

Rise and fall of rotaliid foraminifera across the Paleocene and Eocene times

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ABSTRACT: Rotaliids are one of the groups of larger foraminifera that quickly recolonized the shallow-water environments after the mass extinction at the end of the Cretaceous. Here we present a summary of the state of the art about their stratigraphic distribution and diversity across the Paleocene and Eocene epochs.

Our data suggest that their differentiation at the genus level was very rapid and reached its maximum in the upper Danian SBZ2. Specific diversification, instead, culminated in the upper Thanetian SBZ4, with a second peak during the Cuisian (=upper Ypresian). Successively, the rotaliid diversity definitely declined, whereas other groups of larger foraminifera, and especially *Alveolina* and *Nummulites*, became more widespread and flourished with a large amount of species, up to the lower Bartonian SBZ17, when a final drop in rotaliid diversity is recorded. These major changes appear strictly linked to climate warming events such as Late Danian Event (LDE, generic diversification of rotaliids), Paleocene–Eocene Thermal Maximum (PETM, faunal turnover followed by abrupt decrease in both generic and specific diversity), Early Eocene Climatic Optimum (EECO, increase in number of K-strategists under oligotrophic conditions) and Middle Eocene Climatic Optimum (MECO, ultimate drop in diversity and competition with other larger foraminifera).

Keywords: Rotaliidae, larger foraminifera, diversity, paleoclimate, Paleogene

INTRODUCTION

Rotaliids and related families are benthic foraminifera with complex inner morphology. They can be fully considered as larger foraminifera (LF) for their inner complexity, having evident reproductive dimorphism in some genera, and often reaching a maximum diameter larger than 1 mm. They thrived in shallow to very shallow water environments settling both on vegetated or unvegetated, soft or hard substrates, and also in dysoxic organic-rich bottoms (e.g., Consorti et al. 2018). Because of their structural elements, that require the analysis of differently oriented sections, their identification has been often unreliable and several specialists directed attention to other taxonomic groups. Recently, the seminal monograph by Hottinger (2014) gave new emphasis on the investigation of rotaliids and several researches dealt with this important group of fossil and extant foraminifera (e.g., Benedetti et al. 2011, 2018; Vicedo et al. 2021).

The K/Pg mass extinction swept away almost all larger foraminifera diversified in the latest Maastrichtian; successively, the Paleogene was punctuated by several climatic changes which presumably had effect on the shallow-water communities. We here concentrate our analyses on Paleocene and Eocene, since they were epochs of important changes in benthic communities and, in addition, a few accurate systematic descriptions of the Oligocene are available to contribute to an exhaustive compiling of our list with reliable stratigraphic distribution of each taxon. The Paleocene and Eocene epochs were also characterized by some important environmental perturbations recorded by carbon isotopic excursions. Some of them were caused by hyperthermal events, such as the Latest Danian Event (LDE, 61.7 Ma, Quillévéré et al. 2008; Bornemann et al. 2009), and the Paleocene/Eocene Thermal Maximum (PETM,

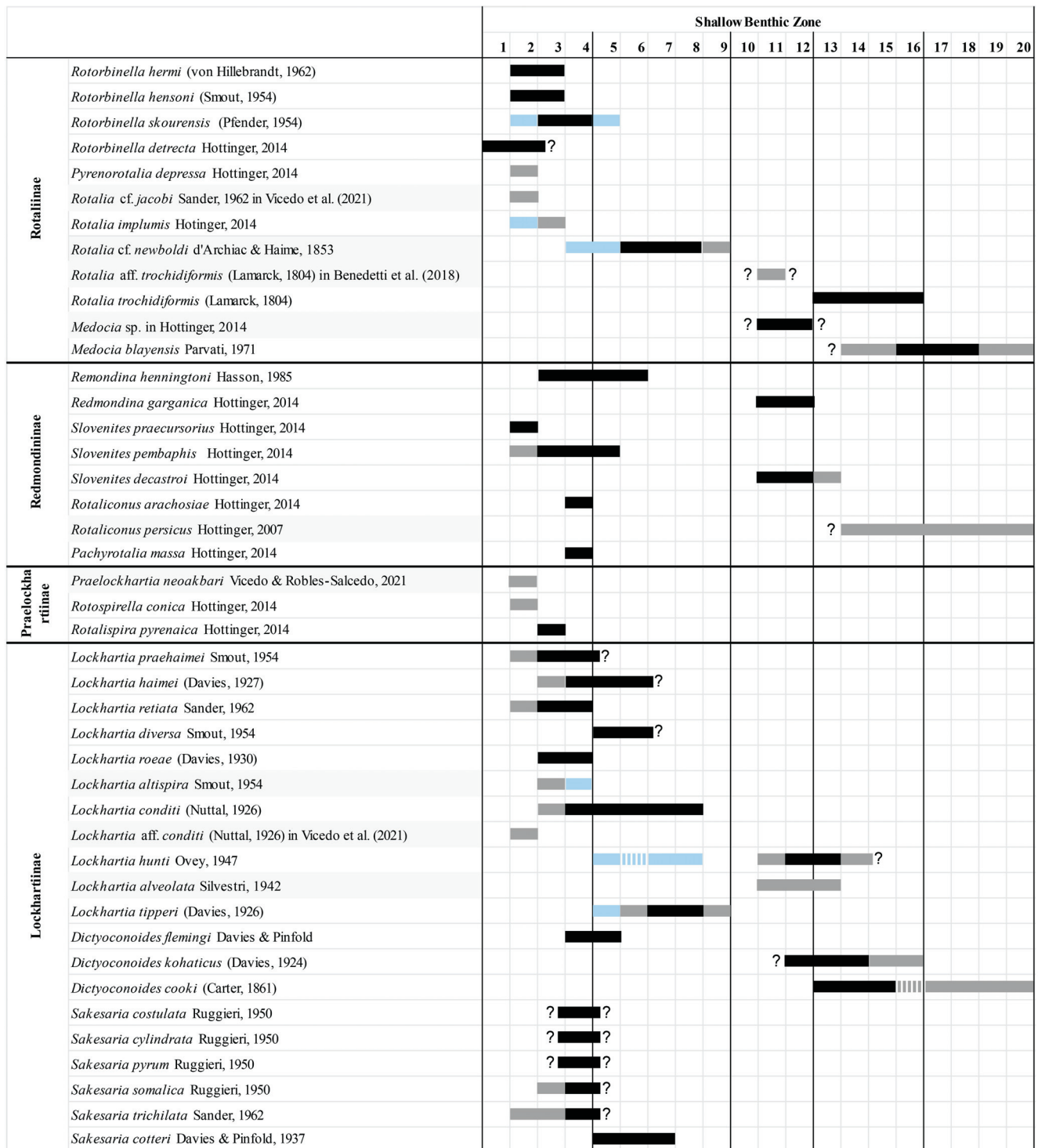
55.5 Ma, e.g., Thomas and Shackleton 1996; Schulte et al. 2013). Other are still to be investigated and apparently not linked to sudden warming, such as the Early Late Paleocene Event (ELPE, 58.4 Ma, e.g., Bralower 2002; Petrizzo 2005; Bernalola et al. 2007), or longer-lasting warmings such as the Early Eocene Climatic Optimum (EECO, 53–49 Ma, Zachos et al. 2001; Luciani et al. 2016) and the Middle Eocene Climatic Optimum (MECO, 40.5–40 Ma, Bohaty and Zachos 2003).

