988

Type-genus. *Praehedbergella* Gorbachik & Moullade, 1973.

Chronostratigraphic range. Middle Valanginian–Cenomanian.

Genera included. *Blefuscuiana* Banner & Desai, 1988; *Gorbachikella* Banner & Desai, 1988; *Praehedbergella* Gorbachik & Moullade, 1973; *Lilliputianella* Banner & Desai, 1988; *Lilliputianelloides* BouDagher-Fadel, Banner & Whittaker, 1997; *Wondersella* Banner & Strank, 1987.

Superfamily GLOBOTRUNCANOIDEA Brotzen, 1942

Type-family. Globotruncanidae Brotzen, 1942.

Chronostratigraphic range. Middle Albian–Maastrichtian.

Families included. Globotruncanidae Brotzen, 1942; Praeglobotruncanidae Ion, 1983; Reissidae Korchagin, 2001.

Family GLOBOTRUNCANIDAE Brotzen, 1942

Type-genus. *Globotruncana* Cushman, 1927.

Chronostratigraphic range. Middle Turonian–Maastrichtian.

Genera included. *Contusotruncana* Korchagin, 1982; *Globotruncana* Cushman, 1927; *Marginotruncana* Hofker, 1956; *Obliquacarinata* Korchagin, 1993; *Sphaerotruncana* Korchagin, 1993; *Ventrotruncana* Korchagin, 1993.

Family PRAEGLOBOTRUNCANIDAE Ion, 1983

Type-genus. *Praeglobotruncana* Bermúdez, 1952.

Chronostratigraphic range. Middle Albian–lower Campanian.

Genera included. *Concavatotruncana* Korchagin, 1982; *Dicarinella* Porthault, 1970, in Donze *et al.* (1970); *Falsotruncana* Caron, 1981; *Rotundina* Subbotina, 1953; *Praeglobotruncana* Bermúdez, 1952; *Verotruncana* Korchagin, 2001.

Genus-level taxa defined as evolutionary lineages (without type species). *Exmouthia* Georgescu, 2013, in Georgescu *et al.* (2013).

Family REISSIDAE Korchagin, 2001

Type-genus. *Globotruncanita* Reiss, 1957.

Chronostratigraphic range. Turonian–Maastrichtian.

Genera included. *Elevatotruncana* Korchagin, 2001; *Globotruncanita* Reiss, 1957; *Kassabiana* Salaj & Solakius, 1984; *Radotruncana* El-Naggar, 1971; *Sigalitruncana* Korchagin, 1982; *Turbotruncana* Korchagin, 1993.

Superfamily PLANOMALINOIDEA Bolli, Loeblich & Tappan, 1957

Type-family. Planomalinidae Bolli, Loeblich & Tappan, 1957.

Chronostratigraphic range. Middle Barremian–Maastrichtian.

Families included. Eohastigerinellidae Loeblich & Tappan, 1984; Globigerinelloididae Longoria, 1974; Planomalinidae Bolli, Loeblich & Tappan, 1957; Schackoinidae Pokorný, 1958.

Family EOHASTIGERINELLIDAE Loeblich & Tappan, 1984

Type-genus. *Eohastigerinella* Morozova, 1957.

Chronostratigraphic range. Turonian–Santonian.

Genera included. *Eohastigerinella* Morozova, 1957; *Hastigerinoides* Brönnimann, 1952.

Family GLOBIGERINELLOIDIDAE Longoria, 1974

Type-genus. *Globigerinelloides* Cushman & ten Dam, 1948.

Chronostratigraphic range. Middle Barremian–Maastrichtian.

Genera included. *Alanlordella* BouDagher-Fadel, 1995; *Allotheca* Ehrenberg, 1843; *Biglobigerinella* Lalicker, 1948; *Blowiella* Kretzchmar & Gorbachik, 1971, in Gorbachik (1971); *Claviblowiella* BouDagher-Fadel Banner & Whittaker, 1997; *Globigerinelloides* Cushman & ten Dam, 1948; *Pseudoschackoina* Verga & Premoli-Silva, 2005.

Family PLANOMALINIDAE Bolli, Loeblich & Tappan, 1957

Type-genus. *Planomalina* Loeblich & Tappan, 1946.

Chronostratigraphic range. Middle Aptian–Cenomanian.

