Carnets Geol. 26 (12)

EISSN 16340744
DOI: 10.2110/carnets.2026.2612

Upper Eocene-Oligocene larger Foraminifera from the westernmost Tethys (Prebetic Range, SE Iberia). Revision of *Austrotrillina* and *Risananeiza*

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Abstract: The study of upper Eocene-Oligocene larger foraminiferal assemblages in two sections of the Prebetic Range in south-eastern Iberia (Ibi and La Font Roja sections) revealed a rich diversity, including species previously known only from the Central Tethys, such as the Eocene *Neorhipidionina* cf. *spiralis*, and the Oligocene *Pfendericonus globulus*, *Austrotrillina howchini*, *Idalina pignattii*, and *Archaias* sp., as well as endemic forms such as *Peneroplis peramplus*, *Spirolinella emmae*, and *Borelis* sp. 1. The continuous record of *Austrotrillina* (Rupelian-Chattian) and *Risananeiza* (upper Chattian) showed evolutionary trends and allowed for a systematic revision. *Austrotrillina asmariensis*, *A. striata*, and *A. brunni* are considered morphotypes of a single species, *A. striata*, evolving anagenetically from the lower Rupelian *A. paucialveolata*, which originated from the Eocene *A. eocaenica*. The two known species of *Risananeiza*, *R. crassaparies* and *R. pustulosa*, were identified for the first time within the same stratigraphic section. They represent successive stages of an anagenetic species throughout the upper Chattian. The biostratigraphic results provide an improved characterization of Shallow Benthic zones SB 21 to 23 in the westernmost Tethys and allow the subdivision of SB 23 (upper Chattian) into two sub-biozones, 23A and 23B, based on the stratigraphic ranges of miogypsinids (*Miogypsinella* spp., *Postmiogypsinella intermedia*) and *Risananeiza*. The Priabonian-Chattian *Neorotalia burdigalensis* also exhibits evolutionary trends with potential biostratigraphic relevance. Overall, the biostratigraphic data obtained indicate diachronous, parallel evolution and extinction in several genera, improving our understanding of diversity patterns and migration pathways in Oligocene larger Foraminifera.

Keywords:

- Rupelian;
- Chattian;
- Priabonian;
- shallow benthic zones;
- *Borelis*;
- *Neorotalia*;
- *Pfendericonus*

Citation: FERRÀNDEZ-CAÑADELL C., GRANERO P. & BOVER-ARNAL T. (2026).- Upper Eocene-Oligocene larger Foraminifera from the westernmost Tethys (Prebetic Range, SE Iberia). Revision of *Austrotrillina* and *Risananeiza*. *Carnets Geol.*, Madrid, vol. 26, no. 12, p. 239-315. DOI: 10.2110/carnets.2026.2612

Résumé : *Grands foraminifères de l'Éocène supérieur-Oligocène de la Téthys occidentale (Prébétique, sud-est de la péninsule ibérique). Révision des genres* Austrotrillina *et* Risananeiza.- L'étude des assemblages de grands foraminifères de l'Éocène supérieur-Oligocène dans deux coupes de la chaîne prébétique du sud-est de la péninsule Ibérique (coupes d'Ibi et de La Font Roja) a révélé une riche diversité, incluant des espèces auparavant connues uniquement de la Téthys centrale, telles que *Neorhipidionina* cf. *spiralis* de l'Éocène, et *Pfendericonus globulus*, *Austrotrillina howchini*,

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Published online in final form (pdf) on August 8, 2026
[Editor: George PLEŞ; language editor: Robert W. SCOTT; technical editor: Bruno GRANIER]

Idalina pignattii et *Archaias* sp. de l'Oligocène, ainsi que des formes endémiques comme *Peneroplis peramplus*, *Spirolinella emmae* et *Borelis* sp. 1. La présence continue d'*Austrotrillina* (Rupélien-Chattien) et de *Risananeiza* (Chattien supérieur) a mis en évidence des tendances évolutives et a permis une révision systématique. *Austrotrillina asma*riensis, *A. striata* et *A. brunni* sont considérées comme des morphotypes d'une seule espèce, *A. striata*, ayant évolué de manière anagénétique à partir d'*A. paucialveolata* (Rupélien inférieur), elle-même issue d'*A. eocaenica* (Éocène). Les deux espèces connues de *Risananeiza*, *R. crassaparies* et *R. pustulosa*, ont été identifiées pour la première fois dans la même coupe stratigraphique. Elles représentent des stades successifs d'une espèce anagénétique tout au long du Chattien supérieur. Les résultats biostratigraphiques permettent une meilleure caractérisation des zones benthiques de faible profondeur SB 21 à 23 dans la Téthys occidentale et la subdivision de SB 23 (Chattien supérieur) en deux sous-biozones, 23A et 23B, en fonction de la répartition stratigraphique des miogypsinidés (*Miogypsinella* spp., *Postmiogypsinella intermedia*) et de *Risananeiza*. La *Neorotalia burdigalensis* (Priabonien-Chattien) présente également des tendances évolutives potentiellement pertinentes sur le plan biostratigraphique. Globalement, les données biostratigraphiques obtenues indiquent une évolution diachronique et parallèle, ainsi que des extinctions chez plusieurs genres, ce qui contribue à une meilleure compréhension des schémas de diversité et des voies de migration chez les grands foraminifères de l'Oligocène.

