

SUPPLEMENTARY INFORMATION

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

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This Supplementary Material contains:

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.

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Supplementary references cited (only including references that are not in the main text).

SUPPLEMENTARY TEXT S1: CLARIFICATION ON THE DATE OF LOEBLICH AND TAPPAN (1987)

It is customary to date the monumental work of Loeblich and Tappan (1987) in 1988, but the authors cautioned that the publisher incorrectly indicated its publication date, and requested to refer to it with the correct date, *i.e.* 1987 (see Loeblich & Tappan, 1989).

SUPPLEMENTARY TEXT S2: TAXONOMIC NOTES ON THE ORDER GLOBOTRUNCANIDA

First appearance of truly planktic foraminifera

Identifying the first occurrence of truly planktic foraminifera is controversial. Many Triassic and Jurassic taxa have been suggested as holoplanktic, but later had to be reinterpreted as benthic (BouDagher-Fadel, 2012, 2015). For example, Fuchs (1967, 1973) described several *Globigerina*-type genera and Fuchs (1975) referred to them as planktic ("protoglobigerinas"). In the Triassic, *Kollmannita* Fuchs, 1967, *Schlagerina* Fuchs, 1967, and *Schmidita* Fuchs, 1967, are the most remarkable, in addition to *Oberhauserella* and *Praegubkinella*, and, in the Jurassic, *Jurassorotalia* Fuchs, 1973, and *Mariannenina* Fuchs, 1973. BouDagher- Fadel *et al.* (1997) rejected that these taxa were planktic, but benthic belonging to the family Oberhauserellidae. However, they had a relevant role in the origin of earliest globotruncanids (favuselloids), as discussed in the main text. Besides proposing *Praegubkinella* as ancestor of *Conoglobigerina*, Fuchs (1975) also proposed that *Hedbergella* Brönnimann & Brown, 1958, derived from the genus *Mariannenina*, which is a direct descendent of the oberhauserellid genus *Schmidita*. In fact, Fuchs

(1975) included *Mariannenina* within the family Hedbergellidae Loeblich & Tappan, 1961. This would make the order Globotruncanida polyphyletic. According to Fuchs (1975), only the descendants of *Praegubkinella* and *Schmidita* retained the planktic mode of life, while the descendants of *Oberhauserella* and *Schlagerina* returned to the benthos. However, BouDagher-Fadel (2012, 2015) warned that *Mariannenina* is a benthic genus of uncertain status, maybe congeneric with *Jurassorotalia* (Loeblich and Tappan, 1987), and phylogenetically disconnected from hedbergellids.

Number of genera and lineages

The globotruncanid classification at the superfamily and family levels should be deeply checked, and will likely change substantially in the coming years, as there appear to be many lineages within hedbergellids, rugoglobigerinids, globotruncanids, rotaliporids, globigerinelloids and planomalinooids that perhaps need to be separate into new families (see, for example, Banner & Desai, 1988; BouDagher-Fadel *et al.*, 1997; Korchagin, 2003; Georgescu, 2008a, 2008b, 2009b, 2012, 2013b, 2013c; Huber & Leckie, 2011). As Huber and Leckie (2011) recommended, the revision of Cretaceous taxa requires more detailed stratophenetic studies. To cite an example, the genera defined in families Globotruncanidae, Hedbergellidae and Rugoglobigerinidae by Korchagin (1982, 1993) and Korchagin (2001), and compiled in a monograph by Korchagin (2003), could be different lineages and be separated into different families or subfamilies. The phylogenetic relationships for these last genera have been based on the notes and suggestions made mainly by Korchagin (2003) as well as the phylogenetic position of their type species. Nevertheless, a more in-depth review will be necessary.

More recently, Georgescu (2012, 2013b) and Georgescu *et al.* (2013) conducted a detailed taxonomic review of globotruncanoids, hedbergelloids, planomalinooids and rugoglobigerinoids from Albian to Maastrichtian. They proposed up to ten new evolutionary lineages of globotruncanids, assigned to different genus-level taxa. The latter were defined and described as evolutionary lineages, and not as genera, *i.e.*, without assigning type species (see below). They grouped the species into evolutionary lineages (iterative and directional lineages) following the principles of an evolutionary classification that takes into account the demonstrated ancestor-descendant relationships as inferred in the fossil record. However, by not having the type species assigned, the validity of all them is questionable according to the International Code of Zoological Nomenclature (ICZN).