This paper represents part of a work in progress about the diversity of shallow-water calcifiers during the Paleogene and their response to climate changes. The aim of this study, in particular, is to investigate the variation in number of rotaliid taxa through the Paleocene–Eocene of the Neotethys and their response to the major environmental changes occurring in this interval.

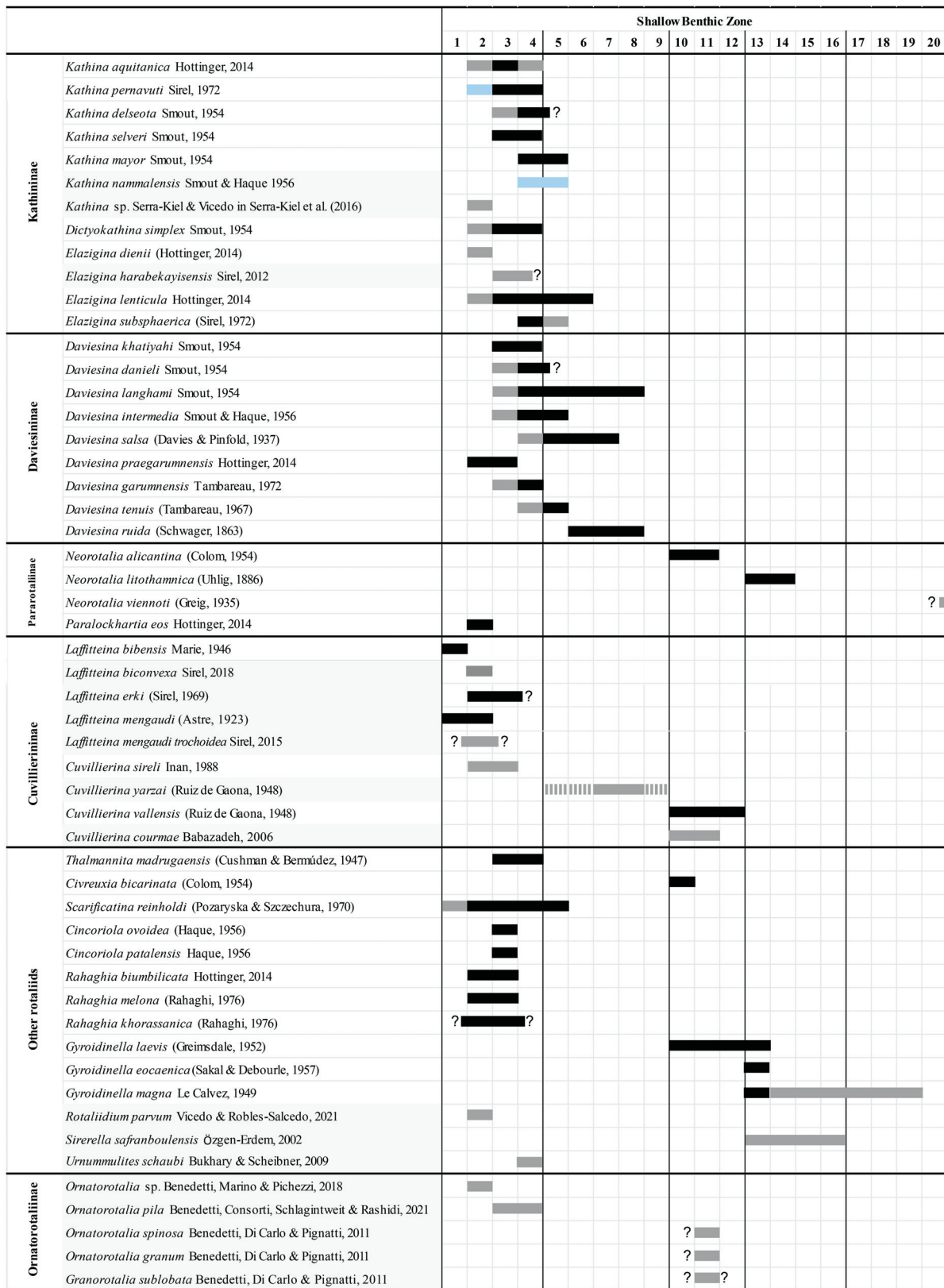
METHODS

To investigate the diversity of rotaliids we provide a list (text-figs. 1-2) of the currently valid taxa and their stratigraphic distribution within the biozonal scheme of Serra-Kiel et al. (1998) recently revised for the Paleocene (Scheibner and Speijer 2009; Serra-Kiel et al. 2020) and the Eocene (Rodríguez-Pintó et al. 2012, 2013; Mochales et al. 2012; Costa et al. 2013; Luciani et al. 2020).

Most of our data derive from the monograph by Hottinger (2014) after a critical revision of the distribution of the species given in the figures and in the text, integrated with data (evidenced in text-figs. 1-2 in light grey) available for other recently discussed species (e.g., Benedetti et al. 2011, 2021; Sirel 2012; Vicedo et al. 2021). We took into account only those species for which an as yet as possible precise stratigraphic interval is given. In compiling our list of rotaliid taxa we decided to in-



TEXT-FIGURE 1
 Range chart of Paleocene-Eocene known species of Rotaliidae belonging to subfamilies Rotaliinae, Redmondinae, Praelockhartiinae and Lockhartiinae. In black data after Hottinger (2014), in grey modification to Hottinger (2014) and additional data from the western Neotethys, in light blue distribution from Tibet (Zhang et al. 2013).