Motsclefs :

• Rupélien ;
• Chattien ;
• Priabonien ;
• zones benthiques de faible profondeur ;
• *Borelis* ;
• *Neorotalia* ;
• *Pfendericonus*

1. Introduction

The late Eocene-Oligocene was characterised by major climatic and palaeoceanographic changes, marking the end of the Eocene's warm conditions and the onset of the cooler and more seasonal climate of the Oligocene (*e.g.*, Berggren & Prothero, 1992; Zachos *et al.*, 2001; Pälike *et al.*, 2006; Liu *et al.*, 2009; Jovane *et al.*, 2009). These environmental changes led to a progressive decline in larger foraminiferal diversity, most evident in the Mediterranean region, and the extinction of major groups that had flourished during the early and middle Eocene, including *Alveolina*, orthophragmines (Discocyclinidae and Orbitoclypeidae), and most lineages of *Nummulites.*

In the Western Tethys, the reduced diversity of larger Foraminifera during the late Eocene-early Oligocene is further compounded by a scarce and discontinuous geological record. For example, the Pyrenean foreland basin (Ebro Basin), which was very rich in larger Foraminifera during the early and middle Eocene, lost its connection with the Atlantic Ocean in the middle Priabonian and became endorheic (Riba *et al.*, 1983; Garcés *et al.*, 2020). Consequently, the late Priabonian and Oligocene were characterized by endorheic deposition, dominated by alluvial, lacustrine, and palustrine successions, including evaporites, carbonates, and siliciclastics. In the Helvetic Alps, the Priabonian record of larger Foraminifera is mainly represented by limestones with hyaline species from relatively deep facies (heterosteginids and orthophragmines), overlain by the deeper-water *Globigerina* marls (*e.g.*, Ferràndez-Cañadell *et al.*, 2023b). A large part of the marine Oligocene deposits from the Western Tethys were either eroded or deformed by tectonic processes, during or after deposition, as noted by Hottinger (1963) for the Betics. A classical Oligocene section in northern Spain, San Vicente de la Barquera (Heck & Drooger, 1984), consists of turbiditic deposits where lepidocyclinids and nummulitids occur together with reworked Eocene nummulitids and orthophragminids, as well as a few Lower Cretaceous orbitolinids (Ferràndez-Cañadell *et al.*, 1999).

Oligocene larger Foraminifera have been extensively studied in the Central Tethys (Iran, Iraq, Oman, Yemen, eastern Turkey; *e.g.*, Henson, 1936, 1937, 1950; Smout & Eames, 1958; Adams, 1968; Sirel, 2003; Gedik, 2008, 2014, 2015; Özcan & Less, 2009; Özcan *et al.*, 2009a, 2010a, 2010b; Işık, 2010; Işık & Hakyemez, 2011; Sirel *et al.*, 2013, 2020a, 2020b; Serra-Kiel *et al.*, 2016). In contrast, studies from the Western Tethys (Mediterranean region-western and central Turkey) are fewer and more limited, particularly regarding shallow-water facies with porcellaneous larger Foraminifera. These facies have only been reported from Malta (Felix, 1973; Brandano *et al.*, 2009), Italy (Pignatti, 1995; Bassi *et al.*, 2007), Mallorca (Colom, 1929, 1935), and SE Spain (Didon *et al.*, 1961; Hottinger, 1963), or are restricted to the nearly monospecific '*Archiacina* beds' in the Paris Basin (Alimen & Lucas, 1945), Aquitaine (Sztrákos & Steurbaut, 2017), Transylvania (Bombita, 1980), and Mallorca (Colom, 1957). Hottinger (1963), Sirel (1997), and Bassi *et al.* (2007) emphasised the scarcity of shallow-water carbonate facies in the Western Tethys ("virtually absent", Sirel, 1997, p. 167).

The global reduction in larger Foraminifera diversity, together with the poor geological record of shallow-platform facies in the Western Tethys, makes Priabonian-Oligocene biozonation particularly challenging. Biostratigraphic correlation is further complicated by multiple migration episodes involving several groups (*e.g.*, Robinson,