SUPPLEMENTARY TEXT S3: TAXONOMIC NOTES ON THE ORDER HETEROHELICIDA

Multiserial heteroheliceid lineages

During the Late Cretaceous, several heteroheliceid lineages became large and complex, multiplying their chambers in one or all planes. There are at least three lineages of large heteroheliceids (Nederbragt, 1991). The first appeared in Coniacian and culminated in Maastrichtian in genera *Racemiguembelina* Montanaro-Gallitelli, 1957, and *Planoglobulina* Cushman, 1927, being his first member *Pseudotextularia* Rzehak, 1891. The second appeared in Santonian and culminated in Campanian in genera *Sigalia* Reiss, 1957, and *Ventilabrella* Cushman, 1928, being his first member *Planulitella* Georgescu, 2010a (Fig. 3). The third appeared in Campanian and culminated in genus *Gublerina* Kikoine, 1948, being his first member

Praegublerina Georgescu, Saupe & Huber, 2009. Names for these lineages were proposed at the subfamily level: Pseudotextulariinae Maamouri and Salaj, 1978, Ventilabrellinae Maamouri & Salaj, 1978 (previously named by Maamouri and Salaj, 1974), and Gublerininae Aliyulla, 1977, respectively. We have elevated these subfamilies to the family rank (see below). The taxa de Maamouri and Salaj (1978) did not have much diffusion, and Loeblich and Tappan (1987) considered them junior synonyms of the family Heterohelicidae Cushman, 1927. Maamouri and Salaj (1978) assigned *Gublerina* to Ventilabrellinae, but this genus belongs to a different lineage and fits better in the family Gublerinidae postulated by Aliyulla (1977). Lineages and phylogenetic relationships between genera of Gublerinidae and Ventilabrellidae were studied in detail by Georgescu *et al.* (2008) and Georgescu (2010a) respectively. Georgescu (2014d) suggested that *Planoglobulina*, which has traditionally been considered descendant of *Pseudotextularia* (see Nederbragt, 1991), as we have tentatively proposed here, could evolve independently from *Mihaia* Georgescu, 2013. If confirmed, the family Pseudotextulariidae would become polyphyletic (Fig. 3).

Spiroplectids

The family Spiroplectidae Cushman, 1911, which was originally defined with the subfamily category, groups biserial heterohelicids with an initial spiral stage. The type genus assigned was *Spiroplecta* Ehrenberg, 1844, a controversial genus that was defined to gather species that are mostly benthic (Cushman, 1911), but was later revalidated by Georgescu and Abramovich (2009a). Aliyulla (1977) attributed this lineage to the subfamily Tesseraellinae, but its type genus, *Tesseraella* Aliyulla, 1977, is now considered a junior synonym of *Spiroplecta*. Georgescu and Abramovich (2009a) concluded that *Spiroplecta*, whose type-species is *Spiroplecta*

americana Ehrenberg, 1844, and *Paraspiroplecta* Georgescu & Abramovich, 2008b, whose type-species is *Paraspiroplecta navarroensis* (Loeblich & Tappan, 1951), although morphologically very similar, come from different ancestors in a process of iterative and convergent evolution: *Spiroplecta* from *Planoheterohelix* Georgescu & Huber, 2009, and *Paraspiroplecta* from *Hendersonites* Georgescu & Abramovich, 2009b. If this hypothesis is verified, the family Spiroplectidae would be polyphyletic (Fig. 3).

Heterohellicids

Georgescu (2013a) proposed phylogenetic relationships between several Cenomanian to Campanian heterohellicid genera, from which several lineages can be deduced (e.g., *Lunatriella*-*Steineckia* and *Pseudoplanoglobulina*-*Laeviheterohelix* lineages). Each of these lineages could be defined as heterohellicid families or subfamilies. In addition, Georgescu (2013b), Georgescu *et al.* (2013) and Georgescu and Henderson (2014) postulated up to nine evolutionary lineages of heterohellicids, six of them new, from Santonian to Maastrichtian, assigned to different genus-level taxa without type species assigned. As in the case of genus-level taxa of *Gobotruncanida* n. ord. described by these authors, their validity could be questioned according to the ICZN. However, we have considered all them due to its usefulness in unraveling the phylogeny in orders Heterohellicida and *Globotruncanida* n. ord.