TEXT-FIGURE 2
 Range chart of Paleocene-Eocene known species of Rotaliidae belonging to the subfamilies Kathiniinae, Daviesiniinae and selected related taxa belonging possibly to different family groups and assigned to the subfamilies Pararotaliinae, Cuvillieriniinae, Ornatorotaliinae and other rotaliid-related species. In black data after Hottinger (2014), in grey modification to Hottinger (2014) and additional data from western Neotethys, in light blue distribution from Tibet (Zhang et al. 2013).

clude in our list also data from central-eastern Tethys, available from Tibet and Pakistan, as they provide a huge amount of data for the diversity of rotaliids, especially as concerns the genus *Lockhartia* (e.g., Kahsnitz et al. 2016) which is nearly absent in the western section, except for *L. retinata* reported from western Aquitaine (Hottinger 2014, fig. 5.2).

As part of our ongoing project, we compare the distribution of rotaliids with the number of species belonging to two of the most representatives shallow-water genera of larger foraminifera: *Alveolina* and *Nummulites*. As concerns *Alveolina*, preliminary data about species distribution derive from the monographs by Hottinger (1960, 1974), Drobne (1977) and Sirel and Acar (2008), with the addition of the first appearance of *Alveolina* from SBZ4 given by Serra-Kiel et al. (2020). *Nummulites* species mostly derive from Schaub (1981) and Serra-Kiel et al. (1998) and subordinately by other single researches. Our data are also compared with those of Whidden and Jones (2012) given for Paleogene diversity of alveolinids, nummulitids and orthophragmines.

Diversity indices were calculated by PAST software (Hammer et al. 2001; Hammer and Harper 2006) and then elaborated graphically.

WHAT, IF ANYTHING, IS A ROTALIID?

As above stated, rotaliids are benthic perforated foraminifera with a lamellar test and a complex system of interocular spaces, canals and with a single intercameral foramen (e.g., Muller-Merz 1980). The most important characters of Rotaliidae are the trochospiral chamber arrangement, allowing us to distinguish both ventral and dorsal sides, the interiomarginal position of the single foramen, the folium and its separation from the main chamber lumen by an umbilical plate (Hottinger 2014). Loeblich and Tappan (1987) defined the family Rotaliidae simply as characterized by a trochospiral test, with radial canals and intraseptal and subsutural canals, and including four subfamilies: Cuvillierinae, Rotaliinae, Pararotaliinae, and Ammoniinae. As concerns the latter subfamilies, a recent updated classification based on ribosomal RNA raised at family rank Ammoniidae and placed modern relatives of Pararotaliinae within Calcarinidae belonging to superfamily Calcarinoidea (Holzmann and Pawlowski 2017). *Cuvillierina* has not modern relatives and it belongs possibly to a different family (Hottinger 2014; Benedetti 2015; Benedetti et al. 2018; Consorti and Rashidi 2019). According to the recent genetic analysis (Holzmann and Pawlowski 2017) no true rotaliids (=Family Rotaliidae Ehrenberg 1839) are present in modern oceans, but this issue deserves more researches to be solved. Before the genetic revision of classification, Loeblich and Tappan (1994) in their monograph on extant foraminifera from northern Australia reported 13 species in the family Rotaliidae, three species of *Pararotalia* within the subfamily Pararotaliinae and six species of *Ammonia*, two of *Asterorotalia*, one of *Challengerella*, and one of *Pseudorotalia* under the subfamily Ammoniinae. In addition, four species of calcarinids are documented. Parker (2009) from Western Australia reported a single species of *Pararotalia* and no calcarinid, in addition to nine species of *Ammonia*. More recently, from Indonesia, Förderer and Langer (2018) reported three rotaliid species (two of *Ammonia* and one of *Neorotalia*) and eight species of calcarinids. Debenay (2012) in his inventory on foraminifera from New Caledonia, under family Rotaliidae listed ten species of *Ammo-*

nia, three of *Pararotalia*, one of *Pseudorotalia* and one of *Neorotalia*, in addition to seven species of calcarinids.

Taking into account the new data on the ribosomal RNA, we can assume that no true rotaliids are currently present in the oceans. However, given the subjectivity in the suprageneric classification of fossil, extinct foraminifera, in this work we adopt the traditionally accepted morphological definition of rotaliids, i.e., trochospiral tests with inner complex canal system composed by intraseptal, spiral and umbilical canals, associated to umbilical plate, toothplate and folium. Moreover, we include in our counts taxa that show functional morphology and occupy ecological niches similar to those of *Rotalia* (e.g., Muller-Merz 1980; Hottinger 2014), as also recently adopted for the Cretaceous taxa (e.g., Consorti et al. 2017; Consorti and Rashidi 2019)