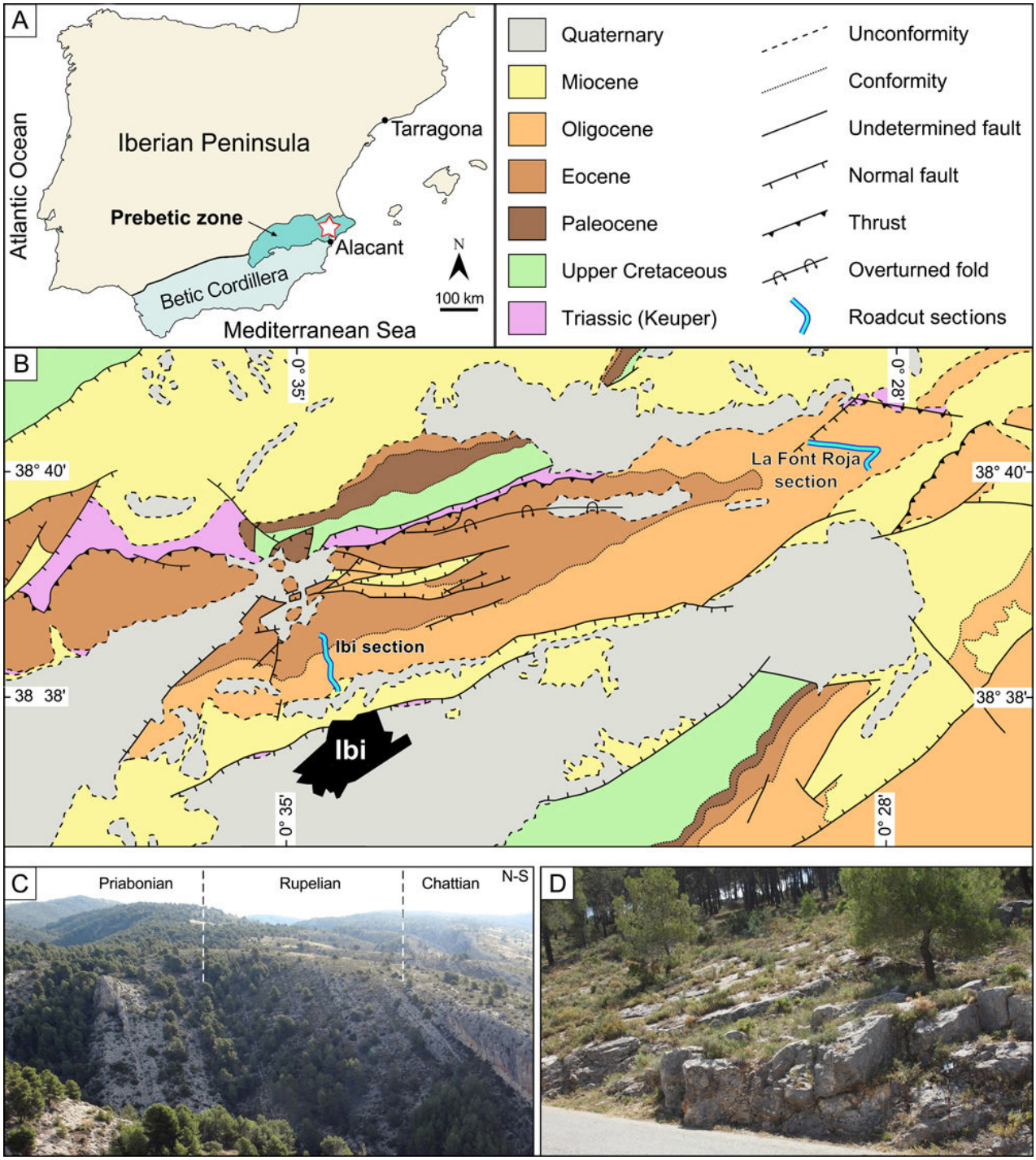


Figure 1: Geographical and geological setting of the study area. **A)** Location of the study area (star) in the eastern part of the Prebetic domain within the Betic Cordillera of the Iberian Peninsula. **B)** Geological map of the study area showing the location of the two sections studied along roadcuts: Ibi and La Font Roja. This map is an adapted version derived from the geological maps by Almela *et al.* (1973), Martínez del Olmo & Benzaquen (1973), Martínez *et al.* (1977), and Colodrón *et al.* (1980), updated from data from Geel (1995) and this study. **C)** Panoramic view of the lower and middle parts of the Ibi section, showing the boundaries between the Priabonian, Rupelian, and Chattian stages based on the biostratigraphic analysis conducted in the present study. **D)** Outcrop view of the upper Chattian succession at La Font Roja section.

1996; Renema, 2002, 2007; Harzhauser & Piller, 2007; Boudagher-Fadel & Price, 2013; Hottinger, 2014; Benedetti *et al.*, 2018; Sarfi & Yazdi-Moghadam, 2024; and references therein). These limitations in the geological and fossil record have led to the assumption that diversity in the Western Tethys during the Priabonian and Oligocene was lower compared to the Central Tethys (*e.g.*, Bassi *et al.*, 2007; Dimou *et al.*, 2024). Bassi *et al.* (2007) further suggesting a gradual reduction in porcellaneous species diversity in the Central-Western Tethys from south-east to north-west.

In this study, we report a rather complete succession of Eocene-Oligocene age (Priabonian-up-

per Chattian) from the Prebetic Range (Figs. 1-2), representing shallow-water platform carbonates developed along the south-eastern coast of the Iberian Peninsula. These deposits contain rich assemblages of both hyaline and porcellaneous larger Foraminifera, unique in the Western Tethys, offering new insights into the diversity and palaeobiogeography of these organisms during the Oligocene. Furthermore, the continuous record throughout the Oligocene enables a detailed analysis of morphological variation and evolutionary trends in several genera, particularly *Austrotrillina*, *Risananeiza*, and *Neorotalia*. These findings provide valuable contributions to biozonation and biostratigraphic correlation, as well as to the interpretation of palaeobiogeographic diversity and migration patterns.

