Marine Micropaleontology 194 (2025) 102423

Contents lists available at ScienceDirect

Marine Micropaleontology

journal homepage: www.elsevier.com/locate/marmicro

Paleoecological and paleoenvironmental insights from Ornatorotaliidae (larger foraminifera)

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ARTICLE INFO

Keywords:
Symbiont-bearing larger benthic foraminifera
Paleogene
Ecological niche
Evolution
Foraminifera

ABSTRACT

The present study deals with the ecology and phylogenetic relationships among species of the genera *Ornatorotalia*, *Granorotalia*, and *Risananeiza* belonging to the Family Ornatorotaliidae. The microfacies analyses allowed us to assign each taxon to its life paleoenvironment within the shallow-water carbonate setting, and to make a comparison with extant species belonging to the family Calcarinidae. While different species of *Ornatorotalia* and *Granorotalia* thrived only in the inner ramp, *Risananeiza* spp. possibly inhabited also deeper environments up to the middle ramp. The phylogenetic relationships among genera and species are here briefly discussed, nonetheless it's still impossible to identify any unambiguous ancestor of this group.

1. Introduction

Larger foraminifera (LF) is an informal name used for a polyphyletic group of symbiont-bearing single-celled foraminifera with a complex inner structure that can reach up to 15 cm in diameter (Hottinger, 2000). Living LF host photosymbiotic algae within their test and thrive in shallow-water environments within the photic zone where they can provide sufficient light for their symbiont needs (e.g., Hohenegger, 2011). Their test size, shape, and density are in equilibrium with the hydrodynamic conditions of the seafloor they inhabit (Seddighi et al., 2015; Briguglio et al., 2017) and in some cases, they can resist transport by staying firmly attached to their substrate (Hohenegger, 2000). Recent studies also provided results on how quickly the cells can respond to temperature variations within shallow-water ecosystems (e.g., Prazeres et al., 2017) and such variations can be considered as proxies to reconstruct accurately paleoenvironments and paleotemperatures (e.g., Gandolfi et al., 2023). The correct taxonomic identification of LF plays therefore a pivotal role in both biostratigraphic and paleonvironmental interpretation of shallow-water carbonate successions (see e.g., Consorti and Schlagintweit, 2020). In addition, LF, with their complex structures and rapid evolutionary trends, offer invaluable insights into the biostratigraphy of shallow-water sedimentary successions (e.g., Benedetti and Schiavinotto, 2023). Some groups of these organisms, such as alveolinids, nummulitids, rotaliids and radial foraminifera are useful biostratigraphic markers. The Shallow Benthic Zones (SBZ, Cahuzac and Poignant, 1997; Serra-Kiel et al., 1998) have been pivotal in dating shallow-water carbonate deposits since their inception, due to the scarcity or absence of planktonic index fossils in shallow-water settings.

Among LF, rotaliids were pioneers in recolonizing the shallow-water environments after the K/Pg mass extinction (Benedetti and Papazzoni, 2022), and also the rotaliid-like groups, such as ornatorotaliids, were important calcifiers widely distributed from the Central to Eastern Neotethys Paleogene carbonate platforms (Benedetti et al., 2011, 2018, 2021; Sirel, 2018; Sirel and Devecíler, 2017). Afterward their recent systematic description (Benedetti et al., 2011), ornatorotaliids have been commonly reported from upper Ypresian (i.e., Cuisian) shallow-water carbonates deposited especially during the warming event known as Early Eocene Climatic Optimum (EECO, 53–49 Ma, Zachos et al., 2001; Luciani et al., 2016). As concern the Neotethys, the Ypresian is traditionally subdivided into the Ilerdian and Cuisian stages by LF scholars, by means of faunal turnover and distinct evolutionary trends observed in nummulitids and alveolinids. Even if these stages are regionally defined and not formally recognized (Pomerol, 1981; Speijer et al., 2020) they are still useful for correlating early Eocene biozones, particularly the SBZ by Serra-Kiel et al. (1998).

More recently, additional species have been reported from the

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https://doi.org/10.1016/j.marmicro.2024.102423
Received 3 October 2024; Received in revised form 27 November 2024; Accepted 27 November 2024

Paleocene of Central and Eastern Neotethys as well as from the Oligocene to Miocene of the Neotethyan Realm (see Fig. 1 for location of the investigated samples).

This study has the following aims: 1) to discuss the paleoecological and paleoenvironmental significance of the extinct species included into the family Ornatorotaliidae Benedetti, 2015a 2) to define their commonly occurring associations and their (paleo)ecological optimum, and finally 3) to discuss their relationships with the specific depositional paleoenvironments.

2. Material and methods

2.1. The family Ornatorotaliidae

2.1.1. Systematic position

The family Ornatorotaliidae has been erected by Benedetti (2015a) to describe rotaliid-like trochospiral foraminifera with open canals on both ventral and dorsal side, including the genera *Ornatorotalia* and *Granorotalia*, to which has been added later also the genus *Risananeiza*. Benedetti and Sinanoğlu (2022) included the family under the superfamily Calcarinoidea that, according to recent molecular analyses by Holzmann and Pawlowski (2017), comprises only the family Calcarinidae, in which they group also *Pararotalia* and *Neorotalia*, belonging to the subfamily Pararotaliinae. Hayward et al. (2021) included *Ornatorotalia*, *Granorotalia*, and *Risananeiza* in the subfamily Pararotaliinae. More recently, Innamorati et al. (2024) considered *Ornatorotalia* within Pararotaliidae. The occurrence of open dorsal canals could be considered as a key diagnostic feature to maintain Ornatorotaliidae within the superfamily Calcarinoidea.

2.1.2. The genus Ornatorotalia

Benedetti et al. (2011) firstly described the genera *Ornatorotalia* and *Granorotalia* from the upper Ypresian (middle Cuisian) of northern Sicily and Maiella Mts. (Central Italy). Pignatti (1995) figured *Ornatorotalia granum* under the unformal name "small rotaliids". Benedetti et al. (2018) reported both taxa from the middle Cuisian of Central Italy. The species *O. granum* has been recently reported from the middle Ilerdian SBZ7–8 of Turkey by Bozkurt and Görmüs, 2021. The identification of the figured specimen is consistent but its proloculus diameter is 35 μm, smaller than the type material, thus suggesting a possible evolutionary trend testified by an increase in embryonic size within the species lineage.

Benedetti et al. (2018) also found a few specimens of *Ornatorotalia* sp. from an SBZ2 assemblage of Central Italy but the available material is insufficient for a complete and accurate description of a new taxon.

Benedetti et al. (2021) described *Ornatorotalia pila* from the upper Thanetian of Iran, occurring also in the lower Thanetian (Sirel and Devecíler, 2017), or more precisely from biozones SBZ3–4 (sensu Serra-Kiel et al., 1998), recently recalibrated as corresponding to Selandian-Thanetian (Serra-Kiel et al., 2020; Papazzoni et al., 2023). *Ornatorotalia pila* has been recorded by Rahaghi (1983) as *Rotalia* sp. and possibly also the specimens identified as *Calcarina* (Rahaghi, 1983; pl. 46, Figs. 1–16) can be referred to this species. In addition, some specimens figured by Samuel et al. (Samuel et al., 1972, pl. 40, Fig. 2) and identified as genus *Rotalia* can be possibly referred to *O. pila* (see Benedetti et al., 2021). Carrasco et al. (2019) and Rivandi and Moosavizadeh (2015) reported, yet not figured, *O. granum* from the Thanetian of North Eastern Iran, which could be possibly referred to *O. pila*.

Benedetti and Sinanoğlu (2022) described from upper Danian (i.e., SBZ2) of easternmost Turkey a different new species, *Ornatorotalia ozgenerdemi,* characterized by small size, small megalospheric embryo, and apparent absence of reproductive dimorphism.

2.1.3. The genus Granorotalia

Granorotalia sublobata has been described from the middle Cuisian of Sicily and Central Italy, where it is routinely found displaced from inner ramp (e.g., Benedetti et al., 2018). Specimens possibly referred to *Granorotalia* have been described from the Lutetian of Western Carpathians by Samuel et al. (1972), in open nomenclature as *Rotalia* sp. 8 (Samuel et al., 1972, pl. 47, Figs. 1–4). Recently, both *Ornatorotalia* and *Granorotalia* have been also reported from the lower Cuisian of Iran (Motamedalshariati, 2023) and up to the lowermost Lutetian of Longobucco, Calabria (Southern Italy, Innamorati, 2022; Innamorati et al., 2024), and they are routinely documented as resedimented in middle ramp to slope deposits of Central Italy (Mangione, 2010; Benedetti et al., 2011, 2018; Tomassetti and Benedetti, 2020; Marino et al., 2022).

No ornatorotaliids are so far documented in literature from Bartonian to lower Rupelian of Neotethys, although we found two individuals (as uncentered sections) possibly referred to *Granorotalia* from upper Eocene assemblages of southern Sicily, near Siracusa (Fig. 2).

2.1.4. The genus Risananeiza

We include the genus *Risananeiza*, with its two species *R. pustulosa* and *R. crassaparies,* within the family because of the open canals on both sides (differing from Pararotaliinae), the type of canal systems, and the single aperture (differing from Calcarinidae). Benedetti and Briguglio (2012) tentatively proposed a systematic affinity between *Risananeiza* and ornatorotaliids, and Benedetti (2015a) erroneously assigned the taxon to the subfamily Cuvillierininae because of the absence of spines in the microspheric generation.