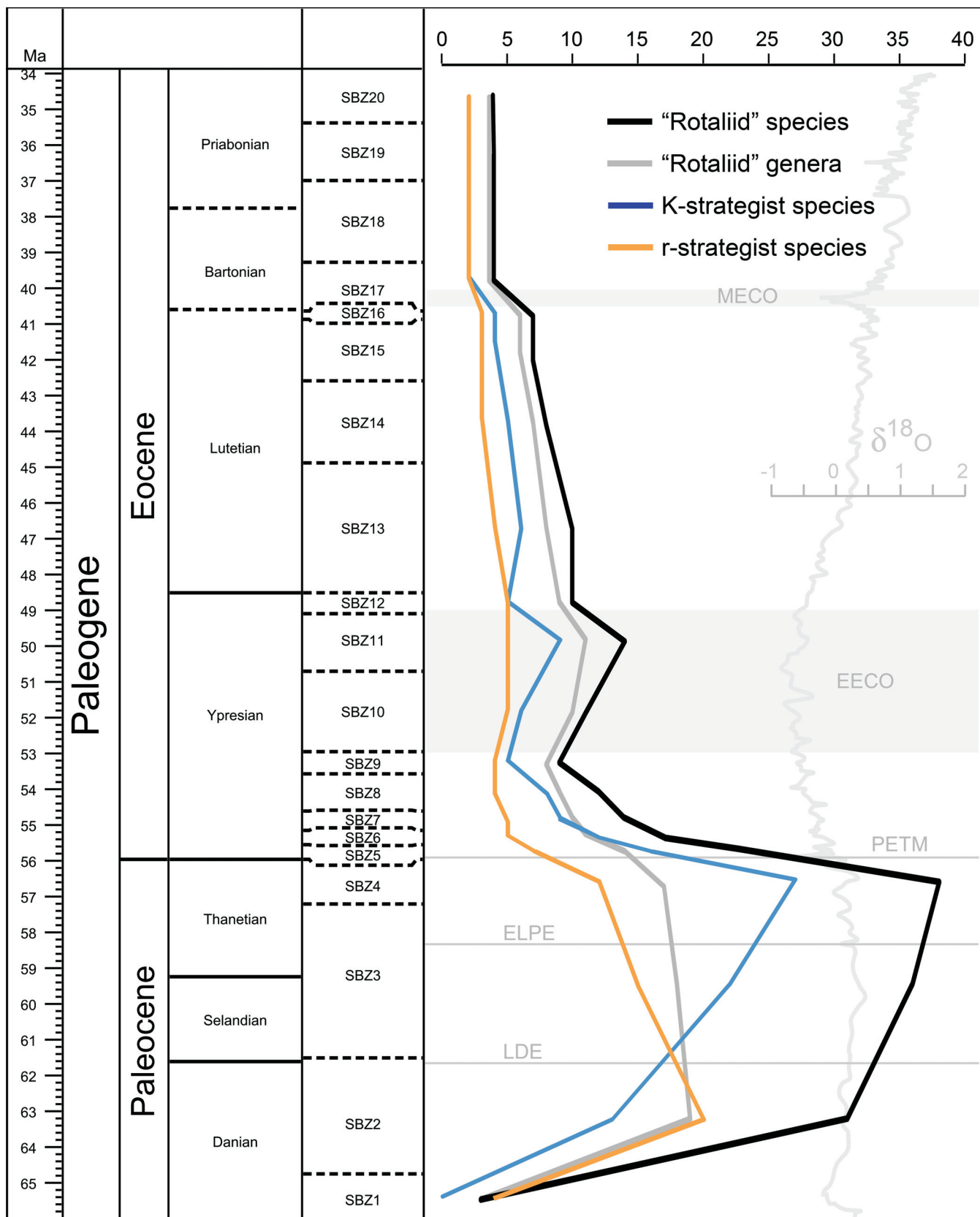
SHALLOW BENTHIC ZONES

The Shallow Benthic Zones (SBZ) have been erected more than two decades ago for the Paleocene-Eocene (Serra-Kiel et al. 1998) and the Oligocene-Miocene (Cahuzac and Poignant 1997). The Paleocene-Eocene biozones are mostly Oppelzones based on the concomitant occurrence of different phylogenetically unrelated taxa (e.g., Pignatti and Papazzoni 2017) and they are not based on the total range or abundance of a single taxon. They are principally, but not exclusively, related to the stratigraphic occurrence of larger foraminifera. With respect to the initial age constraints given by Serra-Kiel et al. (1998), the boundaries among SBZ have been recently recalibrated for the Paleocene (Serra-Kiel et al. 2020), so that SBZ1 spans only the lower part of the Danian and, at least in the western Neotethys, it is barren of larger foraminifera (e.g., Serra-Kiel et al. 1998, 2020); the SBZ2 now embraces the rest of Danian stage; the SBZ3 spans from the base of Selandian to the lowermost Thanetian, and the SBZ4 possibly reaches the Paleocene/Eocene boundary. The Ilerdian (=lower Ypresian) zones were revised by Scheibner and Speijer (2009), and the whole Eocene has been object of several recalibrations (Rodríguez-Pintó et al. 2012, 2013; Mochales et al. 2012; Costa et al. 2013). Luciani et al. (2019) concentrated their efforts on SBZ17–19. We tried to integrate all the new data in producing our stratigraphic scheme but we are aware that, given the general scarcity of information provided by means of continuous shallow-water successions, further studies in the next years could provide evidences of different boundaries. The data obtained from our counts and measurements of diversity indices are plotted, as common rule, in the middle of each biozone.

TAXONOMIC AND BIOSTRATIGRAPHIC REMARKS

Some rotaliids or rotaliid-related taxa were not inserted in the monograph by Hottinger (2014, fig. 1.3). We provide a list as more complete as possible, based on those taxa for which a detailed inner complex morphology is known and the biostratigraphic constraints are available (text-figs. 1-2).

Rotaliconus persicus Hottinger 2007 has been added in the new updated stratigraphic chart (text-fig. 1), in addition to other taxa such as *Praelockhartia neoakbari*, *Rotalia* cf. *jacobi*, *Lockhartia* aff. *conditi* and *Rotalidium parvum* described by Vicedo et al. (2021), *Lockhartia altispira* (recently reported from SBZ4 of Tibet and, in open nomenclature *L. cf. altispira*, from SBZ3 by Vicedo et al. 2021), *Lockhartia alveolata* (Figured in Dinçer and Aşar 2004 and resembling *Lockhartia* cf. *hunti* in Hottinger 2014, plate 5.20) and ornatorotaliids such as *Ornatorotalia pila*, *O. spinosa*, *O. granum*, *O. sp.*, and



TEXT-FIGURE 3
 Generic and specific diversity of rotaliids from Paleocene to Eocene epochs (SBZ1-20). The numbers of r- and K-strategist species are also reported. The absolute ages here and in text-fig. 4 are after Time Scale Creator 7.4. SBZ are recalibrated as explained in the text. Oxygen curve after Cramer et al. (2009).

Granorotalia sublobata (Benedetti et al. 2011, 2018, 2021; Sirel and Deviciler 2017).

Vicedo et al. (2021) suggested that the species figured by Hottinger (2014) under the name *Rotorbinella hensoni* should be considered a new one, whereas *R. detrecta* Hottinger 2014 should be considered fully synonym with *R. hensoni* (Smout 1954). Since a detailed revision of Smout type material is not available, we prefer to adopt a conservative approach and consider as valid the taxonomic identification of Hottinger (2014). Therefore, since the aim of this work is not to review taxonomically the rotaliid taxa, but to provide biodiversity information and to discuss their changes through time, both taxa described by Hottinger (2014) are here considered valid at species-level and their stratigraphic distribution is used accordingly. Zhang et al. (2013) reported *Rotorbinella skourensis* from SBZ2 to SBZ5, thus extending the range given by Hottinger (2014) at least for the eastern Neotethys.

The range chart in Hottinger (2014, fig. 1.3) doesn't report the stratigraphic range for *Rotalia implumis* that can be assigned to SBZ3 according to the type locality in the description of the new species. However, it is also reported in the SBZ2 of Tibet by Zhang et al. (2013). The stratigraphic range of *Rotalia* cf. *newboldi* should be extended upward to the SBZ9, as reported in the text by Hottinger (2014, p. 33) but it is also documented in SBZ4–5 from eastern Neotethys (Zhang et al. 2013).