2. Geological setting

The Betic Cordillera in southeastern Spain forms part of the Western Mediterranean Alpine belt. It is subdivided into an External Zone and an Internal Zone, corresponding respectively to the former passive southern margin of Iberia and a stack of allochthonous nappe complexes (García-Hernández *et al.*, 1980; Geel & Roep, 1999; Vera, 2000). The External Prebetic Domain occupies the northern part of the Prebetic Zone, in a proximal position relative to the southeastern Iberian margin, and consists mainly of platform carbonates, which were periodically interrupted by detrital inputs. On the other hand, the Internal Prebetic is characterised by hemipelagic deposits including turbidites (Martín-Chivelet & Chacón, 2007; Höntzsch *et al.*, 2013). The studied sections record a ~500 m-thick succession of shallow-platform limestones belonging to the External Prebetic, located near the town of Ibi (Fig. 1).

Deposition of upper Eocene-Oligocene deposits in the Prebetic Domain was influenced by the Alpine tectonic activity. Initially, the southern Iberian margin acted as a passive margin, later undergoing an extensional phase before evolving into a thrust-and-fold belt during the Betic orogeny and the opening of the Gulf of València in the late Oligocene-Miocene (Azéma, 1977; Roca & Desegaulx, 1992; Vegas, 1992; Geel, 1995). Consequently, Paleogene palaeogeography and sedimentation in this region were complex and variable (Martín-Martín *et al.*, 2021).

There is no consensus among authors regarding the age of the post-Eocene deposits. In particular, the younger shallow-water limestone beds in the Ibi and surrounding areas were initially interpreted as Aquitanian-Burdigalian (Almela *et al.*, 1973; Martínez del Olmo & Benzaquen, 1973; Martínez *et al.*, 1977; Colodrón *et al.*, 1980), and later reassigned to the Burdigalian (Geel, 1995) or even to the middle Oligocene (Geel, 2000). It should be noted, however, that the chronostratigraphic meaning of these stratigraphic units has varied over time.

The Oligocene larger Foraminifera from the Prebetic of Alacant have been previously studied by Hottinger (1963), Azéma *et al.* (1969), Geel (1995, 2000), Höntzsch *et al.* (2013), Bover-Arnal *et al.* (2017), Ferràndez-Cañadell and Bover-Arnal (2017), Falces-Delgado and Giannetti (2023), and Ferràndez-Cañadell (2024). The pioneering work by Hottinger (1963) revealed an association of porcellaneous forms ("Calcaires à Pénéroplidés de Moratalla"), which he compared to those from the Middle East reported by Henson (1950) and interpreted as late Oligocene in age, based on previous data on molluscs in Durand Delga and Magné (1958). Later studies by Azéma *et al.* (1969), Geel (1995, 2000), and Höntzsch *et al.* (2013) identified larger Foraminifera only at the group or generic level, providing a basic biostratigraphy (supplemented by planktic foraminiferal data in Geel, 1995) and focusing on major stratigraphic sequences and their relation with tectonic evolution and climatic changes. Ferràndez-Cañadell and Bover-Arnal (2017) studied larger Foraminifera from the easternmost Prebetic (Benitatxell Range) and identified a characteristic upper Chattian (SB 23) assemblage containing both porcellaneous and hyaline species. The study by Falces-Delgado and Giannetti (2023), which focused on the palaeoecology of *Kuphus*, reported an upper Rupelian (SB 22A) association of larger Foraminifera from Serra de l'Arguenya, located on the southern flank of the Diapiric Anticline of the Saix-Castalla-Ibi subunit (Martínez *et al.*, 1977), approximately 20 km ESE of Ibi.

The Ibi section (Els Molins ravine, north of Ibi town; Fig. 1) preserves a long record of Palaeogene deposits, ranging from the middle Cuisian, Shallow Benthic zone (SB) 11 (Martín-Martín *et al.*, 2025; Miclăuş *et al.*, 2025), to the late Chattian (SB 23). The Oligocene record of the Ibi section was previously studied by Geel (1995, 2000), who interpreted the facies as back-reef deposits and recognised four Oligocene sedimentary cycles, O1 to O4. Based on the larger Foraminifera assemblages (identified at the group or genus level), together with regional correlations and planktic foraminiferal data, Geel (1995) assigned the ages of these cycles as lower Rupelian (P18-19-20, cycles O1 and O2), upper Rupelian to lower Chattian (P21, cycle O3), and upper Chattian (P22, Cycle O4). In a later paper, Geel (2000) revised this interpretation and considered all these cycles to represent the lower and middle Oligocene. Similarly, Höntzsch *et al.* (2013) used foraminiferal assemblages, recognised at the level of group or genus, to develop a depositional model for the Prebetic Paleogene platform, highlighting the influence of climate changes and tectonics. These earlier studies focused primarily on the sedimentary evolution of the area and did not address the systematics of the Foraminifera at the species level. Consequently, they do not provide information on species diversity. Their biostratigraphic frameworks are based on the first