SUPPLEMENTARY TEXT S4: TAXONOMIC NOTES ON THE ORDER

GUEMBELITRIIDA

Taxonomic position of genus *Cassigerinella*

Steineck and Darrell (1971) classified *Cassigerinella* as belonging to the benthic family Islandiellidae Loeblich & Tappan, 1964 (a junior synonym of the buliminid family Cassidulininae d'Orbigny, 1839). However, the cassigerinellids have been routinely regarded as descendants of chiloguembelinids, both for its planktic mode of life and its initially biserial test and microperforate, smooth or pore-mounded wall (Blow, 1979; Kennett & Srinivasan, 1983; Li, 1986; Huber *et al.*, 2006; BouDagher-Fadel, 2012, 2015; Pearson *et al.*, 2018a). Li and McGowran (1996) also observed textural and morphological similarities between tenuitellids and cassigerinellids, and Huber *et al.* (2006) included the tenuitellids within the guembeltriids. However, recent studies have shown that the tenuitellids are closely related to globigerinitids (Pearson *et al.*, 2018b), and therefore should be excluded from this order (see supplementary text S6).

Taxonomic position of genus *Jenkinsina*

The triserial genus *Jenkinsina* is problematic both due to its evolutionary origin and taxonomic position (see Premec Fucek *et al.*, 2018). Jenkins *et al.* (1998) noted the stratigraphic gap between *Jenkinsina* and its putative ancestor, *i.e.*, the genus *Guembeltria* (or *Chiloguembeltria* according to Arenillas *et al.*, 2017), was too great to be able to establish a phylogenetic relationship between the two. They proposed instead to *Chiloguembelina* as its most probable ancestor. However, the stratigraphic gap between *Jenkinsina* and *Chiloguembeltria* narrowed after the discovery of *Jenkinsina* specimens in the lower Eocene and Paleocene (see Huber *et al.*, 2006, and Premec Fucek *et al.*, 2018). Therefore, although a more exhaustive investigation is necessary to provide more detailed stratophenetic evidence, it is still possible to think of a phylogenetic relationship between both genera (Fig. 3). Finally, *Jenkinsina*

seems to be directly ancestral to the genus *Cassigerinelloita* Stolk, 1965, according to their similarities of wall texture (Li & Radford, 1992; Huber *et al.*, 2006).

SUPPLEMENTARY TEXT S5: TAXONOMIC NOTES ON THE ORDER

GLOBIGERINIDA

Parvularugoglobigerinoids

Hofker (1978) indicated that the wall surface of the genus *Parvularugoglobigerina* (type-genus of the new family Parvularuglobigerinidae) has small pustules and fine pipelike pores (*i.e.*, microperforate, finely pustulate wall). Hofker (1978) also proposed that the pustules are often found in rows as in the Cretaceous genus *Rugoglobigerina*, causing a lot of confusion during decades. Blow (1979) even considered these forms as a relict fauna composed of dwarfed representatives of late Cretaceous genera as *Hedbergella* and *Rugoglobigerina*. However, Toumarkine and Luterbacher (1985) negated the characteristics assigned by Hofker to *Parvularugoglobigerina* and its attribution to *Hedbergella* and *Rugoglobigerina* by Blow (1979). The parvularugoglobigerinid wall texture was initially described as rough or finely pustulate (Luterbacher & Premoli-Silva, 1964), but this feature was later attributed to fossil-diagenetic recrystallization (Smit, 1982). Stainforth *et al.* (1975) and Toumarkine and Luterbacher (1985) claimed that the record of well-preserved specimens of parvularugoglobigerinids are in favour of the original interpretation by Luterbacher and Premoli-Silva (1964), supporting that they exhibit microperforate, smooth wall (Fig. 1). Smooth-walled specimens were later reported by Smit (1982), Brinkhuis and Zachariasse (1988), Li and Radford (1991) and Li *et al.* (1995) among many others. Based on DSDP sites (Sites 384, 758 and 465) and USA Gulf Coast

