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

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 supragenetic 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.

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 stratigraphic 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 and 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 stratigraphic 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 & Gilabet 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 (Guembelitrina Arenillas, Arz & Gilabet n. ord.), two new superfamilies (Parvularugibigerinoidea Arenillas, Arz & Gilabet n. superfam., and Abathomphaloidea Arz, Arenillas & Gilabet n. superfam.) and one new family (Parvularugibigerinidae Arenillas, Arz & Gilabet 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 superfamaly 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), Robasynskiy and Caron (1979), Blow (1979), Salto et al. (1981), Banner (1982), Korchagin (1982), Kennett and Srinivasan (1983), and Robasynskiy 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), Mouliade 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 planomalinois (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 Pokorny, 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 parvularugoglobigerinids, the validity of the families Globigerapsidae Blow, 1979, and Pianorotalitidae BouDagher-Fadel, 2012, the taxonomic position of globanomalinois, 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 foraminifers 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 & Görg, 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 from the family Oberhauserellidae Fuchs, 1970 (Fig. 1), which includes benthic foraminifera with aragonitic tests (order Robertinida Mikhailovich, 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 descendant 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 aragonitic 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 Woeitzina 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.
Fuchs (1975) proposed Conoglobigerina in 1982; it was probably the sole survivor of the Cretaceous–Paleogene boundary (KPB) mass extinction (Smit, 1982, Georgescu et al., 2009). 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, may have derived from the benthic genus Praeplanctonia Georgescu, 2009, a direct descendant 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 an 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 guembelitrids

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 heterohelicids. However, since Guembelitria did not appear until the Santonian (or until Cenomanian in the case that the species of Archaeoguembelitria were considered guembelitrids), 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 guembelitrids (Fig. 2).

There is stronger evidence that the guembelitrids are the ancestor of two incoming Danian lineages (Olsson et al., 1999; BouDagher-Fadel, 2012, 2015): the biserial chiloguembelins, 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 Chiloguembelina Hofker, 1978, played an important evolutionary role because it is the common ancestor of chiloguembelins and globoconusids (Arenillas et al., 2017). The first representative of the chiloguembelins 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 (Muricochedbergella 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 Caucasia 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 Pseudocaucasia Arenillas & Arz, 2016 in Arenillas and Arz (2017), which is morphologically very similar to some Jurassic species of Conoglobigerina. Muricochedbergella is commonly considered the ancestor of two lineages that appeared in the early Danian: globanomalinaids and eogloboconusids (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 Muricochedbergella as the ancestor of both lineages. In addition, Arenillas et al. (2018) raised doubts that Muricochedbergella 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 Guembelitrida 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 Caucasia, 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 parvularugoglobigerinids 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 modern and larger globoconusid genus Trochoguembelitria, whose first appearance occurred almost at the same time as eogloboconids and globanomalinds (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; Ujié & 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 Ujié 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 rotalid genus Praepararotalia Liu, Olsson & Huber, 1998. Since a benthic ancestor has been proposed as the origin of this group (de Vargas et al., 1997; Ujié et al., 2008; Ujié & 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 superfamly 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 globorotaliids 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 globorotaliids 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 globorotaliids) according to the SSU-rDNA molecular studies. In any case, if an independent benthic origin for globorotaliids is demonstrated, the superfamily Globorotalioidea Cushman, 1927, would have to be well established by stratophenetic evidence that both benthic and planktic species, and may have evolved from another, different ancestral benthic lineage (Georgescu, 2009a): the buliminid *Praeplanctonia*, and may have survived 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 heterohelids (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 *Galilaelia* (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 parvularugoglobigerinids 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 *Chiloquembelina* (see, for example, Stainforth et al., 1975; Kennett & Srivivasan, 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 growing 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, Ujié et al. (2008) indicated that the modern triserial genus *Galiliteilla*, 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 globigerinids (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 *Galiliteilla*, 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 preferentially 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).

**Opportuists 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 theoberhauserellids 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 KP3B, when other species became extinct (Kroon & Nederbragt, 1990). Other guembelitrid-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 Pseudocauasina, i.e., Caucasina, has also been considered an opportunist, specifically a phylodetritivore tolerant to eutrophic, dysoxic environments (Poag, 1989, 2012; Koutsoukos & Hart, 1990). The pelagic niches emptied after the KP3B 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, globanomaloinoids, porticulasphaeroids), 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 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 Zeaувigerina), 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 Archaeoguembellitria), Neobulimina (ancestor of Guembellitria), Caucasina (ancestor of Pseudocaucasina), and Stainforthia (ancestor of Gallitella). Streptochilus and Zeaувigerina 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 superfamilly Serioidea by Holzmann and Pawlowski (2017) (see supplementary text S8). This superfamilly also includes to the family Stainforthiidae of the superfamily Serioidea by Holzmann and Pawlowski (2017). This superfamilly also includes to the family Stainforthiidae of the superfamily Serioidea by Holzmann and Pawlowski (2017).
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 Brotzien, 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, Chiloguembeliniidae 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 (chiloguembeliniids, 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, Chiloguembeliniidae, 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 Globotruncanoida. However, they have an independent origin, probably from rugoglobigerinoids as Archaeoglobigerina Pessagno, 1967 (see Caron, 1985).