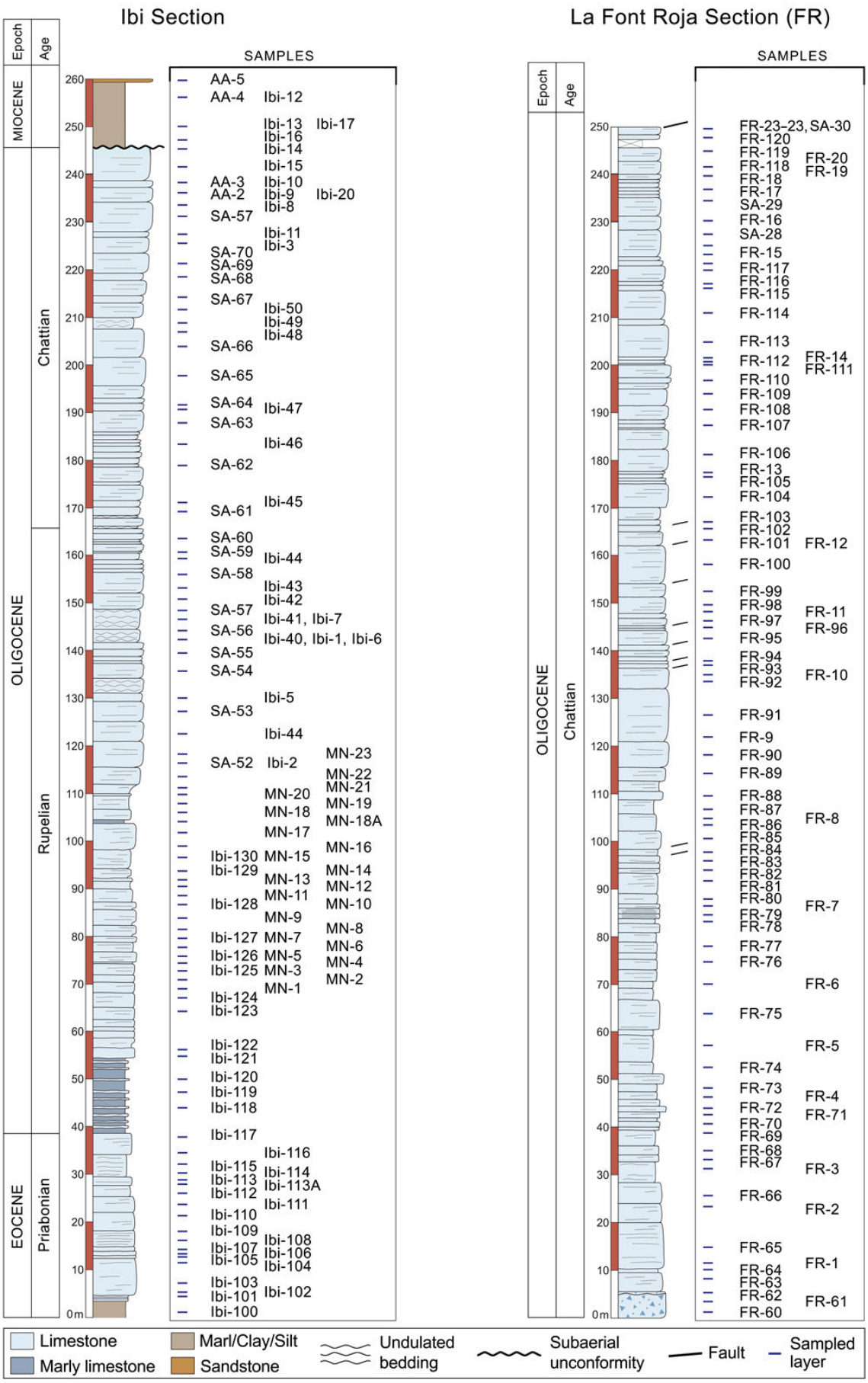


Figure 2: Stratigraphic logs of the studied sections and stratigraphic positions of the samples collected. See Fig. 1 for the location of the sections.