Risananeiza pustulosa, described from the Chattian of northern Egypt (Boukhary et al., 2008), has been also recorded from Turkey (e.g., Sirel and Işik, 2011) and westernmost Neotethys (Ferràndez-Cañadell and Bover-Arnal, 2017). Some specimens described by Bassi et al. (2007) as *N. viennoti* from the upper Chattian of Veneto (Northern Italy) can be more likely referred to this species. *Risananeiza crassaparies*, smaller

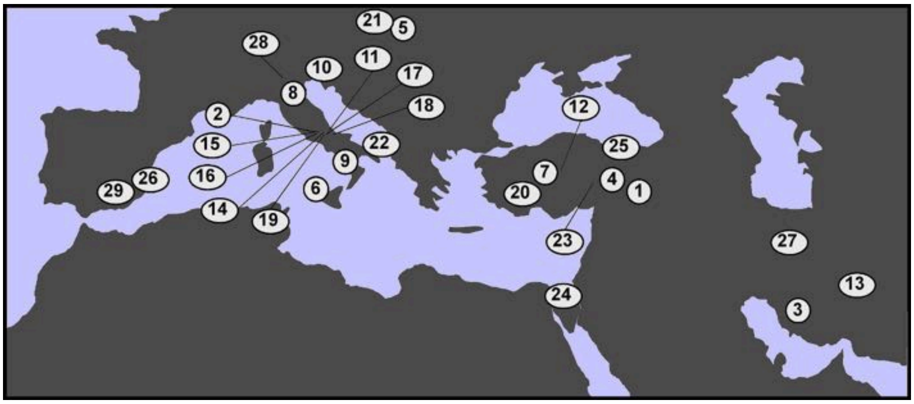

Fig. 1. Simplified location of the investigated samples, numbers as in Table 2.

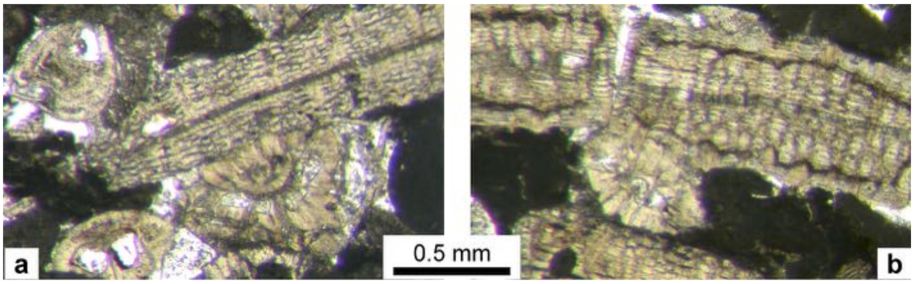

Fig. 2. Two specimens tentatively assigned to *Granorotalia* by the possible occurrence of vertical funnels and spinose periphery of specimen (a) and vertical funnels on both sides of the specimen (b). The specimens are both uncentered and contained in an unsorted larger foraminiferal packstone referred to the Priabonian (SBZ19–20) by the occurrence of *Chapmanina gassinensis*, *Pellatispira madaraszi, Medocia blayensis, Nummulites* ex gr. *incrassatus, Discocyclina* spp., *Asterigerina rotula, Neorotalia* spp. and *Fabiania* sp. (by courtesy of S. Carbone and C. Monaco, University of Catania).

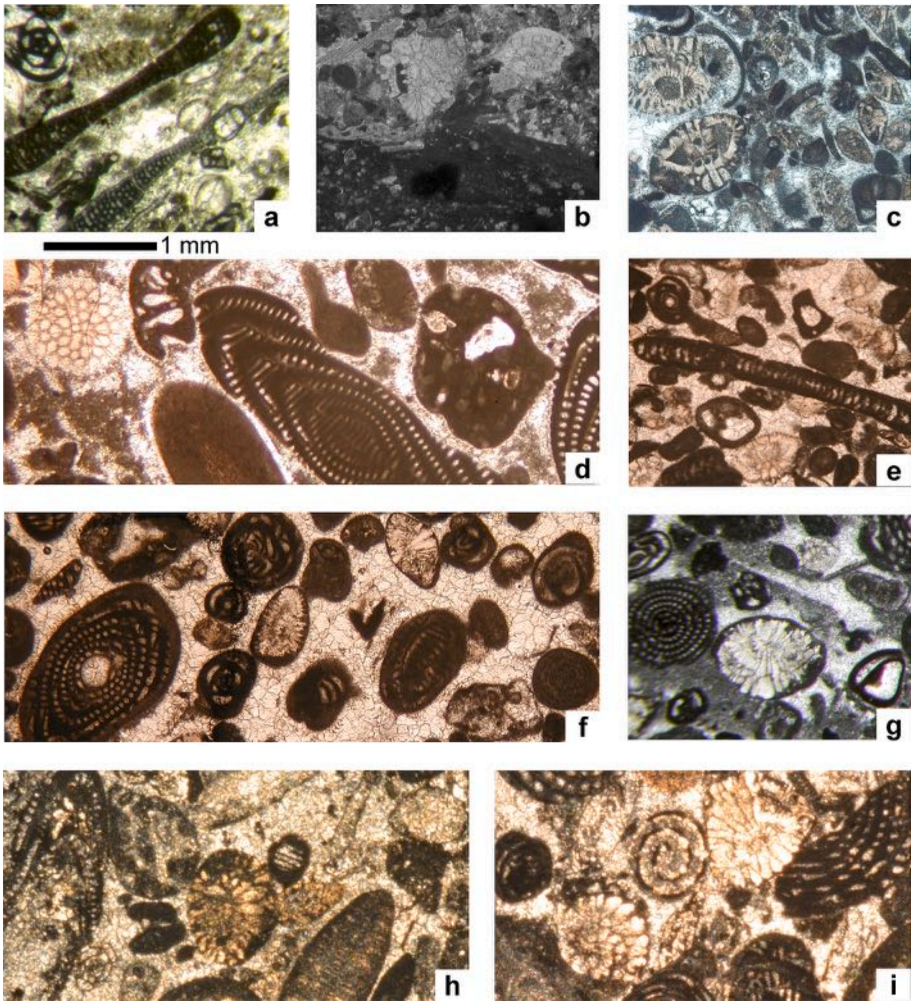

Fig. 3. Microfacies of the investigated ornatorotaliid-bearing samples. a. poorly sorted grainstone with isooriented large and flattened *Mardinella daviesi*, upper Danian (SBZ2) of Becirman (Turkey), sample YGA; b. unsorted bioclastic packstone-wackestones, upper Danian (SBZ2) of Antrodoco (Central Italy), AM46; c. poorly sorted grainstone, upper Thanetian (SBZ4) of Iran, QS31; d. poorly sorted alveolinid-rotaliid packstone-grainstone, middle Cuisian (SBZ11) of northern Sicily, MB14bis; e. unsorted cortoidal-foraminiferal grainstone, middle Cuisian (SBZ11) of Canale (northern Sicily); f. poorly sorted alveolinid grainstone, middle Cuisian (SBZ11) of northern Sicily, CC; g. poorly sorted alveolinid-rotaliid grainstone, middle Cuisian (SBZ11) of Castrovalva, CV1; h. alveolinid grainstone, middle Cuisian (SBZ11) of Monte Postale, PST1302; i. alveolinid grainstone, middle Cuisian (SBZ11) of Monte Postale, PST1434.

than *R. pustulosa* and with flattened test, is documented from the upper Rupelian of Turkey (Gedik, 2020; Gedik and Karadenizli, 2021) to the upper Chattian of Italy (Benedetti and Briguglio, 2012). Although Ferràndez-Cañadell and Bover-Arnal (2017) questioned the differences between these two species, both have been recently reported from Central Italy by Marino et al. (2022) as resedimented from carbonate ramp into basin. The occurrence of the genus from the Oligocene of Iran is also worth of notice (Babazadeh S.A., pers. comm.; Holakouee et al., 2018). Bolívar Feriche (2022) documented *R. crassaparies* from *Neorotalia*-bearing packstone to grainstone inner ramp deposits of Sierra de Marmolance (Granada province, southern Spain); this record is erroneously referred to the Serravallian since figured planktonic foraminifera