New superfamily Parvularugoglobigerinoidea and new family Parvularugoglobigerinidae

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 Parvularugoglobigerinidae, 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 (Parvularugoglobigerinoidea) 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 keels. 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, hispid, punctulate, 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; Globotruncanoida Brotzen, 1942; Planomalinoidea Bolli, Loeblich & Tappan, 1957; Rotaliporoidea Sigal, 1958; Rugoglobigerinoidea Subbotina, 1959.

Superfamily ABATHOMPHALOIDEA Arz, Arenillas & Gilabert n. superfam.


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.


Family ABATHOMPHALIDA Pessagno, 1967

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

Chronostratigraphic range. Maastrichtian.


Family GLOBULIGERINIDAE Loeblich & Tappan, 1984


Chronostratigraphic range. Bathonian–middle Tithonian.


Family ANANIIDAE El-Nakhal, 2010


Chronostratigraphic range. Middle Albian–Maastrichtian.


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

Family HEDBERGELLIDAE Loeblich & Tappan, 1961


Chronostratigraphic range. Middle Aptian–Coniacian.


Family HELVETOGLOBOTRUNCANIDAE Lamolda, 1976

Type-genus. Helvetoglobotruncanana Reiss, 1957.

Chronostratigraphic range. Lower Cenomanian–lower Campanian.


Family PRAEHEDBERGELLIDAE Banner & Desai 1988


Chronostratigraphic range. Middle Valanginian–Cenomanian.


Superfamily GLOBOTRUNCANOIDEA Broten, 1942

Type-family. Globotruncanidae Broten, 1942.

Chronostratigraphic range. Middle Albian–Maastrichtian.


Family GLOBOTRUNCANIDAE Broten, 1942

Type-genus. Globotruncanana Cushman, 1927.

Chronostratigraphic range. Middle Turonian–Maastrichtian.


Family PRAEGLOBOTRUNCANIDAE Ion, 1983

Type-genus. Praeglobotruncanana Bermúdez, 1952.

Chronostratigraphic range. Middle Albian–lower Campanian.


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.


Superfamily PLANOMALINOIDEA Bolli, Loeblich & Tappan, 1957
Type-family. Planomalainidae Bolli, Loeblich & Tappan, 1957.

Chronostratigraphic range. Middle Barremian–Maastrichtian.


Family EOHASTIGERINELLIDAE Loeblich & Tappan, 1984
Type-genus. Eohastigerinella Morozova, 1957.
Chronostratigraphic range. Turonian–Santonian.

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 Kretzschmar & Gorbachik, 1971, in Gorbachik (1971); Claviblowiella BouDagher-Fadel & 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.

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.

Superfamily ROTALIPOROIDEA Sigal, 1958
Type-family. Rotaliporidae Sigal, 1958.
Chronostratigraphic range. Albian–middle Turonian.

Family SUPERFAMILY ROTALIPOROIDEA Subbotina, 1959
Type-family. Rotaliporidae Sigal, 1958
Type-genus. Rotalipora Brotzen, 1942.
Chronostratigraphic range. Middle Albian–middle Turonian.

Family SCHACKOINIDAE Longoria, 1974
Type-genus. Ticanella Reichel, 1950.
Chronostratigraphic range. Albian.

Superfamily RUGOGLOBIGERINOIDEA Subbotina, 1959
Type-family. Rugoglobigerinidae Subbotina, 1959.
Chronostratigraphic range. Turonian–Maastrichtian.
Genera included. Helvetiellidae Longoria & Gamper, 1984; Rugoglobigerinidae Subbotina, 1959.

Family HELVETIELLIDAE Longoria & Gamper, 1984
Chronostratigraphic range. Turonian–Maastrichtian.

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.


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.


Superfamily PARVULARUGOBLIGERINOIDEA 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 PARVULARUGOBLIGERINIDAE Arenillas, Arz & Gilabert n. fam.


Chronostratigraphic range. Lowermost Danian.

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


Superfamily EOGLOBIGERINOIDEA BouDagher-Fadel, 2012


Chronostratigraphic range. Danish–Recent.


Family Eoglobigerinidae Blow, 1979

Type-genus. Eoglobigerina Morozova, 1959.

Chronostratigraphic range. Danish–Langhian.


Family Globoquadrimidae 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


Chronostratigraphic range. Pleistocene.


Family Porticulasphaeridae Banner, 1982

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

Chronostratigraphic range. Middle Ypresian–Priabonian.