Rotalia trochidiformis traditionally groups different defined and undefined species belonging to *Rotalia* or similar genera cited from late Paleocene to middle Eocene (e.g., Pignatti 1995). We here accept the species concept of Hottinger (2014) and consider the taxon described by Benedetti et al. (2018) as *R. aff. trochidiformis. Medocia*, that commonly occurs through the (?whole) middle Eocene (e.g., Hottinger 2007; Serra-Kiel et al. 2016a; Tomassetti et al. 2016), is also reported from the Cuisian in open nomenclature (Hottinger 2014) or, erroneously, as *M. blayensis* (Benedetti et al. 2011). Hottinger (2014) questioned also that the new *Medocia* spans through the lowermost Lutetian SBZ13. The stratigraphic range of *Slovenites pem-baphis* can be extended to the SBZ2 (Papazzoni et al. submitted) although Hottinger (2014, p. 47) restricted its range to the SBZ4–5 (3–5 in the chart). The original chart reported *Slovenites decastroii* only from SBZ11–12, but Hottinger (2014, p. 47) and Tomassetti et al. (2016) reported the species from lowermost Lutetian (SBZ13). The range of *Rotospirella conica* is not given in Hottinger (2014), but it is dated as upper Danian SBZ2, according to Vicedo et al. (2021) and Serra-Kiel et al. (2020).

As concerns the distribution of *Lockhartia*, *L. prehaimeii* has been also reported from the SBZ2 of Tibet (Zhang et al. 2013), while *L. haimeii* is documented from the SBZ3–5 of eastern Neotethys (Zhang et al. 2013) and from the SBZ3 of Oman (Serra-Kiel et al. 2016b). *Lockhartia retiata* has been recently reported also from the SBZ2 of Oman (Serra-Kiel et al. 2016b) and Tibet (Zhang et al. 2013), whereas the range of *L. conditi* is extended to the SBZ3 as reported by Hottinger (2014, pp. 77–78). The vertical distribution of *Lockhartia huntii* is more puzzling, since it was assigned to SBZ12–14 in the scheme of Hottinger, and to SBZ11–13 in the text (Hottinger 2014, p. 79); in addition it was documented in SBZ5, 7, and 8 of Tibet (Zhang et al. 2013), thus the species will require further studies since the total range of this species could be very wide, from the

lower to early-middle Eocene. Also the distribution of *Lockhartia tipperi* is ambiguous, since it is reported from the SBZ7–9 in the scheme of Hottinger (2014), but it is SBZ6–8 in the text (Hottinger 2014, p. 83) and it has been found in the SBZ5, 7, and 8 in Tibet (Zhang et al. 2013). Serra-Kiel et al. (2016a) recently extended the ranges of *Dictyoconoides kohaticus* and *D. cooki* respectively to SBZ16 and SBZ20.

The data about *Sakesaria* are rather incomplete and few is known about the total distribution range of most taxa that are attributed to the SBZ4 by Hottinger (2014); *S. trichilata* is also reported from the SBZ2–3 by Serra-Kiel et al. (2016b), whereas *Sakesaria dukhani* Smout is considered fully synonym of *S. somalica* and it is documented by Sirel (2018) from the SBZ3.

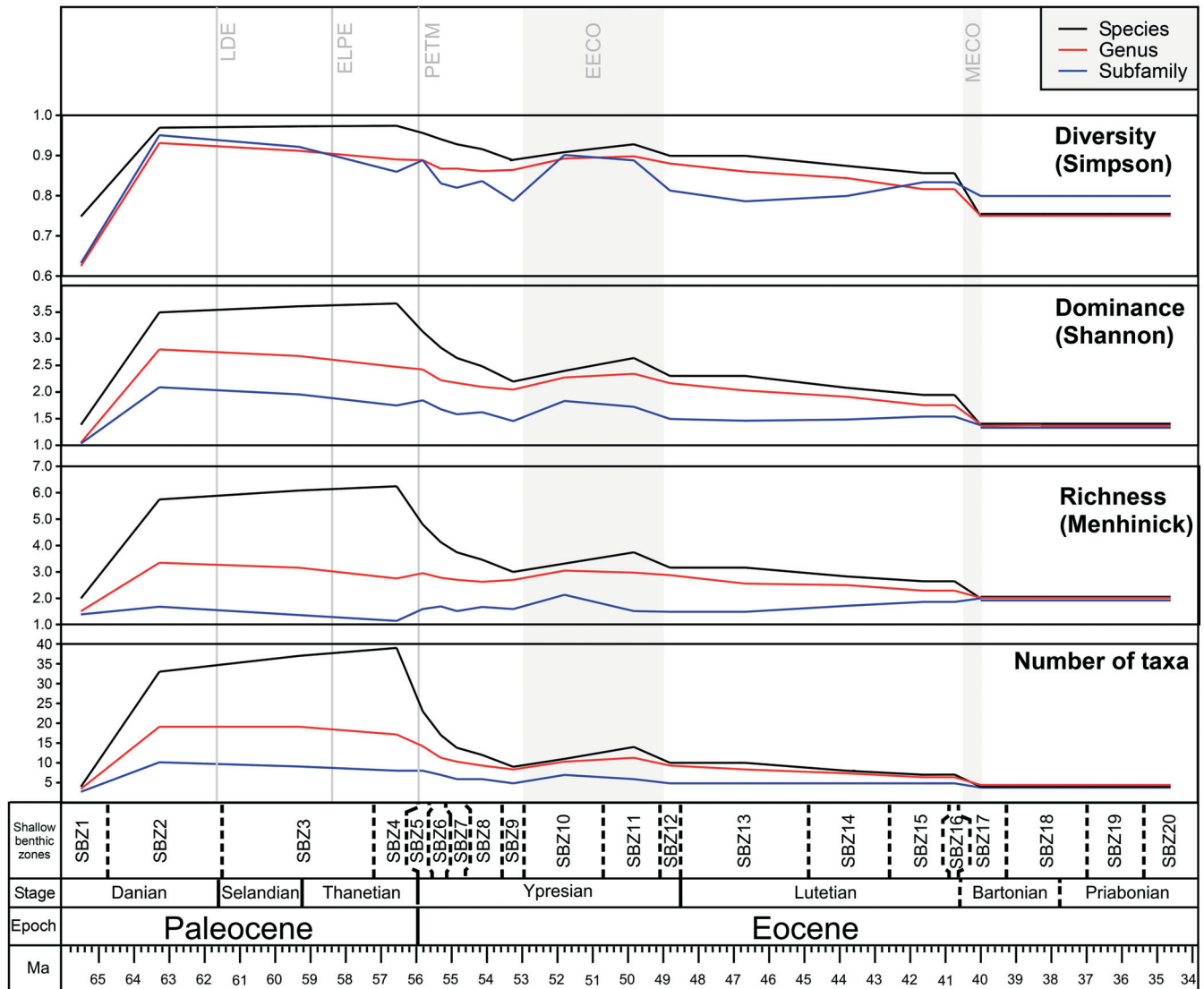
The subfamily Kathininae is characterized by the three genera *Kathina*, *Dictyokathina*, and *Elazigina* (= *Plumokathina* Hottinger). The latter genus could be junior synonym with *Urnummulites*, but the type material figured by Boukhary and Scheibner (2009) is here retained as not apt to compare unambiguously the two taxa, in particular the holotype (Boukhary and Scheibner 2009, pl. 1, fig. 13) is insufficiently illustrated.