Genera included. *Planomalina* Loeblich & Tappan, 1946; *Pseudoplanomalina* Moullade, Bellier & Tronchetti, 2002.

Genus-level taxa defined as evolutionary lineages (without type species). *Bannerina* Georgescu & Sawyer, 2013, in Georgescu *et al.* (2013).

Family SCHACKOINIDAE Pokorný, 1958

Type-genus. *Schackoina* Thalmann, 1932.

Chronostratigraphic range. Aptian–Maastrichtian.

Genera included. *Leupoldina* Bolli, 1957; *Schackoina* Thalmann, 1932.

Genus-level taxa defined as evolutionary lineages (without type species). *Asymetria* Georgescu, 2012; *Groshenyia* Georgescu, 2012; *Neoschackoina* Georgescu, 2012.

Superfamily ROTALIPOROIDEA Sigal, 1958

Type-family. Rotaliporidae Sigal, 1958.

Chronostratigraphic range. Albian–middle Turonian.

Families included. Rotaliporidae Sigal, 1958; Ticinellidae Longoria, 1974.

Family ROTALIPORIDAE Sigal, 1958

Type-genus. *Rotalipora* Brotzen, 1942.

Chronostratigraphic range. Middle Albian–middle Turonian.

Genera included. *Anaticinella* Eicher, 1973; *Pseudothalmanninella* Wonders, 1978; *Rotalipora* Brotzen, 1942; *Thalmanninella* Sigal, 1948.

Family TICINELLIDAE Longoria, 1974

Type-genus. *Ticinella* Reichel, 1950.

Chronostratigraphic range. Albian.

Genera included. *Biticinella* Sigal, 1956; *Claviticinella* El-Naggar, 1971; *Ticinella* Reichel, 1950.

Superfamily RUGOGLOBIGERINOIDEA Subbotina, 1959

Type-family. Rugoglobigerinidae Subbotina, 1959.

Chronostratigraphic range. Turonian–Maastrichtian.

Families included. Helvetiellidae Longoria & Gamper, 1984; Rugoglobigerinidae Subbotina, 1959.

Family HELVETIELLIDAE Longoria & Gamper, 1984

Type-genus. *Helvetiella* Longoria & Gamper, 1984.

Chronostratigraphic range. Turonian–Maastrichtian.

Genera included. *Archaeoglobigerina* Pessagno, 1967; *Bucherina* Brönnimann & Brown, 1956; *Gansserina* Robaszynski, Caron, González-Donoso, & Wonders, 1984; *Globocarinata* Korchagin, 1993; *Helvetiella* Longoria & Gamper, 1984; *Kuglerina* Brönnimann & Brown, 1956.

Genus-level taxa defined as evolutionary lineages (without type species). *Dorbignya* Georgescu, 2013b; *Gandolfia* Georgescu, 2012; *Edgarinella* Georgescu, 2013b.

Family RUGOGLOBIGERINIDAE Subbotina, 1959

Type-genus. *Rugoglobigerina* Brönnimann, 1952.

Chronostratigraphic range. Santonian–Maastrichtian.

Genera included. *Archaeoglobitruncana* Salaj & Maamouri, 1984; *Plummerita* Brönnimann, 1952; *Rugoglobigerina* Brönnimann, 1952; *Rugosocarinata* Korchagin, 1993; *Rugotruncana* Brönnimann & Brown, 1956; *Trinitella* Brönnimann, 1952.

Order GLOBIGERINIDA Lankester, 1885, emended

Type-superfamily. Globigerinoidea Carpenter, Parker & Jones, 1862.

Chronostratigraphic range. Danian–Recent.

Emended Diagnosis. Test trochospiral or planispiral, or mixed trochospiral-planispiral, trochospiral-streptospiral and trochospiral-triserial. Peripheral margin without carinae, or with one carinae or muricocarinae. Aperture bordered by a lip or protected by a porticus, a tooth or a bulla. Microperforate to macroperforate. Wall surface smooth, pitted, cancellate, pustulate, muricate or spinose. Wall hyaline calcitic.

Superfamilies included. Parvularugoglobigerinoidea Arenillas, Arz & Gilabert n. superfam.; Eoglobigerinoidea BouDagher-Fadel, 2012; Globigerinoidea Carpenter, Parker & Jones, 1862; Globorotalioidea Cushman, 1927; Globanomalinidoidea Loeblich & Tappan, 1984; Hantkeninoidea Cushman, 1927; Truncorotaloidinoidea BouDagher-Fadel, 2012.