sections (Millers Ferry), all of them with hiatuses affecting the lowermost Danian (see for example Berggren & Norris, 1997), Liu and Olsson (1992) and Olsson *et al.* (1992, 1999) claimed that parvularugoglobigerinids exhibit pore-mounded wall when specimens are well-preserved. Arenillas *et al.* (2012, 2016) realized that the specimens analysed by these last taxonomists belong to the more modern and larger globoconusid genus *Trochoguembelitra* (Fig. 1), and not the tiny smooth-walled globigeriniforms discovered by Luterbacher and Premoli-Silva (1964). After considering it to be smooth-walled, BouDagher-Fadel (2012, 2015) included *Parvularugoglobigerina* (and parvularugoglobigerinids) in the family Globanomalinidae. On the other hand, Loeblich and Tappan (1987) had previously assigned the specimens of pore-mounded wall to the genus *Postrugoglobigerina*, which was included in the family Globoconusidae by BouDagher-Fadel (2012, 2015). However, Arenillas *et al.* (2012, 2016) warned that holotypes and type-material of the *Postrugoglobigerina* species have been lost and, in addition, there were doubts about the true nature of its wall texture and its biostratigraphic position, thus becoming *nomen dubium non conservandum*.

Globigerapsids and planorotalitids

Most problematic globigerinid lineages are the families Globigerapsidae and Planorotalitidae. The former was postulated by Blow (1979) to group Paleocene–Eocene genera with muricate wall and umbilical aperture, at least in the early stage during the ontogeny. It includes the genera *Muricoglobigerina* Blow, 1979, and *Globigerapsis* Bolli, Loeblich & Tappan, 1957. However, this lineage has been questioned, since the muricae is absent or poorly developed in the wall of *Globigerapsis* and the last representatives of *Muricoglobigerina*. Olsson *et al.* (1999)

and Premoli-Silva *et al.* (2006) detracted from this family, after considering *Muricoglobigerina* a junior synonym of *Acarinina* Subbotina, 1953, and *Globigerapsis* of *Globigerinatheka* Brönnimann, 1952. However, BouDagher-Fadel (2012, 2015) retained both genera as proposed by Blow (1979), and classified them within the truncorotaloids, a taxonomic position tentatively suggested here (Fig. 4). The family Planorotalitidae was postulated by BouDagher-Fadel (2012, 2015) to join Paleocene–Eocene genera with compressed biconvex test and muricocarinae, although considering it to be descended from globanomalinids, as has been traditionally claimed for its type genus *Planorotalites* Morozova, 1957 (e.g., Banner, 1982). This is so because the carinate globanomalinids, which were later separated in the genus *Luterbacheria* Canudo, 1994, were assigned in the past to *Planorotalites* (e.g., Toumarkine and Luterbacher, 1985). However, the presence of muricocarinae in the planorotalitids seems more compatible with the hypothesis that relates this lineage to truncorotalids, as Olsson *et al.* (1999) and Berggren *et al.* (2006) concluded (Fig. 4).

Globanomalinoids

BouDagher-Fadel (2012, 2015) included globanomalinids and pseudohastigerinids in the superfamily Globigerinitoidea, after considering that tenuitellids evolved from pseudohastigerinids as Li (1986) have previously suggested. However, because globigerinitoids appear to be an independent group of planktic foraminifera, globanomalinids must be separated into another superfamily. On these grounds, we have elevated the family Globanomalinidae to the superfamily category.

Globanomalinoids are the first representatives of an extinct Paleogene lineage that also groups superfamilies Hantkeninoidea Cushman, 1927, and Truncorotaloidinoidea BouDagher-Fadel, 2012. This broad lineage was denominated