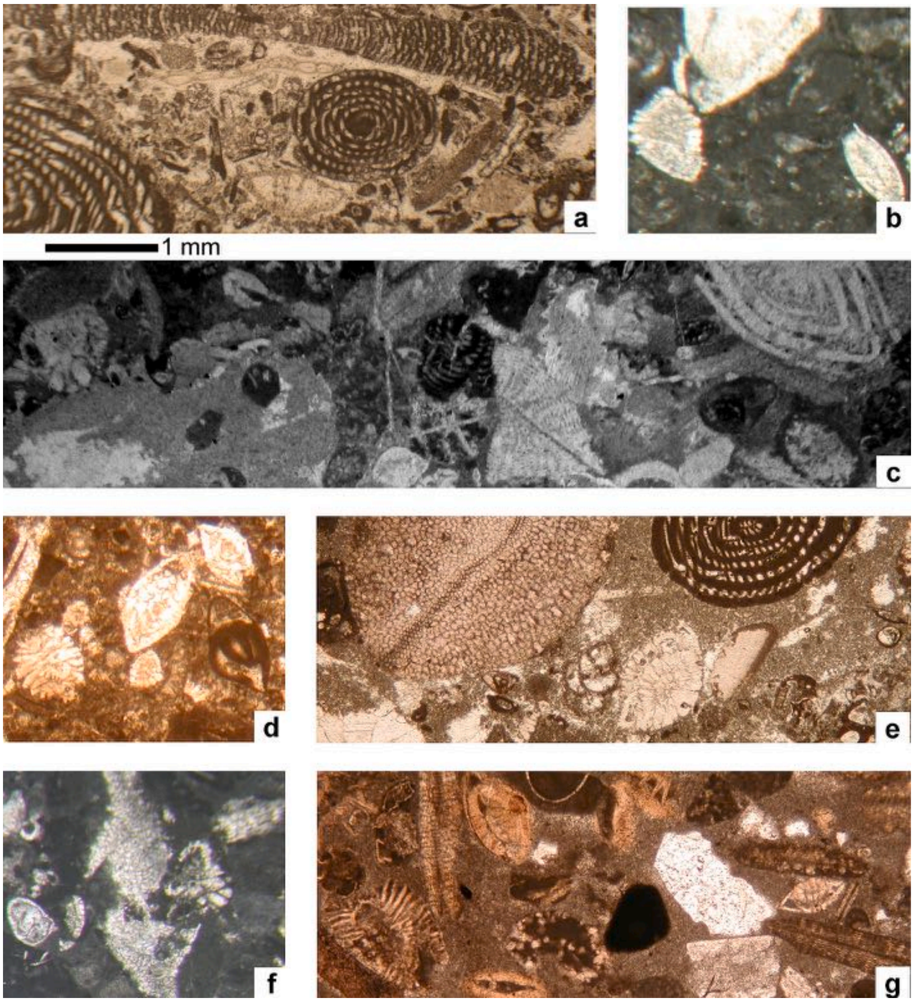

Fig. 4. Microfacies of the investigated ornatorotaliid-bearing samples. a. unsorted alveolinid and *Orbitolites* grainstone, Grado well (Trieste); b. poorly-sorted biodetritic packstone to wackestone, Poggio di Roio (L'Aquila); c. moderately-sorted biodetritic packstone, sample AM52, Antrodoco (Rieti); d. bioclastic packstone, sample MT18, Monte Torretta (L'Aquila); e. bioclastic packstone with alveolinids, rotaliids and discocyclinids, Monte La Rocca (L'Aquila); f. biodetritic floatstone, La Montagnola (Isernia); g. larger foraminiferal packstone matrix in a polygenic breccia, sample 666, Longobucco (Calabria, courtesy of Simone Fabbi).

Table 1
List of the investigated samples and thin sections.

Samples	Locality	Number of examined thin sections	Age	Biozone	Reference
YGA	Becirman (Turkey)	23	Late Danian	SBZ2	Sinanoğlu et al. (2022)
AM46	Antrodoco	1	Late Danian	SBZ2	Benedetti et al. (2018)
Qs26	Shiraz (Iran)	5	Late Thanetian	SBZ4	Benedetti et al. (2021)
LM1	La Montagnola (Isernia, Molise)	1	Middle Cuisian	SBZ11	This work
666	Longobucco (Calabria)	1	Middle Cuisian	SBZ11	This work
567	Longobucco (Calabria)	1	Middle Cuisian	SBZ11	This work
T59–60	Monte La Rocca (L'Aquila, Abruzzi)	2	Middle Cuisian	SBZ11	This work
C5-C20	Grado 1 well (Trieste, Friuli)	9	Middle Cuisian	SBZ11	This work
MB14bis	Buseto Palizzolo (Sicily)	10	Middle Cuisian	SBZ11	Benedetti (2018)
Canale	Buseto Palizzolo (Sicily)	3	Middle Cuisian	SBZ11	Benedetti (2018)
CC	Buseto Palizzolo (Sicily)	4	Middle Cuisian	SBZ11	Benedetti (2018)
MT18	Monte Torretta (L'Aquila, Abruzzi)	1	Middle Cuisian	SBZ11	Tomassetti and Benedetti (2020)
AM52	Antrodoco	1	Middle Cuisian	SBZ11	Benedetti et al. (2018)
CV1	Castrovalva (L'Aquila, Abruzzi)	1	Middle Cuisian	SBZ11	Benedetti et al. (2011)
PR01	Poggio di Roio (L'Aquila, Abruzzi)	1	Middle Cuisian	SBZ11	Benedetti et al. (2011)
Selected samples	Monte Postale (Veneto)	42	Middle Cuisian	SBZ11	Vescogni et al. (2016)
NR1b	Monte La Rocca (L'Aquila, Abruzzi)	1	Late Chattian	SBZ23	This work
R27A	Monte La Rocca (L'Aquila, Abruzzi)	1	Late Chattian	SBZ23	This work
NR26	Monte La Rocca (L'Aquila, Abruzzi)	1	Late Chattian	SBZ23	This work
PB01	Porto Badisco (Apulia)	9	Late Chattian	SBZ23	Benedetti and Briguglio (2012)

and especially the LF assemblage appear more consistent with a late Oligocene age.

2.2. Methods

For this study, each microfacies and respective specimens were analysed to describe paleoenvironmental settings and check for potential taxonomic differentiations. We examined dozens of thin sections from our own collections, and we also discuss data from literature as listed in Table 1.

Carbonate microfacies were defined using the classification of Dunham (1962) and Embry and Klovan (1971), and the methods described by Flügel (2010). The micropaleontological analysis of the bioclastic contents was carried out on microphotographs, by a taxonomic analysis of mainly LF and accompanying shallow water biota (small foraminifera, red and green algae, echinoids, bryozoans, bivalves, etc.). For depositional environment we investigated also the type of cement and abiotic components or lithoclasts (when present). We follow mainly the interpretation given by the standard microfacies scheme provided by Flügel (2010).

2.3. Material

To investigate the paleoecology and paleoenvironmental characterization of ornatorotaliids, we primarily refer to the mentioned literature data. However, here we provide new data (Table 1) about their occurrence (Fig. 1) and microfacies analysis (Table 2). In particular, we found new occurrences of *Ornatorotalia* and *Granorotalia* from the middle Cuisian (SBZ11) of the Monte Postale limestones (both from Monte Postale and Pesciara di Bolca) resulted by an accurate revision of the thin sections analysed by Vescogni et al. (2016) and Papazzoni et al. (2017). Some free-matrix specimens have been also isolated from the volcanoclastics cropping out close to the Pesciara limestone; these volcanoclastics were also referred to the SBZ11 (Papazzoni et al., 2013).

A rich *Ornatorotalia spinosa* assemblage has been identified from limestone samples taken from the Grado 1 well (NE Italy; see e.g., Fig. 5 in Giustiniani et al., 2022) who drilled the upper part of the buried Karst Carbonate platform (also called Adriatic Carbonate platform) succession (Jurkovšek et al., 2016). Such a succession is composed by limestone units ranging from the Lower Cretaceous to the lower Eocene; more precisely the samples with *Ornatorotalia spinosa* belong to the lower Eocene unit “miliolid, *Alveolina* and *Nummulites* limestone” (Consorti et al., 2021, 2024). Limestone facies are characterized by grainstone to packstone, pointing to a high energy shallow-marine environment, very rich in benthic foraminifera such as *Orbitolites*, *Nummulites*, *Alveolina*, orthophragmines, acervulinids, and small rotaliids. The samples belong to a single stratigraphic interval characterized by biostratigraphic markers such as *Alveolina cremae*, *A. distefanoi*, *A. ruetimeyeri*, and *A. rugosa*; this assemblage indicates an Ypresian age belonging to the Shallow Benthic Zone 11 of Serra-Kiel et al. (1998).

New samples from Central Italy show occurrences of both *Granorotalia sublobata* and *Ornatorotalia granum*, especially from slope and toe of slope deposits from Monte La Rocca (L’Aquila), Castrovalva (L’Aquila) and La Montagnola (Isernia). Finally, we also find some specimens in thin sections from the Longobucco Basin (Calabria, southern Italy).

3. Results of micropaleontological and microfacies analyses

The results of the micropaleontological analysis and the microfacies types are listed and detailed in Table 2. In the following subchapters we report briefly some remarks and new observations, following the stratigraphic order.

3.1. Paleocene

The small species *O. ozgenerdemi* has been described from poorly-sorted grainstone with isooriented large and flattened *Mardinella daviesi* associated to *Idalina sinjarica*, rotaliids, and green algae (Benedetti and Sinanoğlu, 2022; Consorti and Sinanoğlu, 2022; Fig. 3a). The microfacies and accompanying biota support the hypothesis of a very shallow vegetated lagoonal environment.

The larger species *Ornatorotalia* sp. figured by Benedetti et al. (2018) cannot be unambiguously constrained to a precise paleoenvironment, since it is still poorly known and it occurs displaced from shallow-water into deeper settings in bioclastic grainstone to packstone with plasticlasts (sensu Folk, 1959) rich in planktonic foraminifera (Fig. 3b). It occurs in an assemblage including *Elazigina dienii*, *Cuvillierina* cf. *sireli* and *Miscellanea* sp. suggesting very shallow original setting in an inner carbonate ramp.

Ornatorotalia pila is reported in poorly-sorted to unsorted grainstones from Iran (Fig. 3c), associated to miliolids, small rotaliids, *Idalina, Daviesina*, *Elazigina, Lockhartia, Dictyokathina, Mardinella*, echinoids, peloids, and dasycladacean algae (Benedetti et al., 2021). This data indicates the presence of vegetated substrates in well-irradiated seafloors. The same taxon is also reported from shallow-water carbonate facies of Harabekayış (Turkey) in assemblage with *Bolkarina*, *Lockhartia, Elazigina, Miscellanea, Planorbulina*, and rare *Discocyclina* (Sirel and Devecíler, 2017; Sirel, 2018).