Superfamily PARVULARUGOGLOBIGERINOIDEA Arenillas, Arz & Gilabert n. superfam.

Type-family. Parvularuglobigerinidae Arenillas, Arz & Gilabert n. fam.

Derivatio nominis. As for the family Parvularuglobigerinidae Arenillas, Arz & Gilabert n. fam.

Chronostratigraphic range. Lowermost Danian.

Diagnosis. Test trochospiral, or mixed trochospiral-triserial. Microperforate to finely perforate. Wall surface smooth.

Families included. Parvularuglobigerinidae Arenillas, Arz & Gilabert n. fam.

Family PARVULARUGLOBIGERINIDAE Arenillas, Arz & Gilabert n. fam.

Type-genus. *Parvularugoglobigerina* Hofker, 1978.

Derivatio nominis. As for the genus *Parvularugoglobigerina* Hofker, 1978.

Chronostratigraphic range. Lowermost Danian.

Diagnosis. See superfamily Parvularugoglobigerinoidea Arenillas, Arz & Gilabert n. superfam.

Genera included. *Pseudocaucasina* Arenillas & Arz, 2016 in Arenillas & Arz (2017); *Palaeoglobigerina* Arenillas, Arz & Náñez, 2007; *Parvularugoglobigerina* Hofker, 1978.

Superfamily EOGLOBIGERINOIDEA BouDagher-Fadel, 2012

Type-family. Eoglobigerinidae Blow, 1979.

Chronostratigraphic range. Danian–Recent.

Families included. Eoglobigerinidae Blow, 1979; Globoquadrinidae Blow, 1979; Neoacarininidae BouDagher-Fadel, 2012; Porticulasphaeridae Banner, 1982.

Family EOGLOBIGERINIDAE Blow, 1979

Type-genus. *Eoglobigerina* Morozova, 1959.

Chronostratigraphic range. Danian–Langhian.

Genera included. *Alicantina* Soldan, Petrizzo & Premoli-Silva, 2018; *Eoclavatorella* Cremades-Campos, 1980; *Eoglobigerina* Morozova, 1959; *Parasubbotina* Olsson, Hemleben, Berggren & Liu, 1992; *Pseudoglobigerinella* Olsson & Pearson, 2006, in Olsson *et al.* (2006b); *Subbotina* Brotzen & Pożaryska, 1961; *Turbeogloborotalia* BouDagher-Fadel, 2012.

Family GLOBOQUADRINIDAE Blow, 1979

Type-genus. *Globoquadrina* Finlay, 1947.

Chronostratigraphic range. Upper Ypresian–Recent.

Genera included. *Dentoglobigerina* Blow, 1979; *Globoquadrina* Finlay, 1947.

Family NEOACARININIDAE BouDagher-Fadel, 2012

Type-genus. *Neoacarinina* Thompson, 1973.

Chronostratigraphic range. Pleistocene.

Genera included. *Neoacarinina* Thompson, 1973.

Family PORTICULASPHAERIDAE Banner, 1982

Type-genus. *Porticulasphaera* Bolli, Loeblich & Tappan, 1957.

Chronostratigraphic range. Middle Ypresian–Priabonian.

Genera included. *Globigerinatheka* Brönnimann, 1952; *Guembelitrioides* El-Naggar, 1971; *Inordinatosphaera* Mohan & Soodan, 1967; *Orbulinoides* Cordey, 1968; *Porticulasphaera* Bolli, Loeblich & Tappan, 1957.

Superfamily GLOBIGERINOIDEA Carpenter, Parker & Jones, 1862

Type-family. Globigerinidae Carpenter, Parker & Jones, 1862.

Chronostratigraphic range. Lower Ypresian–Recent.

Families included. Globigerinidae Carpenter, Parker & Jones, 1862; Globigerinellidae BouDagher-Fadel, 2012; Hastigerinidae Bolli, Loeblich & Tappan, 1957; Orbulinidae Schultze, 1854; Sphaeroidinellidae Banner & Blow, 1959; Turborotalitidae Hofker, 1976.