as nonspinose lineages by Olsson *et al.* (1999) in order to differentiate them from the spinose lineages of the Paleogene, which are clustered in the superfamily Eoglobigerinoidea. The textural distinction between both Paleogene lineages is similar to how non spinose Globorotaliidae and spinose Globigerinidae are distinguished in the Neogene. Loeblich and Tappan (1984) included globanomalinids in the family Hantkeninoidea, but the differences in their arrangements (trochospiral and planispiral respectively) allow them to be separated into two different superfamilies (Fig. 4). We also have tentatively separated pseudohastigerinids of the family Hantkeninoidea, validating the family Pseudohastigerinidae postulated by Canudo (1990). The presence of tubulospines in the hantkeninoids, unlike *Pseudohastigerina* Banner & Blow, 1959, is a character significant enough to differentiate both families, in the same way that in the Cretaceous the tubulospinate schackoinids (family Schackoinidae Pokorný, 1958) were separated from their ancestors globigerinelloidids (family Globigerinelloididae Longoria, 1974). Olsson *et al.* (1999) and Pearson *et al.* (2006) included *Globanomalina* Haque, 1956, in the Cretaceous family Hedbergellidae Loeblich & Tappan, 1961, based on the hypothesis that it evolved from the genus *Muricohedbergella*. Authors of the pforams@mikrotax website (Young *et al.*, 2017) have retaken the family Globanomalinida, but including the genus *Muricohedbergella*. However, Arenillas and Arz (2013a, 2013b) provided high-resolution stratophenetic evidence that eoglobigerinids and globanomalinids evolved from ancestral parvularugoglobigerinids, and therefore that the globanomalinids and hedbergellids are not related and must be taxonomically separated.

Globorotaloids

We have raised to the genus rank the subgenera of *Globorotalia* Cushman, 1927, considered by Kennett and Srinivasan (1983): *Fohsella* Bandy, 1972, *Globoconella* Bandy, 1975, *Hirsutella* Bandy, 1972, *Jenkinsella* Kennett & Srinivasan, 1983, *Menardella* Bandy, 1972, and *Truncorotalia* Cushman & Bermúdez, 1949. They are different *Globorotalia*-type lineages (see pforams@mikrotax website by Young *et al.*, 2017) and some are not phylogenetically related to each other but they are to be the result of a convergent or iterative evolution (see Aze *et al.*, 2011).

Globigerinoids

We have provisionally considered some genera whose species have traditionally been included in the genus *Globigerinoides* Cushman, 1927, for exhibiting all supplementary apertures, but which appear to belong to different lineages (Kennett & Srinivasan, 1983; Bolli & Saunders, 1985; Aze *et al.*, 2011; Spezzaferri *et al.*, 2015; Wade *et al.*, 2018): *Alloglobigerinoides* Huang, 1986; *Globicuniculus* Saito and Thompson, 1976; *Globigerinoidesella* El-Naggar, 1971; and *Trilobigerina* Popescu, 1987. The latter is an objective senior synonym of *Trilobatus* Spezzaferri, Kucera, Pearson, Wade, Rappo, Poole, Morard & Stalder, 2015, since Spezzaferri *et al.* (2015) used the same type species as Popescu (1987).

We have also retained the genus *Zeaglobigerina* Kennett & Srinivasan, 1983, which also contains some *Globigerinoides*-type species. This genus has been considered a junior synonym of *Globoturborotalita* Hofker, 1976 (Olsson *et al.*, 2006a; BouDagher-Fadel, 2012, 2015), but it seems to be useful to group its type-species *Zeaglobigerina woodi* (Jenkins, 1960) and all its *Globoturborotalita*-type descendants (see Cenozoic planktic foraminiferal phylogeny of Aze *et al.*, 2011). *Z. woodi* played a relevant role

in the phylogeny of Neogene planktic foraminifera, from which various *Globigerinoides*-type lineages arose.

SUPPLEMENTARY TEXT S6: TAXONOMIC NOTES ON THE SUPERFAMILY GLOBIGERINITOIDEA

Recent studies have allowed to include *Dipsidripella* in the family Globigerinitidae Bermúdez, 1961 (Pearson *et al.*, 2018b). This genus seems to be closely related to tenuitellids, which may be its descendants. However, since *Dipsidripella* morphologically and texturally differs from tenuitellids (see Pearson *et al.*, 2018b), it is probably also necessary to define a new family for this genus.

SUPPLEMENTARY TEXT S7: HIGHER-RANK CLASSIFICATION OF PLANKTIC FORAMINIFERA

Lee (1990) raised the order Foraminiferida to class Foraminifera, and consequently the suborder Globigerinina to order Globigerinida. Nevertheless, we must note that Mikhalevich (1980) and Sen-Gupta (1999) elevated globigerinids and foraminifera to higher taxonomic categories: subclass Globigerinana and phylum Foraminifera respectively, the first termed subclass Globigerinata by Maslakova (1990).