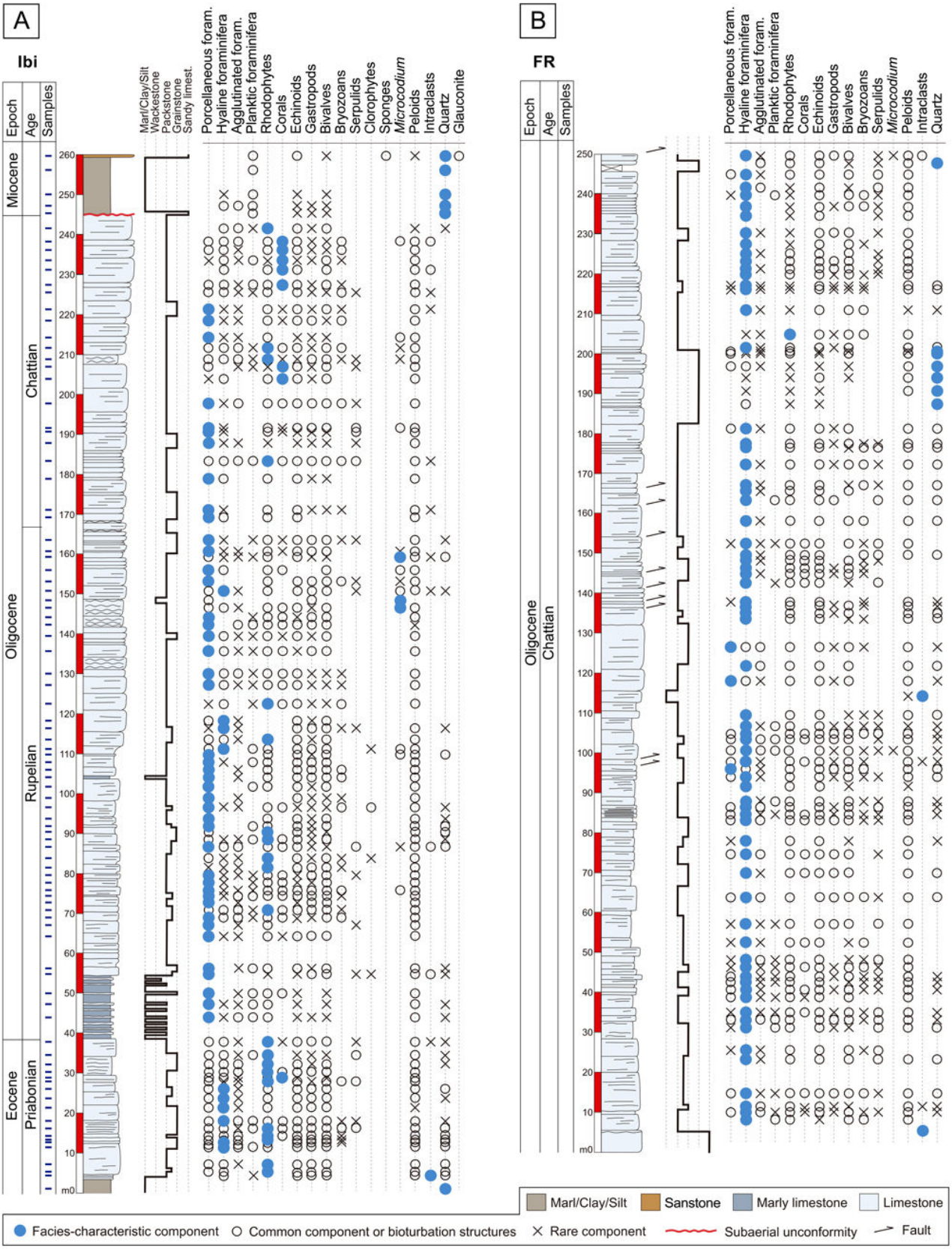


Figure 3: Stratigraphic logs studied, **A)** Ibi section and **B)** La Font Roja section, showing textures and qualitative abundances of skeletal and non-skeletal components. See Fig. 1 for the geographical location of the studied sections.

occurrences and co-occurrences of genera. In this regard, GEEL (2000) used the first occurrences of *Nephrolepidina*, *Eulepidina*, and *Miogypsinoides* to define an 'upper lower Oligocene', a 'middle Oligocene', and an 'upper Oligocene', respectively.

Preliminary results of the present study were given in two congress abstracts (GRANERO *et al.*, 2020, 2022), and in FERRÀNDEZ-CAÑADELL (2024), a paper focused on two early Rupelian new species perhaps endemic to the Prebetic domain.

3. Materials and methods

The studied specimens were documented from over 6,000 microphotographs taken from 385 thin sections of 212 limestone samples, collected along nearly 500 m of stratigraphic section (Fig. 2). Most of the Foraminifera were, therefore, studied in unoriented and non-centred sections. Consequently, the measurements reported in tables and plots are approximate and may be slightly smaller than the real dimensions. Thin sections of the samples were produced in the Laboratories of Palaeontology and Petrology of the Faculty of Earth Sciences of the University of Barcelona. Several microscopes and cameras were used; with the majority of photographs taken using a Zeiss AxioCam MRc 5 digital camera mounted on a Zeiss Axioplan-2 petrographic microscope. The thin sections are deposited at the Faculty of Earth Sciences of the University of Barcelona, except for those containing type material of *Peneroplis peramplus* and *Spirolinella emmae* (FERRÀNDEZ-CAÑADELL, 2024), which are housed at the Museum of Natural Sciences of Barcelona (Museu de Ciències Naturals de Barcelona) in seven thin sections under catalog numbers MGB 94151 (sample MN-6), MGB 94152 (sample MN-18), MGB 94153 (sample Ibi-120), and MGB 94154 (sample Ibi-126). According to MARTINSSON (1979) and EMILIANI (1991), we use the terms "planktic" and "benthic" rather than "planktonic" and "benthonic", which are incorrect derivations from the Greek terms. Original toponymic names in the Catalan language are used instead of the Castilianised forms imposed during the Franco dictatorship found in the literature (*e.g.*, Alacant instead of 'Alicante', Saix instead of 'Sax', Serra de l'Arguenya instead of 'Sierra de la Argueña', and Barranc dels Molins instead of 'Barranco de los Molinos'). To simplify the text and improve readability, full species names are listed in Appendix.