Family GLOBIGERINIDAE Carpenter, Parker & Jones, 1862

Type-genus. *Globigerina* d'Orbigny, 1826, in Parker *et al.* (1865).

Chronostratigraphic range. Lower Ypresian–Recent.

Genera included. *Alloglobigerinoides* Huang, 1986; *Ciperoella* Olsson & Hemleben, 2018, in Olsson *et al.* (2018); *Globigerina* d'Orbigny, 1826, in Parker *et al.* (1865); *Globicuniculus* Saito & Thompson, 1976, in Saito *et al*. (1976); *Globigerinoides* Cushman, 1927; *Globigerinoidesella* El-Naggar, 1971; *Globoturborotalita* Hofker, 1976; *Trilobigerina* Popescu, 1987 (= *Trilobatus* Spezzaferri, Kucera, Pearson, Wade, Rappo, Poole, Morard & Stalder, 2015); *Zeaglobigerina* Kennett & Srinivasan, 1983.

Family GLOBIGERINELLIDAE BouDagher-Fadel, 2012

Type-genus. *Globigerinella* Cushman, 1927.

Chronostratigraphic range. Lower Rupelian–Recent.

Genera included. *Beella* Banner & Blow, 1960; *Bolliella* Banner & Blow, 1959; *Globigerinella* Cushman, 1927; *Orcadia* Boltovskoy & Watanabe, 1982; *Protentella* Lipps, 1964; *Quiltyella* Coxall & Spezzaferri, 2018, in Spezzaferri *et al.* (2018).

Family HASTIGERINIDAE Bolli, Loeblich & Tappan, 1957

Type-genus. *Hastigerina* Thomson, 1876.

Chronostratigraphic range. Middle Tortonian–Recent.

Genera included. *Hastigerina* Thomson, 1876; *Hastigerinella* Cushman, 1927; *Hastigerinopsis* Saito & Thompson, 1976, in Saito *et al*. (1976).

Family ORBULINIDAE Schultze, 1854

Type-genus. *Orbulina* d'Orbigny, 1839.

Chronostratigraphic range. Middle Burdigalian–Recent.

Genera included. *Biorbulina* Blow, 1956; *Candorbulina* Jedlitschka, 1934; *Orbulina* d'Orbigny, 1839; *Praeorbulina* Olsson, 1964.

Family SPHAEROIDINELLIDAE Banner & Blow, 1959

Type-genus. *Sphaeroidinella* Cushman, 1927.

Chronostratigraphic range. Upper Aquitanian–Recent.

Genera included. *Prosphaeroidinella* Ujiié, 1976; *Sphaeroidinella* Cushman, 1927; *Sphaeroidinellopsis* Banner & Blow, 1959.

Family TURBOROTALITIDAE Hofker, 1976

Type-genus. *Turborotalita* Blow & Banner, 1962.

Chronostratigraphic range. Middle Lutecian–Recent.

Genera included. *Berggrenia* Parker, 1976; *Turborotalita* Blow & Banner, 1962.

Superfamily GLOBOROTALIOIDEA Cushman, 1927

Type-family. Globorotaliidae Cushman, 1927.

Chronostratigraphic range. Ypresian–Recent.

Families included. Catapsydracidae Bolli, Loeblich & Tappan, 1957; Globorotaloididae Banner & Blow, 1959; Globorotaliidae Cushman, 1927; Pulleniatinidae Cushman, 1927.

Family CATAPSYDRACIDAE Bolli, Loeblich & Tappan, 1957

Type-genus. *Catapsydrax* Bolli, Loeblich & Tappan, 1957.

Chronostratigraphic range. Lower Ypresian–Bartonian.

Genera included. *Catapsydrax* Bolli, Loeblich & Tappan, 1957; *Globigerinopsoides* Cita & Mazzola, 1970; *Globigerinoita* Brönnimann, 1952; *Velapertina* Popescu, 1969.

Family GLOBOROTALOIDIDAE Banner & Blow, 1959

Type-genus. *Globorotaloides* Bolli, 1957.

Chronostratigraphic range. Ypresian–Recent.

Genera included. *Clavatorella* Blow, 1965; *Globorotaloides* Bolli, 1957; *Protentelloides* Zhang & Scott, 1995.

Family GLOBOROTALIIDAE Cushman, 1927

Type-genus. Globorotalia Cushman, 1927.