3.2. Eocene

The microfacies analysis of the Cuisian carbonate platform from north-western Sicily revealed that *O. spinosa*, and subordinately also *G. sublobata*, settled in vegetated substrate in shallow-water (innermost ramp) settings or also sand shoals in association with peloids and cortoids (Benedetti, 2018; Fig. 3d-f). Reworked *Ornatorotalia spinosa* has been also documented within biodetritic packstone-floatstone in Scaglia type formations of Central Italy (Benedetti et al., 2018; Capotorti and Chiarini, 2023) and from SBZ11–12 shallow-water carbonates of central Turkey (Sirel and Devecíler, 2017), thus suggesting shallow to very shallow-water settings. Innamorati (2022) recently reported *O. spinosa* and other ornatorotaliids within silty matrix of microbreccias of the Paludi Fm. (Longobucco, Calabria) assigned to SBZ11-?12 (middle Cuisian to?lowermost Lutetian). Our investigation of such microbreccias (Fig. 4g) suggests the co-occurrence of nummulitids, orthophragmines, and other LF possibly displaced from different depths down to the slope, with the species *Cuvillierina vallensis* that could restrict the age of the assemblages to SBZ11.

In the Grado well *Ornatorotalia spinosa* occurs in poorly-sorted grainstones characterized by abundant alveolinids, nummulitids, rotaliids (*Rotalia* cf. *trochidiformis*), *C. vallensis, Orbitolites* sp., *Gyroidinella eocenica*, abundant *Cibicides* spp., and hooked acervulinids, thus suggesting vegetated substrate in shallow-water setting (Fig. 4a). Worth of notice is the finding of the species in the Monte Postale limestones (Veneto, Northern Italy) for which the previous accurate micropaleontological and microfacies analysis (Vescogni et al., 2016; Papazzoni et al., 2017) allows us to constrain the occurrence of ornatorotaliids to precise environments. The Monte Postale section, close to the famous “Pesciara di Bolca” Fossil-Lagerstätte, consists mainly of coralgal buildups with abundant coral colonies, calcareous algae, and encrusting organisms, preserved in growth position or in fragments as well, superimposed or interposed by grainstone to packstone with *Alveolina* and other scattered LF such as especially nummulitids and subordinate orthophragmines (Vescogni et al., 2016). We found *O. spinosa* and rare *G. sublobata* specimens only in *Alveolina* grainstone, *Alveolina-Nummuites* packstone and graded *Alveolina* grainstone currently interpreted as linked to bioclastic sands within coralgal rims, lagoon and fore-reef (Fig. 3h-i). No ornatorotaliids occur in association with *Discocyclina*, corals or encrusting biota.

Table 2

Ornatorotaliid occurrences in the western to eastern Neotethys (numbers refer to those in Fig. 1).

Species	Biozone	Age	Locality	Microfacies	Paleoenvironment	Reference	Fig. 1
Ornatorotalia ozgenerdemi	SBZ2	Late Danian	Becirman (Turkey)	Poorly sorted grainstone with isooriented and flattened *Mardinella daviesi,* rotaliids and dasycladales	Shallow-water, vegetated	Benedetti and Sinanoglu, 2022 Sinanoglu et al., 2022	1
Ornatorotalia sp.	SBZ2	Late Danian	Antrodoco (Central Italy)	Larger foraminiferal bioclastic grainstone to packstone with plasticlasts consisting of planktonic foraminiferal wackestone to packstone	Middle to outer ramp	Benedetti et al., 2018	2
Ornatorotalia pila	SBZ4	Thanetian	Shiraz (S Iran)	Poorly sorted to unsorted grainstone with large rotalids (*Daviesina*), small rotaliids, miliolids, echinoids, peloids and dasycladaleans algae	Shallow-water, vegetated	Benedetti et al., 2021	3
	SBZ3	Selandian-early Thanetian	Harabekayış section, Elazığ (E Turkey)	Not specified, associated to *Elazigina harabekayisensis*, Hottingerina anatolica, *Bolkarina* sp., *Miscellanea yvettae*, *Lockhartia diversaa*, *Pseudokathina selveri* and *Discocyclina* sp.	Shallow-water	Sirel and Deveciler, 2017	4
		late Danian-Thanetian	Hričovské Podhradie (Slovakia)	"Reef" limestone clasts dominated by algae and encrusting foraminifera with subordinate larger foraminifera such as *Discocyclina.*	Shallow-water	Samuel et al., 1972	5
Ornatorotalia spinosa	SBZ11	Middle Cuisian	Northern Sicily	Alveolinid.rotaliid packstone. grainstone; peloidal-cortoidal foraminiferal grainstone; rhodolith-nummulitid floatstone (transported); larger foraminiferal floatstone (transported)	Shallow-water vegetated and unvegetated inner ramp and sand shoals	Benedetti et al., 2011 Benedetti, 2018	6
	SBZ11	Middle Cuisian	Antrodoco (Central Italy)	Biodetritic packstone-floatstone	Middle to outer ramp	Benedetti et al., 2018	2
	SBZ11–12	Middle late Cuisian	S Polatlý, SW Ankara, central Turkey	Not specified - hard, gray-light brown coloured limestone with *Alveolina cuspidata*, *A. schwageri*, *A.* cf. *cremae*, *A. minuta*, *A. oblonga*, *A. decastroi*, *A. boscii*, *Glomalveolina minutula, Lockhartia conditi, Linderina* sp., *Corkinolina liburnica, Nummulites burdigalensis, N. fossulatus* and *Assilina placentula*	Shallow to very shallow water	Sirel and Deveciler, 2017	7
	SBZ11	Middle Cuisian	Monte Postale, Veneto (Northern Italy)	*Alveolina* grainstone; *Alveolina-Nummuites* packstone; graded*Alveolina* grainstone	Bioclastic sands within coralgal rims, lagoon, fore-reef	Vescogni et al., 2016 Papazzoni et al., 2017	8
	SBZ11-?12	Middle Cuisian-lowemost Lutetian	Longobucco Basin, Calabria (Southern Italy)	Microbreccias with larger foraminifera in silty matrix	Turbiditic deposits in basin (displaced from shallow water)	Innamorati, 2022	9
	SBZ11	Middle Cuisian	Grado, Trieste (NE Italy)	Unsorted *Alveolina* grainstone with peloids, rotaliids, *Orbitolites* and rare nuulitids	Shallow-water vegetated environment, shoal	This work	10
Ornatorotalia granum	SBZ11	Middle Cuisian	Decontra, Maiella Mountain (Central Italy)	Unsorted *Alveolina* packstone	Inner to middle carbonate ramp	Benedetti et al., 2011 Pignatti, 1995	11
	SBZ11–12	Middle.late Cuisian	Çayraz section, N of Haymana, S Ankara, central Turkey	Not specified - hard, gray-light brown coloured upper Ypresian (middle-upper Cuisian) limestone with *Alveolina cuspidata*, *A. schwageri*, *A.* cf. *cremae, A. minuta*, *A. oblonga*, *A. decastroi*, *A. boscii*, *Glomalveolina minutula, Lockhartia conditi, Linderina* sp., *Corkinolina liburnica, Nummulites burdigalensis, N. fossulatus* and *Assilina placentula*	Shallow to very shallow water	Sirel and Deveciler, 2017	12
	SBZ10	Lower Cuisian	Birjand, East of Iran	Calcarenite with terrigenous particles associated with *Nummulites atacicus*, *N. subramondi, N, partschi, Alveolina solida, Orbitolites* sp., *Pseudolituonella* sp., *Assilina plana*, *Asterocyclina* sp., *Discocyclina* sp., and *Orbitoclypeus* sp.	?Middle ramp	Motamedalshariati, 2023	13

(*continued on next page*)

Table 2 (*continued*)