List of abbreviations: FR: La Font Roja, SB: Shallow Benthic (biozone), FO: first occurrence, *EI*: elongation index (= test length/width), *P*: internal equatorial diameter of the megalospheric proloculus (excluding chamber wall thickness).

4. Results

Two sections were studied in the south-eastern Iberian Peninsula: Ibi and La Font Roja (Figs. 1-4). Both belong to the External Prebetic Domain, which comprises a mixed carbonate-siliciclastic succession of Triassic to Miocene age, deposited along the South Iberian passive continental margin of the Tethys (GARCÍA-HERNÁNDEZ *et al.*, 1980; VERA, 2000; HÖNTZSCH *et al.*, 2013). No formal lithostratigraphic units have yet been defined for the succession analysed.

The Ibi section was logged along the Molins ravine (Barranc dels Molins), north of Ibi town in Alacant province (Fig. 1). The section, corresponding to the 'Ibi west' section of GEEL (1995, 2000), includes a continuous record of platform limestones from the middle Eocene to the late Chattian, which is cut by an erosional surface unconformably overlain by middle Miocene marls and sandstones containing planktic Foraminifera. The part of the Ibi section studied here (base: 38°38'13"N, 0°34'43"W) shows a continuous series of shallow-water limestones ranging from the uppermost Eocene (Priabonian) to the upper Chattian (Figs. 1-5). The *La Font Roja* section (FR), located 9 km to the east-north-east, lies within the Carrascar de la Font Roja Natural Park (Figs. 1-5) and roughly corresponds to the 'Ibi-east' section of GEEL (1995).

Ibi succession

The sedimentary succession logged at Ibi is 260 m thick (Figs. 2, 3A) and is mainly composed of well-bedded limestone beds ranging from centimetre- to metre-scale thickness. Locally, the limestones display nodular bedding and are interbedded with marl layers of comparable thickness. The limestones predominantly exhibit packstone to grainstone textures, although wackestone textures are also locally present. Porcellaneous Foraminifera constitute the main skeletal component of these platform carbonates. However, beds dominated by hyaline Foraminifera, corals, rhodophytes, or *Microcodium* also occur. Beds dominated by hyaline Foraminifera are mainly found in the lower part of the section, between metres 11 and 26, and metres 111 and 120 (Fig. 3A). Like hyaline Foraminifera, rhodophytes are also common throughout the succession but become locally dominant between metres 3 and 39, 113 and 122, and 209 and 241. The Rhodophyta observed include geniculate and non-geniculate species, some of which form rhodoliths. In certain intervals, such as between metres 239 and 245 (Fig. 3A), these rhodoliths accumulate to form a distinct rhodolith bed (Fig. 4A-B). Locally, hook-shaped morphologies of crustose rhodophytes were also identified. Coral-dominated beds occur in both the lowermost and uppermost parts of the section, specifically between metres 29 and 30, and metres 204 and 239, respectively (Fig. 3A). The coral colonies observed were not reef-builders but rather level-bottom communities displaying a loose growth fabric, or they formed coral biostromes (Fig. 4C). *Microcodium* was observed in 13 samples across the succession (Fig. 4D), with notable dominance in three samples from the stratigraphic interval between metres 155 and 160 (Fig. 3A). Other common skeletal components in the limestones include bivalves, gastropods, bryozoans, serpulids, planktic Foraminifera, and agglutinated Foraminifera, including encrusting forms. Remains of chlorophytes are rare. Among the non-skeletal components, peloids and silt- to fine sand-sized quartz grains are common, whereas intraclasts are present but rare. Stratigraphic intervals with siliciclastic influence occur between metres 0 and 66, and 89 and 117. At metre 245, an erosional surface marks the top of the carbonate platform succession (Figs. 3A, 4E-F). This irregular surface