Chronostratigraphic range. Lower Ypresian–Recent.

Genera included. Dentigloborotalia Brummer, 1988; Fohsella Bandy, 1972; Globoconella Bandy, 1975; Globorotalia Cushman, 1927; Hirsutella Bandy, 1972; Jenkinsella Kennett & Srinivasan, 1983; Menardella Bandy, 1972; Neogloboquadrina Bandy, Frerichs

& Vincent, 1967; Paragloborotalia Cifelli, 1982; Truncorotalia Cushman & Bermúdez, 1949.

Family PULLENIATINIDAE Cushman, 1927

Type-genus. *Pulleniatina* Cushman, 1927.

Chronostratigraphic range. Messinian–Recent.

Genera included. *Pulleniatina* Cushman, 1927.

Superfamily GLOBANOMALINIDOIDEA Loeblich & Tappan, 1984

Type-family. Globanomalinidae Loeblich & Tappan, 1984.

Chronostratigraphic range. lower Danian–Rupelian.

Families included. Globanomalinidae Loeblich & Tappan, 1984.

Family GLOBANOMALINIDAE Loeblich & Tappan, 1984

Type-genus. *Globanomalina* Haque, 1956.

Chronostratigraphic range. Lower Danian–Rupelian.

Genera included. *Carinoturborotalia* BouDagher-Fadel, 2012; *Globanomalina* Haque, 1956; *Luterbacheria* Canudo, 1994; *Planoglobanomalina* Olsson & Hemleben, 2006; *Turborotalia* Cushman & Bermúdez, 1949.

Superfamily HANTKENINOIDEA Cushman, 1927

Type-family. Hantkeninidae Cushman, 1927.

Chronostratigraphic range. Lower Ypresian–middle Rupelian.

Families included. Pseudohastigerinidae Canudo, 1990; Hantkeninidae Cushman, 1927.

Family PSEUDOHASTIGERINIDAE Canudo, 1990

Type-genus. *Pseudohastigerina* Banner & Blow, 1959.

Chronostratigraphic range. Lower Ypresian–middle Rupelian.

Genera included. *Pseudohastigerina* Banner & Blow, 1959.

Family HANTKENINIDAE Cushman, 1927

Type-genus. *Hantkenina* Cushman, 1924.

Chronostratigraphic range. Middle Ypresian–Priabonian.

Genera included. *Applinella* Thalmann, 1942; *Aragonella* Thalmann, 1942; *Clavigerinella* Bolli, Loeblich & Tappan, 1957; *Cribrohantkenina* Thalmann, 1942; *Hantkenina* Cushman, 1924.

Superfamily TRUNCOROTALOIDINOIDEA BouDagher-Fadel, 2012

Type-family. Truncorotaloididae Loeblich & Tappan, 1961.

Chronostratigraphic range. Lower Danian–lower Rupelian.

Families included. Globigerapsidae Blow, 1979; Planorotalitidae BouDagher-Fadel, 2012; Truncorotaloididae Loeblich & Tappan, 1961.

Family GLOBIGERAPSIDAE Blow, 1979

Type-genus. *Globigerapsis* Bolli, Loeblich & Tappan, 1957.

Chronostratigraphic range. Upper Selandian–upper Priabonian.

Genera included. *Globigerapsis* Bolli, Loeblich & Tappan, 1957; *Muricoglobigerina* Blow, 1979.

Family PLANOROTALITIDAE BouDagher-Fadel, 2012

Type-genus. *Planorotalites* Morozova, 1957.

Chronostratigraphic range. Lower Ypresian–middle Bartonian.

Genera included. *Astrorotalia* Turnovsky, 1958; *Planorotalites* Morozova, 1957.

Family TRUNCOROTALOIDIDAE Loeblich & Tappan, 1961.

Type-genus. *Truncorotaloides* Brönnimann & Bermúdez, 1953.

Chronostratigraphic range. Lower Danian–lower Rupelian.

Genera included. *Acarinina* Subbotina, 1953; *Igorina* Davidzon, 1976; *Morozovella* McGowran, 1964; *Morozovelloides* Pearson & Berggren, 2006; *Pearsonites* Soldan, Petrizzo & Premoli-Silva, 2014; *Praemurica* Olsson, Hemleben, Berggren & Liu, 1992; *Pseudogloboquadrina* Jenkins, 1966; *Testacarinata* Jenkins, 1971; *Truncorotaloides* Brönnimann & Bermúdez, 1953.