Species	Biozone	Age	Locality	Microfacies	Paleoenvironment	Reference	Fig. 1
	SBZ11	Middle Cuisian	Antrodoco (Central Italy)	biodetritic packstone	Resedimented from inner ramp to outer ramp up to the slope	Benedetti et al., 2018	2
	SBZ11	Middle Cuisian	Poggio di Roio, L'Aquila (Central Italy)	Wackestone to packstone	Middle ramp	Benedetti et al., 2011; this work	14
	SBZ11	Middle Cuisian	Monte Torretta, L'Aquila (Central Italy)	Bioclastic packstone-grainstone to wackestone-mudstone (floatstone)	Resedimented from inner ramp along the slope	Tomassetti and Benedetti, 2020	15
	SBZ11	Middle Cuisian	Monte La Rocca, L'Aquila (Central taly)	Bioclastic packstone to wackestone with alveolinids, nummulitids and discocyclinids	Middle ramp	This work	16
	SBZ11	Middle Cuisian	Castrovalva (Central Italy)	Larger foraminiferal, peloidal grainstone	Shallow-water	This work	17
	SBZ11	Middle Cuisian	La Montagnola, Isernia (Central Italy)	Biodetritic larger foraminiferal packstone-floatstone	Middle ramp proximal slope	This work	18
	SBZ11–12 (13?)	Middle Cuisian-lowemost Lutetian	Longobucco Basin, Cosenza (Southern Italy)	Microbreccias with larger foraminifera in silty matrix	Turbiditic deposits in basin (displaced from shallow water)	Innamorati, 2022; Innamorati et al., 2024	9
	SBZ10–11	Lower-middle Cuisian	Collarmele (Central Italy)	Grainstone to packstone with *Alveolina* and rare *Nummulites*	Shallow-water; inner to middle carbonate ramp	Mangione, 2010	19
	SBZ7–8	Ilerdian	Keçiborlu, Isparta, SW Turkey	Not specified - from photographs undorted *Alveolina* grainstone to wackestone	Lagoon to low energy shallow-water with normal salinity	Bozkurt and Görmüş, 2021	20
Granorotalia sublobata	SBZ11	Middle Cuisian	Northern Sicily	Alveolinid.rotaliid packstone. grainstone; peloidal-cortoidal foraminiferal grainstone	Shallow-water vegetated and unvegetated inner ramp and sand shoals	Benedetti et al., 2011 Benedetti, 2018	6
	SBZ11	Middle Cuisian	Monte Torretta, L'Aquila (Central Italy)	Bioclastic packstone-grainstone to wackestone-mudstone (floatstone)	Resedimented from inner ramp along the slope	Tomassetti and Benedetti, 2020	15
	SBZ11	Middle Cuisian	Antrodoco (Central Italy)	Biodetritic packstone-floatstone	Middle to outer ramp	Benedetti et al., 2018	2
	SBZ10–11	Lower-middle Cuisian	Collarmele (Central Italy)	Grainstone to packstone with *Alveolina* and rare *Nummulites*	Shallow-water; inner to middle carbonate ramp	Mangione, 2010	19
	SBZ11-?12	Middle Cuisian-lowemost Lutetian	Longobucco Basin, Cosenza (Southern Italy)	Microbreccias with larger foraminifera in silty matrix	Turbiditic deposits in basin (displaced from shallow water)	Innamorati, 2022	9
	SBZ11–12	Middle.late Cuisian	Çayraz section, N of Haymana, S Ankara, central Turkey	Not specified - hard, gray-light brown coloured upper Ypresian (middle-upper Cuisian) limestone with *Alveolina cuspidata*, *A. schwageri*, *A.* cf. *cremae, A. minuta*, *A. oblonga*, *A. decastroi*, *A. boscii*, *Glomalveolina minutula, Lockhartia conditi, Linderina* sp., *Corkinolina liburnica, Nummulites burdigalensis, N. fossulatus* and *Assilina placentula*	Shallow to very shallow water	Sirel and Deveciler, 2017	12
	SBZ10	Lower Cuisian	Birjand, East of Iran	Calcarenite with terrigenous particles associated with *Nummulites atacicus*, *M. aturicus*, *N. subramondi*, *N*, *partschi*, *N. mamillatus*, *Alveolina solida*, *A. regularis,* Orbitolites sp., *Opertorbitolites* sp.*Pseudolituonella* sp., *Assilina plana*, *A. granulosa*, *Asterocyclina* sp., *Discocyclina* sp., *Orbitoclypeus* sp. and *Neorotalia alicantina*	?Middle ramp	Motamedalshariati, 2023	13
	?SBZ13	Lower Lutetian	Oveiarsko (Slovakia)	Arenaceous limestone	Resedmented from inner ramp	Samuel et al., 1972	21
	SBZ11	Middle Cuisian	Poggio di Roio, L'Aquila, Central Italy	Wackestone to packstone	Middle ramp	Benedetti et al., 2011	14
Risananeiza crassaparies	SBZ23	Late Chattian	Porto Badisco, Apulia (Southern Italy)	Grainstone-packstone with lepidocyclinids, nummulitids, peloids and coralline algae	30–50 mwd	Benedetti and Briguglio, 2012	22
	SBZ23	Late Oligocene	Monte La Rocca, L'Aquila (Central taly)	Lepidocyclinid floatstone with rare planktonic foraminifera	Middle-outer ramp	This work	16
	SBZ22 (not 21)	Late Rupelian-lower Chattian	Akçadağ (Turkey)	Not specified - Limestone	Outer ramp	Gedik, 2020	23

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Table 2 (*continued*)

Species	Biozone	Age	Locality	Microfacies	Paleoenvironment	Reference	Fig. 1
	SBZ23	?Langhian-Serravallian according to the Author; more likely late Oligocene by the assemblage	Sierra de Marmolance, Granada province (southern Spain)	Corals packstone-grainstone with miliolids, encrusting foraminifera, *Amphistegina, Austrotrillina striata*, Neorotalia *viennoti,* echinoderms, bryozoans, very rare *Nephrolepidina, Sorites, Peneroplis, Planorbulina, Sphaerogypsina, Ditrupa*and planktonic formaminifera. *Neorotalia* packstone-grainstone with *Risananeiza,* corals, bryozoans, miliolids, *Heterostegina assilinoides, Eulepidina dilatata-formosoides, Nephrolepidina tournoueri, Amphistegina,* bivalves, *Borelis inflata, Peneroplis, Sorites, Sphaerogypsina, Planorbulina, Operculina complanata, Ditrupa,* green algae (*Halimeda*), brachiopods, and planktonic foraminifera.	Proximal middle ramp-distal inner ramp; reef, low to moderate energy	Bolívar Feriche, 2022	29
Risananeiza pustulosa	SBZ23	Late Chattian	Risan Aneiza, Northern Sinai (Egypt)	Clayey marls with rodoids and larger foraminifera	Offshore deltaic system	Boukhary et al., 2008	24
	SBZ23	Late Chattian	Sogukpınar section, Maras (Turkey)	Algal biosparite	Shallow-water	Sirel and Isik, 2011	25
	SBZ23	Late Chattian	Benitatxell Range, Prebetic Domain (SE Spain)	Rudstone with larger foraminfiera, coralline algae and corals	Distal ramp	Ferrandez-Canadell and Bover-Arnal, 2017	26
	SBZ23	Late Chattian	Qom, Central Iran	Packstone with larger benthic foraminifera (*Miogypsinoides, Postmiogypsinella, Spiroclypeus, Operculina, Amphistegina*, and *Risananeiza*) and coralline algae	shallow-marine environment (middle ramp) and oligotrophic conditions	Yazdi-Moghadam et al., 2023	27
	SBZ23	Late Chattian	Veneto, NE Italy	Bioclastic peloidal wackestone to rudstone-packstone	Near-shore, high-energy conditions in the upper photic zone	Bassi et al., 2007	28

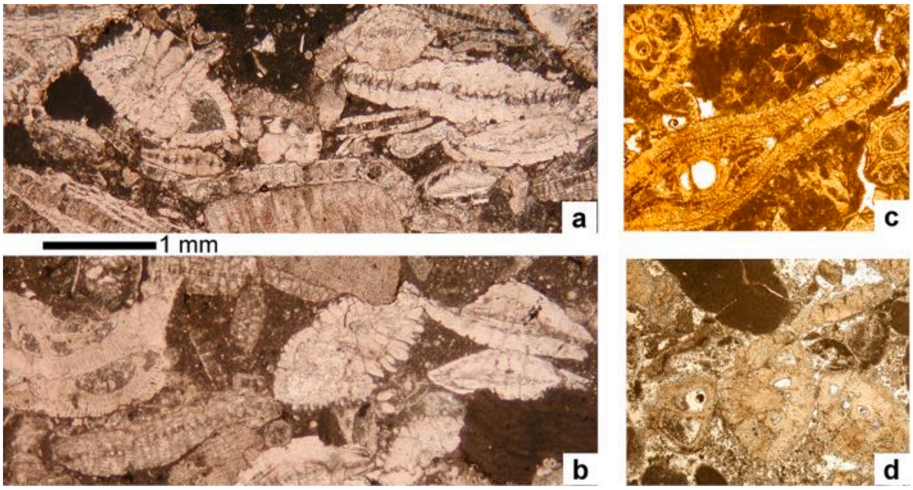

Fig. 5. Microfacies of the investigated ornatorotaliid-bearing samples. a-b. bioclastic packstone with foraminifera and red algae, Monte La Rocca (L'Aquila); a. sample NR1b; b. sample NR26; c. packstone with lepidocyclinids, *Spiroclypeus*, rotaliids, and red algae, Porto Badisco, Apulia, sample B01 in Benedetti and Briguglio (2012); d. grainstone with red algae and rotaliids, sample P18I of Brandano et al. (2010). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Ornatorotalia granum has been originally reported from unsorted *Alveolina* packstone microfacies of Decontra (Maiella Mts., Central Italy) (Pignatti, 1995; Benedetti et al., 2011) and it is frequently found associated to *Granorotalia sublobata*, resedimented from inner into outer ramp up to basin in the Scaglia-type formations (Scaglia Rossa and Scaglia Detritica) of Central Italy (Benedetti et al., 2011, 2018; Tomassetti and Benedetti, 2020; Marino et al., 2022; Capotorti and Chiarini, 2023). We here report similar settings from other successions in Central Italy, such as Monte La Rocca (L'Aquila) (Fig. 4e) and La Montagnola (Isernia) (Fig. 4f), where biodetritic and bioclastic larger foraminiferal packstones are documented through the Paleogene deposits. Although the so-called "Paleogene hiatus" has been generally described as a long period of lack in carbonate sedimentation in the Latium-Abruzzi succession (Colacicchi, 1966; Accordi and Carbone, 1988), and a fully-developed platform has never been recognized (e.g., Brandano, 2017), scattered Cuisian shallow-water deposits crop out near Collarmele and Castrovalva (Pignatti, 1995; Mangione, 2010) showing the presence of *O. granum* and *G. sublobata*. They mainly occur in larger foraminiferal-peloidal grainstone or in grainstone to packstone (Fig. 3g) with *Alveolina* and rare *Nummulites*, thus suggesting inner ramp setting. These deposits have been described from the member named “calcareniti a nummuliti e discocycline” within the formation “Calcareniti a Macroforaminiferi” in the Geological Map of Italy, sheet 378 “Scanno” (Miccadei et al., 2012), and they represent usually thin remains of an articulated Paleogene carbonate platform pertaining to the Latium-Abruzzi domain.

Ornatorotalia granum, although generally reported from the middle Cuisian SBZ11, has been recently documented from the lower Ypresian (i.e., Ilerdian), in lagoonal to low-energy shallow-water environments of Turkey (Bozkurt and Görmüs, 2021) and lower Cuisian of Iran (Motamedalshariati, 2023), possibly in inner to middle ramp deposits (see Table 2 for details). Innamorati et al. (2024) reported a possible occurrence of *O. granum* from the Lutetian SBZ13, but they did not support their statement with data.