The range of *Kathina aquitanica* has been recently changed to the SBZ2–4 (Serra-Kiel et al. 2020) and it also occurs from the SBZ2 of Tibet (Zhang et al. 2013) in association, among others, with *Kathina pernavuti*. Serra-Kiel et al. (2016b) documented *K. delseota* from the SBZ3 in Oman. Vicedo et al. (2021) reported also a specimen *K. cf. major* from the SBZ3 of Oman.

Kathina nammalensis Smout and Haque has been recently reported by Zhang et al. (2013) from the SBZ4–5 of Tibet. Hottinger (2014) considered *K. nammalensis* as possible synonym of *K. selveri*, although further studies are needed on the type material. Several “*Kathina*” have been described in open nomenclature in the last decades from SBZ2 to SBZ4 of Neotethys: some of them belong to *Elazigina* species, but other are possibly new, not yet defined taxa. We decided to retain only one of the most recent finding from the SBZ2 by Serra-Kiel et al. (2016b) which contributed also to extend the range of *Dictyokathina simplex* to the SBZ2. *Elazigina lenticula* has the widest stratigraphic distribution among *Elazigina* in having recently been also documented from the SBZ2 (Papazzoni et al. submitted). *Elazigina harabekayisensis* (text-fig. 2), not reported in the scheme by Hottinger (2014), is referred to the SBZ 3 (Sirel 2012; Serra-Kiel et al. 2016b), although it has been also found in SBZ 4 (Benedetti et al. 2021), and *E. subsphaerica* can be attributed to the SBZ4–5 according to Sirel (2012).

The distributions of *Daviesina* given in Fig. 1.3 by Hottinger (2014) are evidently erroneous, since in the text the author reported *D. danieli*, *D. langhami*, *D. intermedia*, and *D. garumnensis* also from the SBZ3 (Hottinger 2014, pp. 128, 130, 136); in addition *D. salsa* and *D. tenuis* are reported also from the SBZ4 (Hottinger 2014, pp. 141, 148). Although Hottinger (2014) did not specify the foraminiferal assemblages in describing each taxon, thus preventing us to unambiguously constrain the biozonal attribution of some species, from the figure captions is clearly evident that he attributed to SBZ3 all the taxa from the lower Lockhart Formation and to SBZ4 those from the upper Lockhart Formation (e.g., Hottinger 2014, p. 130).

Very few data are available for the stratigraphic distribution of fossil representatives of the genus *Neorotalia*. Hottinger (2014) reported three species that require further detailed investigation



TEXT-FIGURE 4
Number of rotaliid taxa, richness, dominance and selected diversity indices variations through Paleocene to Eocene.

since some specimens figured as *Neorotalia alicantina* possibly belong to *Ornatorotalia granum*, according to Benedetti et al. (2018). Sztrákos (2005) signalled *Neorotalia gr. tuberculata* from the upper Paleocene and lower Ypresian of the North Pyrenean (France), but the specimens are figured only from external view and Benedetti et al. (2011) raised their possible relation with *Ornatorotalia*.

The representatives of the subfamily Cuvillierinae Loeblich and Tappan, 1964, senior synonym of Laffiteinae Hottinger, 2014 are more puzzling, since Hottinger (2014) considered valid only one species of *Laffiteina* from lower Danian, i.e., *L. bibensis*, but Sirel (2018) reported up to five species from the Paleocene of Turkey, and again in Hottinger (2014) only two species of *Cuvillierina* are discussed. In our list we added also *C. yarzai* from the Ilerdian and *C. cormae* from the lower-middle Cuisian.

Ornatorotaliids (sensu Benedetti 2015) are also added since they present some taxonomic characters similar to those of the real rotaliids.

According to Serra-Kiel et al. (2020) *Haymanina danica* Sirel 2012 from the SBZ1 is considered as a junior synonym of *Scarificatina reinholdi* thus extending its range into the lower Danian. *Sirelella safranboulensis* Özgen-Erdem 2002 is here considered a rotaliid, according to Hayward et al. (2018), although detailed investigation of the inner structure are needed to clarify its systematic attribution. *Caldegina* (Sirel 2018) is not included in our counts because of its inner structure and wall texture that require further works on well-preserved tests. *Soriella bitlisica* Sirel 1998 is considered by Hottinger (2014) as a synonym with two other taxa. As stated by Hottinger (2014) *Soriella* Haque will require more detailed studies to understand its systematic position. *Gyroidinella*, not a rotaliid or related form, is not taken into account in this work for the biodiversity

evaluation. The type species, assigned by Sirel (2012) to the new genera *Pseudodictyokathina* and *Postorbiokathina* are considered by Hottinger (2014) fully synonym of *Dictyokathina* and are not included in our count.

As above debated, *Urnummulites schaubi* Boukhary and Scheibner 2009 could be considered senior synonym of *Elazigina*, but it is listed in text-figure 2, although it is not included in the count for biodiversity considerations, since it is possibly synonym with *Elazigina lenticula*.

GHOST TAXA

To provide a reliable inventory of the number of extinct rotaliids, we completed the list with ghost taxa that are possibly still missing from the fossil record. As 'ghost taxa' we consider all those taxa whose existence is inferred from the discontinuous stratigraphic range of a genus. A ghost taxon is inserted to fill the gaps and to complete the stratigraphic range of a genus. Indeed, rotaliids are one of the few groups of LF to pass the K/Pg crisis event as documented by the occurrence of the same genera in the uppermost Cretaceous and upper Danian. Consorti and Rashidi (2018) documented *Elazigina siderea* from the Maastrichtian of Iran as a possible ancestor of *Elazigina dienii* (SBZ2), thus suggesting the theoretical occurrence of *Elazigina* also in the SBZ1. Similarly, also *Rotalispira*, *Pyrenerotalia* and *Daviesina* are reported both for Upper Cretaceous and upper Danian (Boix et al. 2009; Hottinger 2014). *Rotorbinella* is instead recorded in temporal continuity from the Cenomanian (e.g., Consorti et al. 2017).

Most of the rotaliid genera in our scheme have not as yet known complete stratigraphic range or their related species are still missing, for example *Rotalia*, *Medocia*, but especially *Redmondina*, *Slovenites*, *Rotaliconus*, and *Dictyoconoides*. The latter three genus are actually represented by few taxa that appear not phylogenetically correlated.