Order HETEROHELICIDA Fursenko, 1958, emended

Type-superfamily. Heterohelicoidea Cushman, 1927.

Chronostratigraphic range. Upper Albian–Maastrichtian.

Emended Diagnosis. Test biserial, or mixed planispiral-biserial, biserial-multiserial and biserial-uniserial.

Microperforate to macroperforate. Wall surface smooth, pore-mounded, striate or costate. Wall hyaline calcitic.

Superfamilies included. Heterohelicoidea Cushman, 1927.

Superfamily HETEROHELICOIDEA Cushman, 1927

Type-family. Heterohelicidae Cushman, 1927.

Chronostratigraphic range. Upper Albian–Maastrichtian.

Families included. Gublerinidae Aliyulla, 1977; Heterohelicidae Cushman, 1927; Pseudotextulariidae Maamouri & Salaj, 1978; Pseudoguembelinidae Aliyulla, 1977; Spiroplectidae Cushman, 1911; Ventilabrellidae Maamouri & Salaj, 1978.

Family GUBLERINIDAE Aliyulla, 1977

Type-genus. *Gublerina* Kikoïne, 1948.

Chronostratigraphic range. Lower Campanian–Maastrichtian.

Genera included. *Gublerina* Kikoïne, 1948; *Lipsonia* Georgescu & Abramovich, 2008a; *Praegublerina* Georgescu, Saupe & Huber, 2008.

Family HETEROHELICIDAE Cushman, 1927

Type-genus. *Heterohelix* Ehrenberg, 1843.

Chronostratigraphic range. Upper Albian–Maastrichtian.

Genera included. *Braunella* Georgescu, 2007a; *Bronnimannella* Montanaro-Gallitelli, 1956; *Globoheterohelix* Georgescu & Huber, 2009; *Fleisherites* Georgescu, 2009c; *Hartella* Georgescu & Abramovich, 2009a; *Heterohelix* Ehrenberg, 1843; *Huberella* Georgescu, 2007b; *Laeviheterohelix* Nederbragt, 1991; *Lunatriella* Eicher & Worstell, 1970a; *Planoheterohelix* Georgescu & Huber, 2009; *Protoheterohelix* Georgescu & Huber, 2009; *Pseudoplanoglobulina* Aliyulla, 1977; *Steineckia* Georgescu, 2009c; *Striataella* Aliyulla, 1977; *Texasina* Georgescu, 2010a.

Genus-level taxa defined as evolutionary lineages (without type species). *Ehrenbergites* Georgescu, 2013b; *Lazarusina* Georgescu, 2013b; *Magellanina* Georgescu, 2014a; *Mihaia* Georgescu, 2013, in Georgescu *et al.* (2013); *Nederbragtina* Georgescu, 2014a.

Problematic taxa (other benthic origins). *Bifarina* Parker & Jones, 1872 (?family Gublerinidae); *Rectoguembelina* Cushman, 1932 (?family Gublerinidae); *Zeauvigerina* Finlay, 1939 (?family Eouvigerinidae Cushman, 1927, o family Loxostomatidae Loeblich & Tappan, 1962).

Family PSEUDOTEXTULARIIDAE Maamouri & Salaj, 1978.

Type-genus: *Heterohelix* Ehrenberg, 1843.

Chronostratigraphic range. Coniacian–Maastrichtian.

Genera included. *Planoglobulina* Cushman, 1927; *Pseudotextularia* Rzehak, 1891; *Racemiguembelina* Montanaro-Gallitelli, 1957.

Family PSEUDOGUEMBELINIDAE Aliyulla, 1977

Type-genus. *Pseudoguembelina* Brönnimann & Brown, 1953.

Chronostratigraphic range. Lower Santonian–Maastrichtian.

Genera included. *Leptobimodalia* Georgescu, 2014a; *Pseudoguembelina* Brönnimann & Brown, 1953.

Genus-level taxa defined as evolutionary lineages (without type species). *Eicheriella* Georgescu, 2014b.

Family SPIROPLECTIDAE Cushman, 1911

Type-genus. *Spiroplecta* Ehrenberg, 1844.