Granorotalia sublobata seems to share its distribution both with *O. spinosa* and *O. granum*, being well adapted to a wider environmental and depth gradient because of its lower degree of specialization. It is also figured up to lower Lutetian assemblages (Samuel et al., 1972; Innamorati, 2022) and future studies are needed to investigated its occurrence also in the upper-middle to upper Eocene of Neotethys. No middle to late Eocene ornatorotaliids have been so far recognized in the fossil record, although their occurrence cannot be ruled out pending future researches.

3.3. Oligocene

Risananeiza pustulosa has been originally described from matrix-free material extracted from clayey marls with rodoliths and LF (Boukhary et al., 2008) and it is also reported from coeval, i.e., SBZ23, shallow-water algal biosparite of Turkey (Sirel and Işik, 2011 as well from distal ramp deposits of SE Spain, resedimented in rudstone with LF, coralline algae and corals. Yazdi-Moghadam et al. (2023) also recently reported *Risananeiza pustulosa* from central Iran and they refer the assemblages to middle ramp environments (see Table 2 for details).

The species seems to be clearly linked to rhodalgal-dominated environments, with the exception figured by Bassi et al. (2007) as *Neorotalia viennoti*, from bioclastic peloidal wackestone to rudstone-packstone of the upper Chattian of Veneto (NE Italy).

Also *Risananeiza crassaparies* has been previously documented from similar environments, being described from grainstone-packstone with lepidocyclinids, nummulitids, peloids and coralline algae (Fig. 5c-d) of the Porto Badisco Calcarenites (Apulia, SE Italy) (Benedetti and Briguglio, 2012). The accompanying LF, described in detail by Parente and Less (2019), include: *Miogypsinoides complanatus-formosensis*, *Heterostegina assilinoides*, *Spiroclypeus margaritatus, Operculina complanata*, *Nummulites kecskemetii, Cycloclypeus mediterraneus*, *Eulepidina dilatata*, *E. anatolica*, *Nephrolepidina* ex. interc. *Morgani-praemarginata*, and *N.* aff. *Musensis*, suggesting unambiguously the upper Chattian SBZ23. Brandano et al. (2010) interpreted the rhodolith-rich lithofacies of the Porto Badisco Calcarenites as deposited in the oligophotic zone, compatible with a water depth of about 30–50 m for the abundance of red algae.

We here document *R. crassaparies* from lepidocyclinid floatstone with rare planktonic foraminifera of the Monte La Rocca succession (L’Aquila, Central Italy, Fig. 4; Table 2); this species also occurs displaced in similar or deeper settings in other areas of the Central Italy (e.g., Marino et al., 2022) within the Chattian Scaglia Cinerea Detritica Formation (Capotorti and Chiarini, 2023) in assemblage with *Nephrolepidina morgani, Eulepidina formosoides, Neorotalia viennoti, Victoriella conoidea, Nummulites* sp., *Heterostegina* sp., *Cycloclypeus* sp., and *Spiroclypeus* sp. Gedik (2020) reported *R. crassaparies* from the Rupelian (more likely upper Rupelian) of Turkey, in limestones interpreted as deposited in outer ramp.

Bolívar Feriche (2022) documented *R. crassaparies* in two different microfacies from a sedimentary succession of Sierra de Marmolance, Granada province (south-eastern Spain): coral packstone-grainstone and *Neorotalia* packstone-grainstone. The coral packstone-grainstone is characterized by coral colonies associated with coralline algae and subordinate foraminifera, echinoderms, and bryozoans, suggesting a proximal middle- to distal inner ramp setting (Table 2). The *Neorotalia* packstone-grainstone is characterized by the abundance of *Neorotalia viennoti* associated with echinoderms, coralline algae, and especially *Risananeiza*. Subordinate components include corals, bryozoans, miliolids, lepidocyclinids, *Amphistegina*, bivalves, and siliciclastics. Red algae occur mostly as debris, and are rare as rhodoliths. This microfacies indicates distal inner ramp in moderate energy setting.

4. Discussion

4.1. Paleobiology, paleoecology, and paleoenvironmental distribution of ornatorotaliids

Ornatorotaliids do not have currently living species to allow direct comparison with fossil counterparts. However, the paleoecological and paleoenvironmental characteristics of extinct LF are typically inferred by analogy with extant taxa. Our data indicate that ornatorotaliids are characterized by strong and heavy shell ornamentation and thrived, from the lower Paleocene to the Oligocene, almost exclusively in shallow-water, moderate- to high-energy environments, on well-irradiated seafloors. In recent oceans, the modern counterpart can be identified with calcarinids, which seem to possess very similar ornamentation and comparable ecological requirements (e.g., Hohenegger, 2011).

Ornatorotaliids and calcarinids are only related as both belong to the Rotalioidea superfamily and share a common ancestor that perhaps had very little test ornamentation and surely had a classic heterotrophic lifestyle with “r” type reproduction strategy. Both taxa therefore evolved following similar patterns by increasing shell ornamentation, reaching almost autothrophy and developing “K” type reproduction strategy. Another simplesiomorphic trait is given by the evidence that spines are canaliculated in both ornatorotaliids (Benedetti et al., 2011; Benedetti, 2015a) and calcarinids. This could be a clear case of convergent evolutionary pattern (Hottinger, 2000; Hohenegger, 2009).

Short spines are also characteristic of *Neorotalia* and *Pararotalia*, genera recently both included within the subfamily Pararotaliinae under superfamily Calcarinoidea according to molecular genetic classification (Holzmann and Pawlowski, 2017). *Neorotalia calcar* settles on substrate characterized by low water motion (e.g, Hohenegger, 2011) in a depth range between 0 and 30 m (Hallock, 1984; Hohenegger, 1994, 2011; Troelstra et al., 1996; Renema and Troelstra, 2001; Förderer and Langer, 2018; Pignatti et al., 2012), whereas *Pararotalia* has been reported also from modern deeper settings in meso- to eutrophic conditions, in sandy to muddy seafloors (e.g., Goeting et al., 2018).

In LF, the occurrence of similar morphological characters is strictly linked to the type of substrate on which a species lives and to other environmental factors such as water motion, illumination, salinity, depth (e.g., Beavington-Penney and Racey, 2004).

Ornatorotaliids were described as characterized by clear reproductive dimorphism, in which the microspheric generation show usually four large spines (Benedetti, 2015a), differently than smaller megalospheric specimens, which in most cases do not present such large structures.

In modern calcarinids spines support anchoring, and thick lenticular to spherical tests can resist to strong hydrodynamics thus reducing test damages. As a consequence, modern calcarinids are almost all restricted to the euphotic zone (Hohenegger, 2009); the only exception is the genus *Baculogypsinoides*, with more rounded shape and in which spines are much reduced in size and number. Its depth distribution in clear waters can go down to 70–80 m depth. The genus *Calcarina* is restricted to the Indo-Pacific bioprovince spanning from the central Indian Ocean, i.e., Maldivian archipelago (Parker and Gischler, 2011; Benedetti et al., 2023), to Japan (Hohenegger, 2011) passing through the so-called Coral Triangle (e.g., Goeting et al., 2018, 2022). The living calcarinids generally colonize firm substrate, in reefal and peri-reef environments, but they also occur as epiphyte on seagrasses or large algae. They are also frequent in the coralgal unconsolidated sediments of very shallow tropical settings (e.g., Renema and Troelstra, 2001; Benedetti et al., 2024).

Ornatorotaliids can be considered to have occupied a very similar ecological niche as modern calcarinids do. In particular, the genus *Ornatorotalia* can be constrained to very shallow-water settings (Fig. 6) characterized by elevated water motion and vegetated substrate, as documented from the microfacies analyses of the type horizons (Pignatti, 1995; Benedetti et al., 2011, 2021; Benedetti, 2018; Benedetti and Sinanoğlu, 2022), and the herein added data. However, some specimens could be displaced along slopes (Benedetti et al., 2011, 2018). Ornatorotaliids lived in high illuminated environments, thus supporting the hypothesis of algal symbiosis and consequently the development of K-strategy and enhanced alternation of generations; a still disputable exception regards *O. ozgenerdemi* for which dimorphism cannot yet be considered (Benedetti and Sinanoğlu, 2022).

Ornatorotalia spinosa is characterized by few solid spines suggesting, by similarities with calcarinids, inhabiting vegetated and unvegetated sand shoals periodically affected by high hydrodynamic energy, or bioclastic sands within coralgal rims, and the fore-reef (Table 2). This species is not being so far reported from reef crest.

Ornatorotalia ozgenerdemi can be actually considered a small species, possibly with an epiphyte mode of life, that thrived in shallow-water settings characterized by moderate water motion (Benedetti and Sinanoğlu, 2022; Sinanoğlu et al., 2022). Benedetti et al. (2021) suggested that *O. pila* thrived under very shallow water depth and low water motion conditions. The occurrence of the soritid foraminifera *Mardinella* associated with miliolids in the type assemblages suggests vegetated substrate. However, compared to *O. spinosa*, the less-developed spines suggest calmer water conditions, thus we interpret *O. pila* as typical of shallow-water restricted environment in lagoon or innermost carbonate ramp (Fig. 6). Both *O. ozgenerdemi* and *O. pila* occur in assemblage with flattened *Mardinella* and other epiphytic foraminifera in sediments rich in green algae; the skeletal content is consistent with the green algae (GA) foralgal assemblage of Brandano et al. (2019), which generally characterizes tropical seawater with low-density seagrass meadows where green algae may develop in well-illuminated substrates.