As mentioned above, also for *Pararotalia*, *Neorotalia* and *Cuvillierina* our knowledge is still fragmentary, thus some as yet undetermined species should occur. Although the genera *Pararotalia* and *Neorotalia* are signalled since the Late Cretaceous (e.g., Consorti et al. 2017), we cannot establish here that they can be unambiguously accepted as ancestor of modern representatives of both genera. To maintain a conservative approach, we prefer to add, when possible, only one ghost (not yet discovered) species to fill the gap. As suggested by Benedetti et al. (2021) at least one as yet not recovered *Ornatorotalia* should be present in the lower Ypresian. As discussed above, a good candidate could be *Neorotalia tuberculata*.

REPRODUCTIVE STRATEGIES AND ECOLOGICAL IMPLICATIONS

Most rotaliids, as other LF, show reproductive dimorphism, with small megalospheric (larger proloculus) A form and large microspheric (smaller proloculus) B forms, although the difference in embryo size is not always evident. The occurrence of a dimorphic cycle, the occurrence of symbionts in extant LF (e.g., Hohenegger 2011) and the long life of larger forms, lead to the conclusion that, among foraminifera, LF are in general considered as K-strategists, adapted to stable, oligotrophic environments (e.g., Hottinger 1997). However, among LF Hottinger (1999) suggested that the A-forms can be considered more opportunists (r-strategists) and the B-forms more specialists (K-strategists).

High fecundity, large number of offspring, small-sized tests are typical features of r-strategists, whereas on the contrary low fecundity, small number of offspring and large tests are characteristic of K-strategists. Environmental stresses (eutrophication, low temperature, insufficient food or light, high salinity, water turbidity, oxygen depletion and low pH) tends to favour r-strategists, whereas K-strategists dominate under stable conditions (oligotrophic environment, good illumination, relatively high temperature, normal values of salinity, pH, and oxygen content).

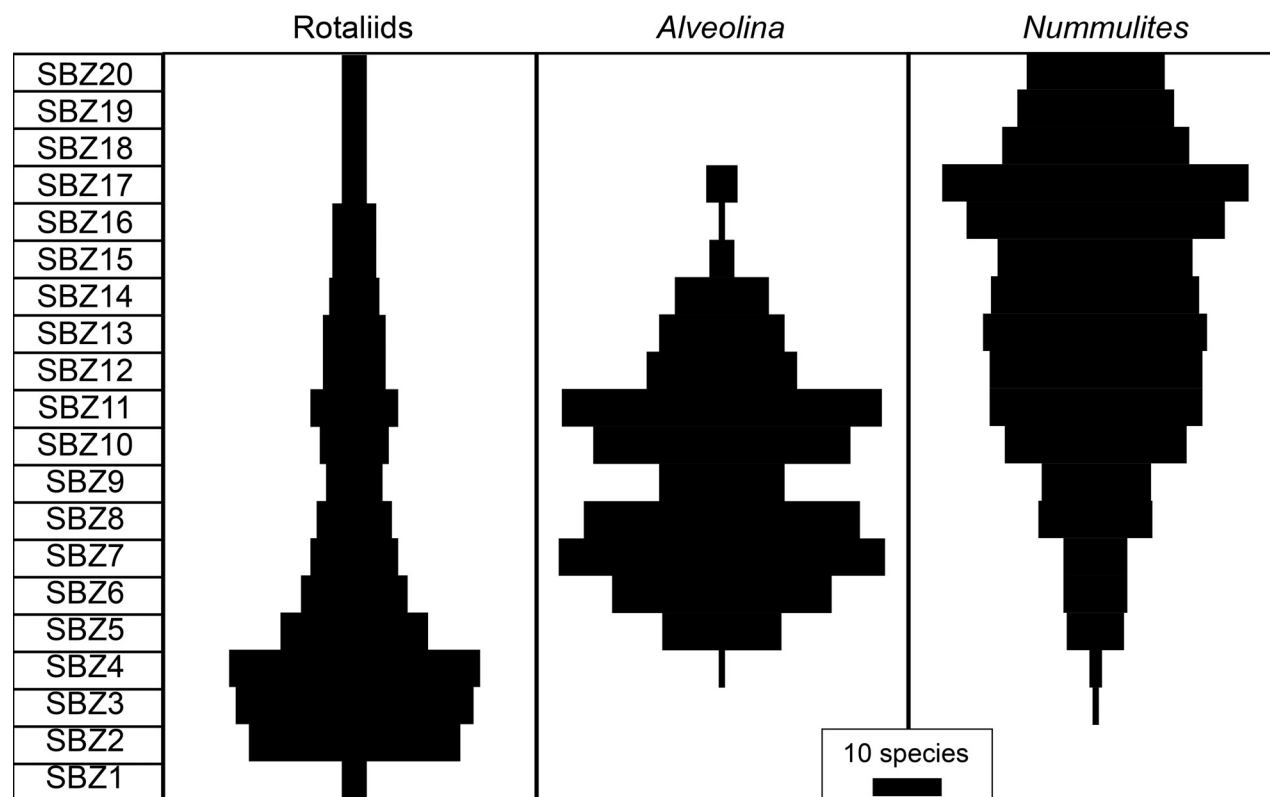
Among rotaliids, the K-strategists are principally recognized on the basis of the occurrence of dimorphism, large test and complex morphology. Hottinger (2014) reported the relative frequencies of K-strategist taxa within rotaliids to discuss them in terms of Global Community Maturation (GCM sensu Hottinger 2001). We followed the criteria of Hottinger to recognize r- and K-strategists among the listed species.

The species belonging to Rotaliinae, Redmondinae, Praelockhartiinae and most of rotaliid-related forms are considered as r-strategists, due to their small size and to the lacking of true microspheric generation. *Laffitteina* is apparently an opportunistic genus able to bypass the K/Pg event (Hottinger 1997). Within Lockhartiinae, only *Sakesaria* is r-strategist, whereas Kathiniinae and Daviesiniinae are fully K-strategists, as are Pararotaliinae and Cuvillieriniinae. Hottinger (2014) included also *Thalmanita* in the group of K-strategist. Among ornatorotaliids, *Ornatorotalia spinosa* has been erected on the basis of both A and B forms by Benedetti et al. (2011), and only later a microspheric specimen of *Granorotalia sublobata* has been detected (Benedetti 2015), thus suggesting that both genera were possibly K-strategists.