Chronostratigraphic range. Lower Santonian–Maastrichtian.

Genera included. *Hendersonites* Georgescu & Abramovich, 2009b (new name for *Hendersonia* Georgescu & Abramovich, 2008b); *Paraspiroplecta* Georgescu & Abramovich, 2008b; *Spiroplecta* Ehrenberg, 1844.

Genus-level taxa defined as evolutionary lineages (without type species). *Neohendersonites* Georgescu, 2014c.

Family VENTILABRELLIDAE Maamouri & Salaj, 1978

Type-genus. *Ventilabrella* Cushman, 1928.

Chronostratigraphic range. Santonian–Maastrichtian.

Genera included. *Planulitella* Georgescu, 2010a; *Proliferania* Georgescu, 2010a; *Sigalia* Reiss, 1957; *Ventilabrella* Cushman, 1928.

Order GUEMBELITRIIDA Arenillas, Arz & Gilabert n. ord.

Type-superfamily. Guembelitrioidea Montanaro-Gallitelli, 1957.

Derivatio nominis. As for the superfamily Guembelitrioidea Montanaro-Gallitelli, 1957.

Chronostratigraphic range. Santonian–Serravallian.

Diagnosis. Test triserial, biserial, or trochospiral, or mixed triserial-biserial, triserial-trochospiral, or biserialstreptospiral. Microperforate to finely perforate. Wall surface smooth, pore-mounded, rugose, hispid or pustulate. Wall hyaline calcitic.

Superfamilies included. Cassigerinelloidea Bolli, Loeblich & Tappan, 1957; Guembelitrioidea Montanaro-Gallitelli, 1957; Chiloguembelinoidea Reiss, 1963; Globoconusoidea BouDagher-Fadel, 2012.

Superfamily CASSIGERINELLOIDEA Bolli, Loeblich & Tappan, 1957

Type-family. Cassigerinellidae Bolli, Loeblich & Tappan, 1957.

Chronostratigraphic range. Bartonian–Serravallian.

Families included. Cassigerinellidae Bolli, Loeblich & Tappan, 1957.

Family CASSIGERINELLIDAE Bolli, Loeblich & Tappan, 1957

Type-genus. *Cassigerinella* Pokorný, 1955.

Chronostratigraphic range. Middle Bartonian–Serravallian.

Genera included. *Cassigerinella* Pokorný, 1955; *Riveroinella* Bermúdez & Seiglie, 1967.

Superfamily GUEMBELITRIOIDEA Montanaro-Gallitelli, 1957

Type-family. Guembelitriidae Montanaro-Gallitelli, 1957.

Chronostratigraphic range. Santonian–lower Bartonian.

Families included. Guembelitriidae Montanaro-Gallitelli, 1957.

Family GUEMBELITRIIDAE Montanaro-Gallitelli, 1957

Type-genus. *Guembelitria* Cushman, 1933.

Chronostratigraphic range. Santonian–lower Bartonian.

Genera included. *Cassigerinelloita* Stolk, 1965; *Guembelitria* Cushman, 1933; *Chiloguembelitria* Hofker, 1978; *Jenkinsina* Haynes, 1981.

Problematic taxa (other benthic origins). *Archaeoguembelitria* Georgescu, 2009a (family Praeplanctonidae Georgescu, 2009a); *Gallitellia* Loeblich & Tappan, 1986 (?family Stainforthiidae Reiss, 1963, or family Virgulinellidae Loeblich & Tappan, 1984); *Guembelitriella* Tappan, 1940 (?family Turrilinidae Cushman, 1927).

Superfamily CHILOGUEMBELINOIDEA Reiss, 1963

Type-family. Chiloguembelinidae Reiss, 1963.

Chronostratigraphic range. Lowermost Danian–lower Rupelian.

Families included. Chiloguembelinidae Reiss, 1963.

Family CHILOGUEMBELINIDAE Loeblich & Tappan, 1956

Type-genus. *Chiloguembelina* Loeblich & Tappan, 1956.

Chronostratigraphic range. Lowermost Danian–lower Rupelian.

Genera included. *Chiloguembelina* Loeblich & Tappan, 1956; *Woodringina* Loeblich & Tappan, 1957.

Problematic taxa (other benthic origins). *Streptochilus* Brönnimann & Resig, 1971 (family Bolivinidae Glaessner, 1937).