Ornatorotalia granum is widely documented from grainstones and packstones associated with peloids, alveolinids, miliolids, and nummulitids in middle ramp to slope deposits where it may occur frequently displaced from shallower environments. We can argue that *O. granum* inhabited both inner and middle ramp, thus showing a wider depth range in respect to previously discussed species, characterizing both low-energy lagoons and high- to moderate-energy shallow environments in the photic zone.

Granorotalia sublobata usually shares its depositional environments with both *O. spinosa* and *O. granum*. Large microspheric specimens of *Granorotalia* show large spines growing along the periphery (Benedetti, 2015a), thus suggesting again homoplasy with calcarinids or with other carinate and spinose species, such as recent *Elphidium aculeatum* that is considered strictly linked to phytal substrate (e.g., Langer, 1993; Benedetti and Frezza, 2016).

The other ornatorotaliid, i.e., *Risananeiza*, was more likely confined in the deepest euphotic to mesophotic zone (Fig. 6), since it lacks spines in both generations and it is generally documented in association with lepidociclynids, nummulitids such as *Nummulites, Operculina, Heterostegina*, *Cycloclypeus* (Ferràndez-Cañadell and Bover-Arnal, 2017), and miogypsinids (Benedetti and Briguglio, 2012). *Risananeiza crassaparies* also possesses granules and heavy ornamentation on the outer surface, somehow similar to the pillars of *Baculogypsinoides*, which is also the deepest of the calcarinids. On the contrary, it seems that *R. pustulosa* could thrive in shallower marine environments, due to its presence in rudstone with other LF, corals and coralline algae. Granero Ordóñez et al. (2022) reported *Risananeiza pustulosa* from shallow-water <40 m settings, although the occurrence of *Cycloclypeus* in the samples could indicate deeper environments or enhances mesotrophic conditions, linked to low seafloor irradiations. Bolívar Feriche (2022) reported *Risananeiza crassaparies* from distal-inner ramp to proximal-middle

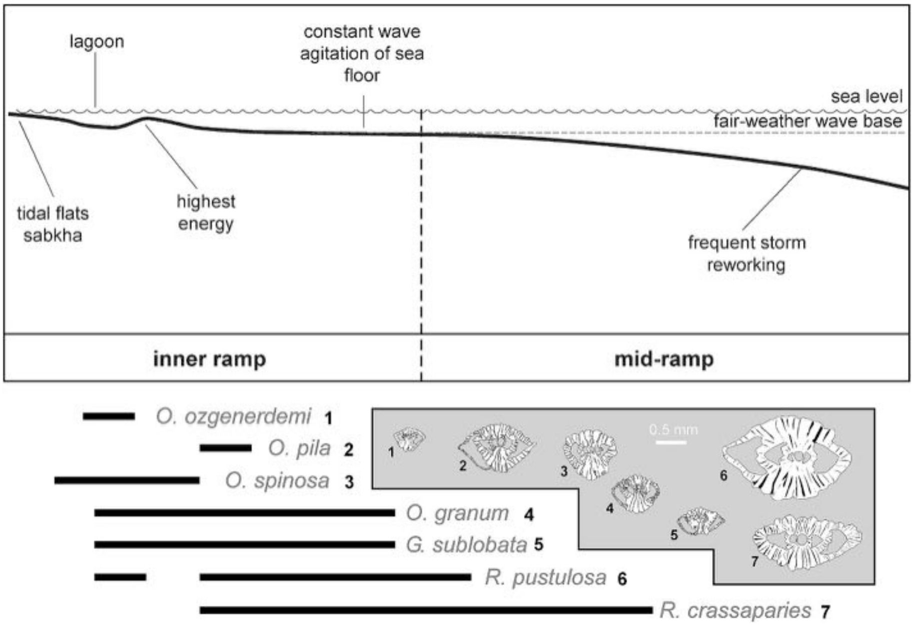

Fig. 6. Depth distribution of the investigated ornatorotaliids according to the results of microfacies analysis. Carbonate ramp model modified after Burchette and Wright (1992).

ramp and reef environments, where it is rare.

Similarly to our analysis, Robles-Salcedo (2014) suggested a functional homoplasy in the extinct Cretaceous representatives of the family Siderolitidae, with the genus *Praesiderolites*, lacking spines, usually found in wackestone to packstone textures characterizing open shelf and lower photic zone in scarce to moderate water motion, as also for the genus *Wannierina*. The flattened *Arnaudiella* settled on soft or hard substrate of relatively deeper waters, similarly to the recent *Baculogypsinoides*, in having supplementary chamberlets, *Pseudosiderolites* is usually found in packstones and subordinately grainstones along the platform margin, whereas *Siderolites* inhabited shallow-water environments in analogy with recent calcarinids with large spines, on hard substrate and high energy settings.

The species *O. spinosa*, *O. pila*, as well as *Granorotalia* and *Risananeiza*, can be interpreted as K-strategists on the basis of the presence of both asexual and sexual generations (Benedetti and Briguglio, 2012; Benedetti, 2015a; Benedetti et al., 2021) with more prominent dimorphism in shallower environments. As concerns *O. granum* and *O. ozgenerdemi*, there has been no evidence so far of reproductive dimorphism. Benedetti and Sinanoğlu (2022) interpreted *O. ozgenerdemi* as a possible r-strategist. However, the reproductive strategy of foraminifera, i.e., especially gamogony vs schizogony, can be influenced by water depth and consequently hydrodynamic conditions on the seafloor (e.g., Benedetti, 2015b; Eder et al., 2018; Hohenegger et al., 2019). For this reason, shallow-water calcarinids exhibit a predominantly asexual reproductive mode, with microspheric agamonts being rather rare (e.g., Hohenegger, 2011). These rare agamonts are only possibly due to the dense populations of calcarinids which can build thick forams' carpets on the reef edge, which are strongly anchored on the substrate, thus facilitating gametes' encounter and fertilization. On the other hand, oligophotic adapted taxa, such as *Cycloclypeus*, *Planostegina* and *Planoperculina* (e.g., Hohenegger, 2004; Briguglio et al., 2016), tend to be more prone to sexual reproduction because gametes can interact due to hydrodynamic conditions being less intense, and agamonts are consequently more abundant (e.g., Eder et al., 2018). At present, we are unable to be so specific concerning ornatorotaliids, but future discoveries will aid in providing a solution.

4.2. Climate and ornatorotaliids

The current known distribution of ornatorotaliids seems almost limited to the Paleocene (SBZ2–4), upper Ypresian-?lowermost Lutetian (SBZ10–12), upper Chattian (SBZ23). Very few occurrences are documented from the lower Ypresian (Ilerdian) and the lower Oligocene (compare Table 2), and no data are so far available from the middle to upper Eocene, apart a possible occurrence from upper Eocene of southern Sicily (the quality of material is not sufficient to investigate taxonomically two single individuals).

The relatively high abundance of ornatorotaliids in the middle Cuisian carbonate systems and in the upper Chattian ramps might suggest a direct correlation with major climate warming events, such as EECO and LOWE (Late Oligocene Warming Event, e.g., Zachos et al., 2001). The best known species of the family, such as *O. spinosa*, *O, granum*, and *G. sublobata*, have been in fact mostly reported from the SBZ11 (see Table 2 for complete references), roughly corresponding to the EECO, whereas the LOWE only partly coincides with the SBZ23, from which *Risananeiza pustulosa* and *R. crassaparies* have been frequently documented (see Table 2 for detailed references). The types of *R. crassaparies* where described from the Porto Badisco Calcarenites Fm., that has been recently considered as deposited right after the LOWE (Bosellini et al., 2021). Moreover, Sinanoğlu et al. (2022) argued about a possible link between the SBZ2 rotaliid-bearing assemblage with *O. ozgenerdemi* and the Late Danian Event (LDE, Quillévéré et al., 2008; Bornemann et al., 2009) but the current knowledge is insufficient to check this assessment.

Finally, there are currently no traces of ornatorotaliids from the Middle Eocene Climatic Optimum (MECO) occurred during the Bartonian.

Ongoing and future taxonomic studies could provide new evidences of ornatorotaliids species to fill the existing gap, and might check the supposed link between climate and this group of LF. Anyway, we have to consider the possibility that the apparent distribution of this group could be an artefact due to the wide occurrence of shallow-water deposits related to these global phases, in which shallow-water settings were more widespread.

4.3. Evolutionary history

Previous thoughts on the phylogeny of recent *Calcarina* excluded relationships with both *Neorotalia* and *Pararotalia*. Updated systematics based both on both functional morphology (Hottinger et al., 1991) and on ribosomal DNA within extant Calcarinoidea (Holzmann and Pawlowski, 2017) demonstrated instead a common origin and shared morphological features including, among all, umbilical plug and spiral canal forming tooth-plates. Recent taxa grouped into Calcarinidae by genetic traits include *Neorotalia*, *Baculogypsina*, *Calcarina*, and *Pararotalia*. *Ornatorotalia* as well as the other related Cenozoic calcarinids may have originated from a small-sized r-strategists rotaliid which survived the K/Pg crisis and radiated after occupying the vacant niches in shallow-water settings. Based on these morphological keys, possible candidates must be in some way related to those phylogenetically related species displaying features such as tooth-plate, canaliculated spines, and/or multiple apertures. The genus *Pararotalia* would fit into this frame and might be a valid candidate, considering its long stratigraphic range starting from the Upper Cretaceous, thus suggesting ability to withstand geological crisis such as the Cenomanian-Turonian hypertemal – related to the Oceanic Anoxic Event 2 – and the K/Pg (see e.g. Boix et al., 2009; Piuz and Meister, 2013; Consorti et al., 2017; Křížová et al., 2024). The Cretaceous *Pararotalia tuberculifera* or *Pararotalia boxiae* show morphological affinities with ornatorotaliids, because of their low trochospiral coiling, strongly ornamented test, acute chamber periphery and tooth-plates. However, they lack dorsal canals. Similarly, the Late Cretaceous genus *Pilatorotalia* Consorti et al. (2017) display a clear tooth-plate but differs from ornatorotaliids in lacking dorsal ornamentation and a widespread enveloping canal system. As possible ornatorotaliids Benedetti and Sinanoğlu (2022) also mentioned *Neorotalia*? *cretacea* and *Neorotalia*? *pinetensis*. Both species appeared during Campanian and share a marked dorsal ornamentation (=enveloping canal system?), but they have been left in open nomenclature (see Vicedo and Robles-Salcedo, 2022), due to the lack of some diagnostic features such as open canals on dorsal side, which make a thoughtful architectural comparison difficult. The Upper Cretaceous species *Calcarinella schaubi* displays, by comparative anatomy, close affinities with Cenozoic calcarinids, especially for the occurrence of heavy ornamentation, multiple apertures and a pervasive enveloping canal system, suggesting ability to thrive in high-energy bottoms.