Mikhalevich (1980, 2004, 2013) considered the subclass Globigerinana Mikhalevich, 1980, as belonging to the class Rotaliata Mikhalevich, 1980, together with the subclasses Rotaliana Mikhalevich, 1980, and Textulariana Mikhalevich, 1980. More recently, Podobina (2015, 2017) again separated globigerinids from rotaliids and textularids in different subclasses within the class Foraminifera.

Based on molecular studies (SSU rDNA), Pawłowski *et al.* (2013) concluded that orders Rotaliida Lankester, 1885, Textulariida Delage & Hérouard, 1896, Robertinida

Mikhalevich, 1980, and Carterinida Mikhalevich, 1980, form a clade that they named class Globothalamea, and proposed that all or most of planktic foraminifera were part of Rotaliida. However, for the reasons stated, it seems more appropriate to separate planktic foraminifera from the rotaliids and divide them at least into four orders, following the same path to how textulariids have been divided into five orders: Textulariida s.s., Astrorhizida Lankester, 1885, Lituolida Lankester, 1885, Trochamminida Saidova, 1981, and Loftusiida Kaminski & Mikhalevich, 2004 (in Kaminski, 2004), and rotaliids into two: Rotaliida s.s. and Buliminida Fursenko, 1958 (see Loeblich & Tappan, 1992, and Kaminski, 2005). Recently, Podobina (2015, 2017) upheld to elevate these last orders to subclasses Rotaliata Mikhalevich, 1980, and Buliminata Podobina, 2014, dividing them in several orders: Rotaliata in orders Rotaliida, Nonionida Podobina, 2014 and Elphidiida Podobina, 2014, and Buliminata in orders Buliminida, Bolivinitida Podobina, 2015, Pleurostomellida Podobina, 2014, and Cassidulinida Voloshinova, 1970 (in Voloshinova *et al.*, 1970). However, members of some of the aforementioned orders are so closely related in molecular phylogenies that it seems difficult to consider them of different orders, as for example textulariids and trochamminids (Pawłowski *et al.*, 2013). Schweizer *et al.* (2008) also concluded that the molecular phylogenetic analyses contradict the traditional separation of rotaliids and buliminids, which was based only on morphological criteria. Instead, they showed the existence of three major rotaliid clades, one of them (clade 3) grouping some rotaliid families (e.g., family Cibicididae Cushman, 1927) together with the family Buliminidae Jones, 1875 (in Griffith and Henfrey, 1875), another (clade 2) grouping the rest of rotaliids, and third (clade 1) grouping families (e.g., Uvigerinidae Haeckel, 1894, Cassidulinidae d'Orbigny, 1839, and Bolivinidae Glaessner, 1937) traditionally considered as belonging to the

buliminids. The same happens with the current planktic foraminifera (globigerinids), which are closely related with the clade 1 of Schweizer *et al.* (2008), hindering their separation from the rotaliids in a different order (Pawłowski *et al.*, 2013). Recently, Holzmann and Pawłowski (2017), after obtaining similar but more detailed results in molecular phylogeny, named the clade 1 of Schweizer *et al.* (2008) as the superfamily Serioidea. They kept clade 3 unnamed although, in order to preserve the traditional names, it could be attributed to the order Buliminida after being this emended. Until new studies in molecular and stratophenetic phylogeny are conducted to resolve these uncertainties, a compromise solution would be for now to divide the rotaliids into three orders, emending Rotaliida and Buliminida, and raising superfamily Serioidea to order Serioida. Some of the rotaliid and buliminid orders suggested by Mikhalevich (2004, 2013) and Podobina (2015, 2017) might also be useful in naming some of the minor clades identified by Schweizer *et al.* (2008) and Holzmann and Pawłowski (2017). All of them could be gathered together with the orders of planktic foraminifera in the subclass Rotaliana Mikhalevich, 1980. The only exception could be the order Globotruncanida in case that its phylogenetic relationship with Robertinida is confirmed. The subclass Rotaliana would be part of the class Globothalamea Pawłowski, Holzmann & Tyszka, 2003, and, consequently, the class Foraminifera Lankester, 1885, should be raised to the category of phylum, as Sen-Gupta (1999) did.

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