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

Chronostratigraphic range. Lower Ypresian–Recent.


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.


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. Biobulina 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. Prospaheroidinella Ujiié, 1976; Sphaeroidinella Cushman, 1927; Sphaeroidinellopsis Banner & Blow, 1959.

Family TURBOROTALITIDAE Hofker, 1976


Chronostratigraphic range. Middle Lutecian–Recent.


Superfamily GLOBOROTALIOIDEA Cushman, 1927

Type-family. Globorotaliidae Cushman, 1927.

Chronostratigraphic range. Ypresian–Recent.

Families included. Catapsydracidae Bolli, Loeblich & Tappan, 1957; Globorotalioidae 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.


Family GLOBOROTALOIDIDAE Banner & Blow, 1959


Chronostratigraphic range. Ypresian–Recent.


Family GLOBOROTALIIDAE Cushman, 1927

Type-genus. Globorotalia Cushman, 1927.

Chronostratigraphic range. Lower Ypresian–Recent.

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

Superfamily HANTKENINOIDEA Cushman, 1927
Type-family. Hantkeninidae Cushman, 1927.
Chronostratigraphic range. Lower Ypresian–Middle Bartonian.
Genera included. Applinella Thalmann, 1942; Aragonella Thalmann, 1942; Clavigerinella Bolli, Loeblich & Tappan, 1957; Cribrohantkenina Thalmann, 1942; Hantkenina Cushman, 1924.

Order HETEROHELICIDA Fursenko, 1958, emended
Type-superfamily. Heterohelicoida 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.

Family GUBLERINIDAE Aliyulla, 1977
Type-genus. Gublerina Kikoïne, 1948.
Chronostratigraphic range. Lower Campanian–Maas- trichtian.

Family HETEROHELICIDAE Cushman, 1927
Type-genus. Heterohelix Ehrenberg, 1843.
Chronostratigraphic range. Upper Albian–Maastrichtian.

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).

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–Maas- trichtian.
Genera included. Leptobimodalina Georgescu, 2014a; Pseudoguembelina Brönnimann & Brown, 1953.
Genus-level taxa defined as evolutionary lineages (without type species). Neohendersonites Georgescu, 2014c.

Family SPIROPLECTIDAE Cushman, 1911
Type-genus. Spiroplecta Ehrenberg, 1844.
Chronostratigraphic range. Lower Santonian–Maas- trichtian.
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 biserial-
streptospiral. Microperforate to finely perforate. Wall surface smooth, pore-mounded, rugose, hispid or pustulate. Wall hyaline calcitic.


Superfamily CASSIGERINELLOIDEA Bolli, Loeblich & Tappan, 1957

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

Chronostratigraphic range. Bartonian–Serravallian.


Family CASSIGERINELLIDAE Bolli, Loeblich & Tappan, 1957


Chronostratigraphic range. Middle Bartonian–Serravallian.


Superfamily GUEMBELITRIOIDEA Montanaro-Gallitelli, 1957

Type-family. Guembelitriidae Montanaro-Gallitelli, 1957.

Chronostratigraphic range. Santonian–lower Bartonian.


Family GUEMBELITRIIDAE Montanaro-Gallitelli, 1957

Type-genus. Guembelitria Cushman, 1933.

Chronostratigraphic range. Santonian–lower Bartonian.


Superfamily CHILOGUEMBELINOIDEA Reiss, 1963


Chronostratigraphic range. Lowermost Danian–lower Rupelian.


Family CHILOGUEMBELINIDAE Loeblich & Tappan, 1956

Type-genus. Chiloguembelina Loeblich & Tappan, 1956.

Chronostratigraphic range. Lowermost Danian–lower Rupelian.


Superfamily GLOBOCONUSOIDEA BouDagher-Fadel, 2012


Chronostratigraphic range. Lowermost–upper Danian.


Family GLOBOCONUSIDAE BouDagher-Fadel, 2012


Chronostratigraphic range. Lowermost–upper Danian.


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


Superfamily GLOBIGERINOIDEA BouDagher-Fadel, 2012, emended


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


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
Chronostratigraphic range. Upper Burdigalian–lower Langhian.

Family GLOBIGERINITIDAE Bermúdez, 1961
Type-genus. Globigerinita Brönnimann, 1951.
Chronostratigraphic range. Chattian–Recent.

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; Tenuitella Li, 1987.

Family ? (unnamed)
Chronostratigraphic range. Middle Lutecian–lower Rupelian.


Supplementary information. Supplementary material of this manuscript is available at the Spanish Journal of Palaeontology web-site (https://sepalaeontologia.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 Guembelitrida; Supplementary Text S5: Taxonomic notes on the order Globigerinida; Supplementary Text S6: Taxonomic notes on the superfamily Globohelicitoidea; Supplementary Text S7: Higher-rank classification of planktic foraminifera.

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Competing Interest. We declare no competing interests

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