The occurrence of true canaliculated spines among the Upper Cretaceous *Siderolites* and *Canalispina* indicates a possible phylogenetic relationship with the Cenozoic calcarinids and ornatorotaliids. Robles-Salcedo (2014) discussed in detail the reasons on comparing them with fossil and living *Calcarina*, *Baculogypsina*, and *Baculogypsinoides*, and suggests a close paleoenvironmental preference for agitated seafloors. However, these taxa display a planispiral pattern, a complex network of canals and no tooth-plates, challenging straight genetic relationships with the ornatorotaliids; they are only roughly morphologically comparable, probably because of a convergent adaptation to similar environments. The roots of Ornatorotaliidae and Calcarinoidea phylogeny could be found among fossil *Pararotalia* or *Neorotalia* species, a group of taxa bearing both spines or pseudospines in their modern representatives, e.g. *Neorotalia calcar* and *Pararotalia stellata*.

Despite the few data still available, ornatorotaliids appear widely scattered from western to eastern Neotethys since the Paleocene up to the Oligocene, where *Risananeiza* is documented also in the isolated

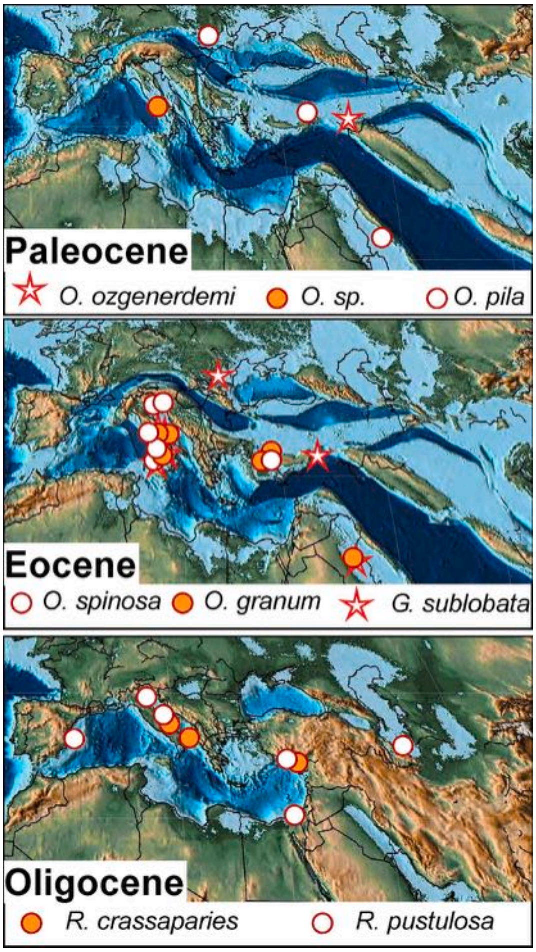

Fig. 7. Palaeogeographic distribution of ornatorotaliid species during the Paleocene (SBZ2 to SBZ4), the Eocene (mainly SBZ10–11) and Oligocene (SBZ23). Palaeogeographic maps after Scotese (2014).

Qom basin (Fig. 7).

Ornatorotalia spans from the upper Danian to the whole Ypresian (Benedetti and Papazzoni, 2022), whereas *Granorotalia*, so far described from the upper Ypresian to lowermost Lutetian (i.e., SBZ10–12), possibly rooted from *Ornatorotalia* or from a different calcarinoid. A schematic stratigraphic summary of the distribution of herein investigated ornatorotaliids is provided in Fig. 8. Given the historical emphasis on nummulitids, alveolinids, and orthophragmines in middle to upper Eocene stratigraphy, the potential presence of *Granorotalia* in younger sediments may have been underestimated and therefore cannot be definitely ruled out.

Risananeiza, restricted to the Oligocene-Miocene, possibly rooted from a species belonging to *Neorotalia*. Gedik (2020) suggested that it rapidly evolved in *Miogypsinella* but this hypothesis appears at present only speculative.

5. Conclusions

Ornatorotaliids widely occurred from the western to the eastern Neotethys during the Paleogene, although further studies are needed to characterize the areal extension of each single taxon. They are recently recognized as useful markers for biostratigraphic interpretation of shallow water sedimentary successions, but so far we have few data about their complete stratigraphic range because of lacking of dedicated studies.

Here, based on the microfacies analysis, comparison with literature data, and according to the ecological behaviours of extant calcarinids, we suggest that the different known species were linked to particular paleoenvironments. The upper Danian species *Ornatorotalia ozgenerdemi* was a generalist small species thriving in vegetated inner ramp or lagoons. The Thanetian *O. pila* more likely inhabited inner ramp settings with moderate-high hydrodynamics and possibly vegetated seafloors. *Ornatorotalia spinosa* colonized both innermost ramps and lagoons, as well as more or less vegetated sand shoals, together with alveolinids; with its strong spines, it was adapted to high-energy conditions. *Ornatorotalia granum* and *Granorotalia spinosa* usually coexisted in a wider depth and paleoenvironmental gradient always within the inner ramp setting.

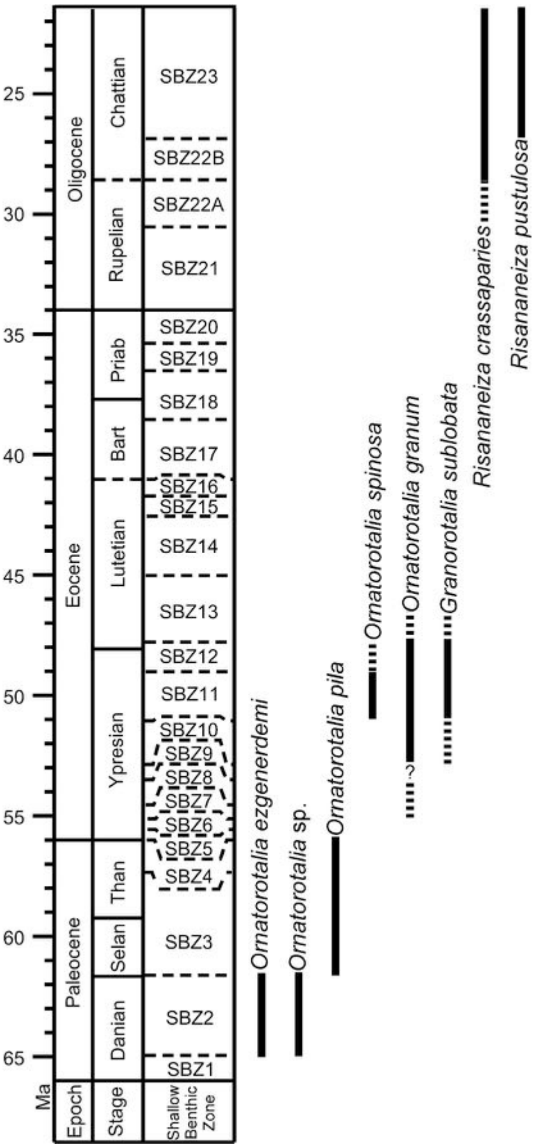

Fig. 8. Stratigraphic distribution of the known taxa belonging to the Ornatorotaliidae family.

The Oligocene *Risananeiza pustulosa* and *R. crassaparies* possibly represent two different ecomorphotypes, the first one characteristic of innermost ramp to uppermost middle ramp, whereas the flattened *R. crassaparies* characterized both high-energy inner ramp zones and middle ramp.

At the present state of knowledge, the phylogenetic relationship among the species, the possible ancestors and descendants could only be hypothesized but more data are required to check the different options.

CRediT authorship contribution statement

Andrea Benedetti: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Antonino Briguglio:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Formal analysis. **Lorenzo Consorti:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Data curation. **Cesare Andrea Papazzoni:** Writing – review & editing, Writing – original draft, Validation, Investigation, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Special thanks to Marco Brandano (Sapienza University, Rome), Carmine D'Amico, Simone Fabbi (Sapienza University, Rome), Ruggero Matteucci (Sapienza University, Rome), Johannes Pignatti (Sapienza University, Rome), Francesco Schiavinotto (Sapienza University, Rome), Serafina Carbone (University of Catania), Carmelo Monaco (University of Catania), Pietro Di Stefano (University of Palermo), Romana Melis (University of Trieste) and Derya Sinanoğlu (Batman University, Turkey), for providing thin sections. Two anonymous reviewers and the editor Valeria Luciani are thanked for their suggestions that contribute to improve the manuscript. This study was funded by the Italian Ministry of Instruction, University and Research (MIUR), funds PRIN 2017: project "Biota resilience to global change: biomineralization of planktic and benthic calcifiers in the past, present and future" (prot. 2017RX9XXY).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marmicro.2024.102423.

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