RESULTS AND DISCUSSION

The results of counts of total number of rotaliid species and genera and relative r- and K-strategist taxa are illustrated in text-figure 3. No K-strategist rotaliids are recorded from the SBZ1 and their number increase almost linearly up to the end of the Paleocene. The opportunists that survived after the K/Pg mass extinction and other r-strategist taxa rapidly increase during the Danian, possibly up to the hyperthermal LDE, close to the end of the lower Paleocene. A 10 million years interval was required for the first diversification of the K-strategist LF, covering the whole Paleocene (Hallock et al. 1991; Hottinger 1997, 2001), even if the first recovery (SBZ 1–2) was indeed quite rapid. The maximum differentiation of the K-strategist rotaliids is following the ELPE, also known as MPBE, an interval of warm, oligotrophic surface waters fully occurring within SBZ3 and roughly coinciding with the first occurrences of the orthophragminids, *Glomalveolina*, and *Nummulites* (e.g., Whidden and Jones 2012). After this event, larger and more complex tests such as *Elazigina subsphaerica*, some *Lockhartia* and *Daviesina* species appeared. While opportunistic genera appear as widely distributed across the entire Neotethys, some regional differences occur among K-strategists, since *Lockhartia* is mainly confined in the eastern Neotethys, where *Nummulites* and *Alveolina* were instead absent or very rare (e.g., Speijer et al. 2012).

Species, genera and subfamily diversities indices are calculated for the investigated interval and reported in text-figure 4. As concerns the number of genera, their richness and diversity, a rapid increase from the SBZ1 to the SBZ2 is noteworthy, thus



TEXT-FIGURE 5
Total number of rotaliid species for each biozone compared with distribution of *Alveolina* and *Nummulites* species per biozone.

suggesting that from the lower to upper Danian a rapid radiation of rotaliids occurred. The rotaliids, after surviving the K/Pg crisis, very soon occupied some vacant niches left by the extinction of shallow-water LF at the end of Cretaceous. Moreover, the number of subfamilies followed the same trend as the genera during the whole Paleocene. The generic diversity decreased from the SBZ2 to the SBZ4, whereas species diversity increased, revealing that in the SBZ4 the rotaliids reached their maximum richness at species level, although some genera became extinct (e.g., *Laffitteina*, *Praelockhartia*, *Rotospirella*, *Rotalispira*, *Cincoriola*, *Rahaghia*). Hottinger (2001) similarly recognized a first generic diversification of all LF starting from SBZ2 and a specific one from SBZ3 in the frame of CGM cycle. At the end of the Paleocene, the shallow-water communities were highly diversified and alveolinids and nummulitids were starting their evolutionary diversification.

After the PETM, the number of rotaliids steadily decreased, whereas other LF such as *Alveolina* and *Nummulites* show a sudden increase (text-fig. 5) as documented also by Whidden and Jones (2012). Rotaliids were typical of shallow-water environments as for their modern analogous Calcarinidae. During the Paleocene, they occupied lagoonal to reefal environments. However, after the PETM the rapid radiation of *Alveolina* (text-fig. 5) seems to replace them both at generic and specific level. At higher depth, the rapid evolution of *Nummulites* (text-fig. 5) and also orthophragmines (Whidden and Jones 2012) most probably played an analogous role.

The abrupt decrease in the number of rotaliid species corresponds to a slight increase of both genera and subfamilies diversity and richness as displayed by the values of Simpson and Menhinick indices (text-fig. 4).

During the early Ilerdian, the vacant shallow-water settings were rapidly recolonized by *Alveolina* that increased up to the SBZ7-8 (Drobne et al. 2011). The sudden depression of SBZ9 (text-figs. 3-5) is considered by Hottinger (2001, 2014) as an artefact due to the scarcity of sedimentary deposits that can host K-strategist foraminifera in that interval. This drop is then followed by a second favourable phase for K-strategists, corresponding to the long-lasting EECO event and culminating in the middle Cuisian SBZ11. A new generic and especially subfamily diversification is recorded in the SBZ10, followed by a species increase in the SBZ11. During the EECO, under oligotrophic condition, several K-strategists LF dominated the shallow-water settings. Rotaliid and ornatorotaliid genera generally occur associated with several *Alveolina* species with a weak peak in the middle Cuisian SBZ11 (Drobne et al. 2011) possibly generated by the rising of the sea surface temperatures.

After the EECO our data suggest a decline in the species richness, diversity, and in the number of both K- and r-strategists.

Finally, in the SBZ17 the number of rotaliid species, the diversity and richness dropped and a few K-strategists survived, whereas *Alveolina* and especially *Nummulites*, that reached their maximum size, had a peak in response to the MECO event.

Global warming events are always associated with sea level changes that affect especially the shallow-water biota, such as LF. Due to these sea level changes, the sedimentary record of carbonate shelves is inherently discontinuous, therefore our analysis suffers for the lacking of high-resolution data, being the biozones too coarse for a detailed analysis. At present, we are not able to investigate the response of rotaliid abundance and diversity to local or short-term global variations of the shallow-water environments.

CONCLUSIONS

The climatic events played a pivotal role in the diversification of rotaliids and of the LF in general, by combining principally increase of surface water temperatures with changes towards oligotrophic conditions. The shift from eutrophic to oligotrophic conditions is most probably the main factor contributing to the LF (and rotaliids) differentiation during the Paleocene–Eocene.

The rotaliids are resilient taxa that survived the mass extinction occurred at the end of the Cretaceous. The diversification of rotaliids started very rapidly and culminated at genus level in the upper Danian, earlier than previously accepted (e.g., Hottinger 2001), whereas the Thanetian peak for species diversification is confirmed. Differently to other taxonomic groups, i.e., alveolinids and nummulitids, for which a single genus during the whole Eocene gave rise to numerous species, the rotaliid genera are usually characterized by a low number of species, possibly due to the intense competition with the other shallow water K-strategist taxa (*Alveolina* and *Nummulites*) established after the PETM event.

The long-lasting oligotrophic conditions recorded during the EECO contributed to a great diversification of several shallow-water LF, such as alveolinids (Drobne et al. 2011; Whidden and Jones 2012) and K-strategist rotaliids.

The competition with other K-strategist LF probably contributed to the decline of rotaliids in the middle Eocene up to the MECO event, when a last dramatic drop is recorded by the known fossil record.

This work provides a first detailed analysis of the diversity of a still poorly known group of shallow-water foraminifera, suggesting that an adaptive radiation in the lower Paleocene, right after the K/Pg event, lead to a rapid evolutive differentiation of several rotaliid genera. We aim to add further works on a larger amount of data about LF to investigate the biodiversity pattern of this informal group of shallow-water organism, their response to climate changes and their resilience capacity after sudden crisis events.

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