Superfamily GLOBOCONUSOIDEA BouDagher-Fadel, 2012

Type-family. Globoconusidae BouDagher-Fadel, 2012.

Chronostratigraphic range. Lowermost–upper Danian.

Families included. Globoconusidae BouDagher-Fadel, 2012.

Family GLOBOCONUSIDAE BouDagher-Fadel, 2012

Type-genus. *Globoconusa* Khalilov, 1956.

Chronostratigraphic range. Lowermost–upper Danian.

Genera included. *Globoconusa* Khalilov, 1956; *Trochoguembelitria* Arenillas, Arz & Náñez, 2012.

Order ? (unnamed)

Chronostratigraphic range. (middle Lutecian?) upper Bartonian–Recent.

Diagnosis. See Superfamily Globigerinitoidea BouDagher-Fadel, 2012, emended.

Superfamily GLOBIGERINITOIDEA BouDagher-Fadel, 2012, emended

Type-family. Globigerinitidae Bermúdez, 1961.

Chronostratigraphic range. (middle Lutecian?) upper Bartonian–Recent.

Emended Diagnosis. Tests trochospiral, or mixed triserial-trochospiral. Microperforate to finely perforate. Wall surface smooth, finely pustulate. Wall hyaline calcitic.

Families included. Candeinidae Cushman, 1927; Globigerinatellidae BouDagher-Fadel, 2012; Globigerinitidae Bermúdez, 1961; Tenuitellidae BouDagher-Fadel, 2012; Family ? (unnamed).

Family CANDEINIDAE Cushman, 1927

Type-genus. *Candeina* d'Orbigny, 1839.

Chronostratigraphic range. Tortonian–Recent.

Genera included. *Candeina* d'Orbigny, 1839.

Family GLOBIGERINATELLIDAE BouDagher-Fadel, 2012

Type-genus. *Globigerinatella* Cushman & Stainforth, 1945.

Chronostratigraphic range. Upper Burdigalian–lower Langhian.

Genera included. *Globigerinatella* Cushman & Stainforth, 1945.

Family GLOBIGERINITIDAE Bermúdez, 1961

Type-genus. *Globigerinita* Brönnimann, 1951.

Chronostratigraphic range. Chattian–Recent.

Genera included. *Globigerinita* Brönnimann, 1951; *Mutabella* Pearson, Norris & Empson 2001; *Polyperibola* Liska, 1980; *Tinophodella* Loeblich & Tappan, 1957.

Family TENUITELLIDAE BouDagher-Fadel, 2012

Type-genus. *Tenuitella* Fleisher, 1974.

Chronostratigraphic range. Upper Bartonian–Recent.

Genera included. *Praetenuitella* Li, 1987; *Tenuitella* Fleisher, 1974; *Tenuitellinata* Li, 1987; *Tenuitellita* Li, 1987.

Family ? (unnamed)

Genera included. *Dipsidripella* Brotea, 1995.

Chronostratigraphic range. Middle Lutecian–lower Rupelian.

Problematic taxa (other benthic origins). *Antarcticella* Loeblich & Tappan, 1987 (?family Rotaliidae Ehrenberg, 1839.

Supplementary information. Supplementary material of this manuscript is available at the Spanish Journal of Palaeontology web-site (https://sepaleontologia.es/spanish-journal-palaeontology/) linked to the corresponding contribution. Supplementary Text S1: Clarification on the date of Loeblich & Tappan (1987); Supplementary Text S2: Taxonomic notes on the order Globotruncanida; Supplementary Text S3: Taxonomic notes on the order Heterohelicida; Supplementary Text S4: Taxonomic notes on the order Guembelitriida; Supplementary Text S5: Taxonomic notes on the order Globigerinida; Supplementary Text S6: Taxonomic notes on the superfamily Globigerinitoidea; Supplementary Text S7: Higher-rank classification of planktic foraminifera.

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Author details. **Ignacio Arenillas, José Antonio Arz** & **Vicente Gilabert.** Departamento de Ciencias de la Tierra, and Instituto Universitario de Investigación en Ciencias Ambientales de Aragón, Universidad de Zaragoza, E-50009 Zaragoza, Spain; ias@unizar.es, josearz@unizar.es, vgilabert@unizar.es

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