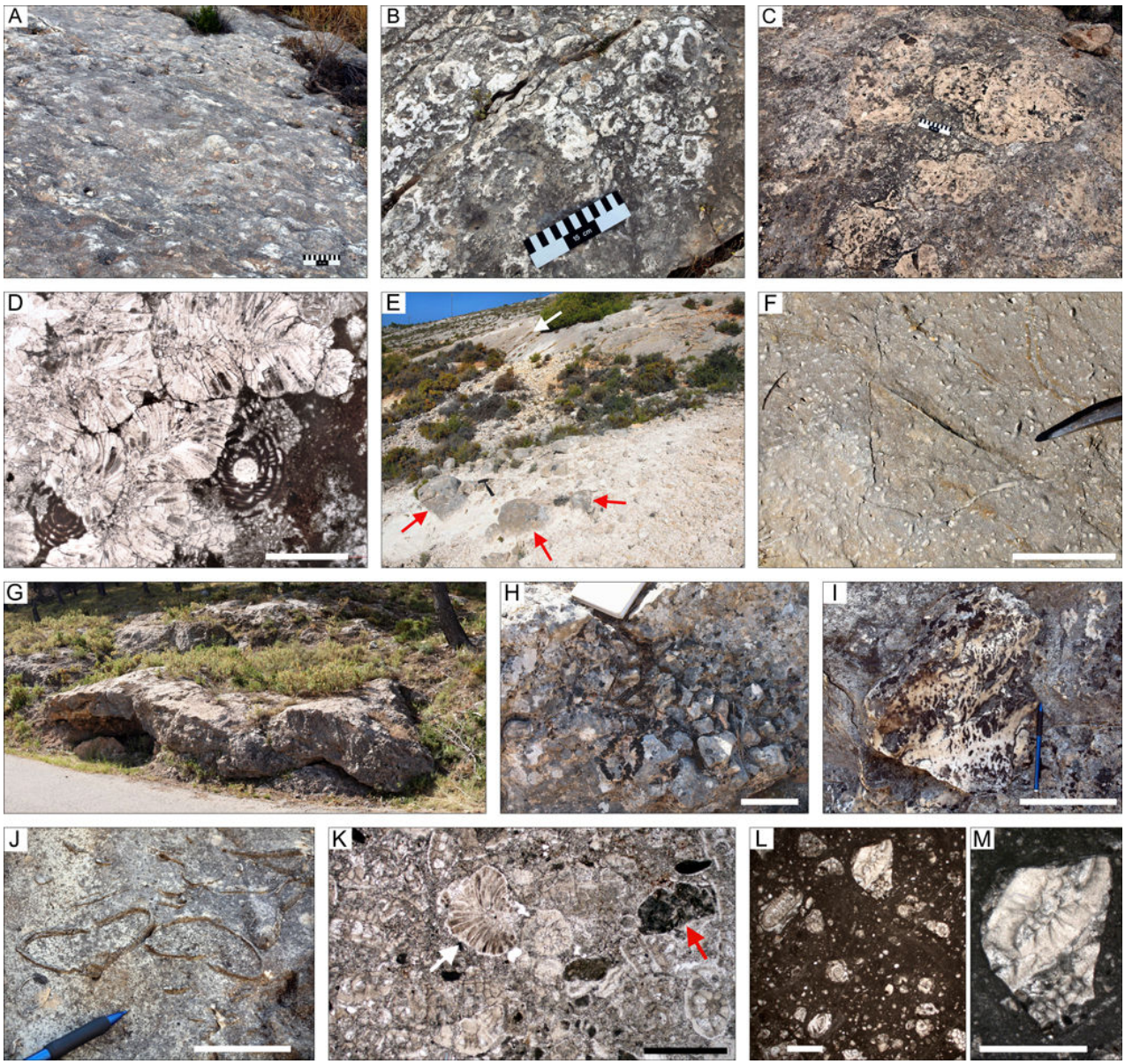


Figure 4: Sedimentary and fossil features from the Ibi and La Font Roja sections. **A-B)** Outcrop view (A) and detail (B) of an upper Chattian rhodolith bed, upper part of the Ibi section. Note the nodular appearance of the surface, reflecting the accumulation of rhodoliths; ruler = 15 cm. **C)** Outcrop view of an upper Chattian coral biostrome, upper part of the Ibi section. Coral colonies can be distinguished by their lighter beige coloration; ruler = 15 cm. **D)** Microphotograph showing *Microcodium* invading *Borelis* tests, late Rupelian, sample SA-57, Ibi section metre 148, scale bar = 1 mm. **E)** Irregular erosional surface capping the upper Chattian platform carbonate succession at the top of the Ibi section (white arrow). This unconformity is overlain by marls containing scleractinian coral colonies in growth position (red arrows). Hammer = 32 cm. **F)** Detail of the rockground at the top of the Ibi section (white arrow in *e*) with bioerosional features associated with the unconformity. Scale bar = 5 cm. **G-H)** Outcrop view (G) and detail (H) of an undulated breccia bed conforming to an underlying irregular palaeotopography in the lowermost part of the FR section; scale bar = 15 cm. **I)** Coral colony in growth position from La Font Roja section, at 145 m (Figs. 2, 3b); scale bar = 5 cm. **J)** Outcrop photograph of echinoid tests from La Font Roja section, at 35 m (Figs. 2, 3b); scale bar = 5 cm. **K)** Photomicrograph of a grain-supported texture showing reworked *Microcodium* (white arrow), hyaline Foraminifera tests, and intraclasts (red arrow), sample SA-30. **L-M)** Photomicrograph (L) and detail (M) of sample FR-8 (late Chattian, La Font Roja section) showing intraclasts, most of which contain fragments of hyaline larger Foraminifera tests; scale bars = 1 mm.

shows widespread bioerosion features (Fig. 4F). Above it lies an alternation of marls, silts, and sandy limestones. The sandy limestones contain abundant planktic Foraminifera. Hyaline and agglutinated Foraminifera, sponge remains, and fragments of echinoids and molluscs also occur. In addition to quartz grains, common non-skeletal components include glauconite and peloids. Locally, marly deposits overlying the erosional surface host level-bottom coral communities preserved in life position, exhibiting a loose growth fabric (Fig. 4E). Samples of the Ibi section are numbered as Ibi-x, Ibi-MN-x, SA-x, and AA-x, corresponding to different field campaigns (2013/2016/2018) or to different subsections (Fig. 2).

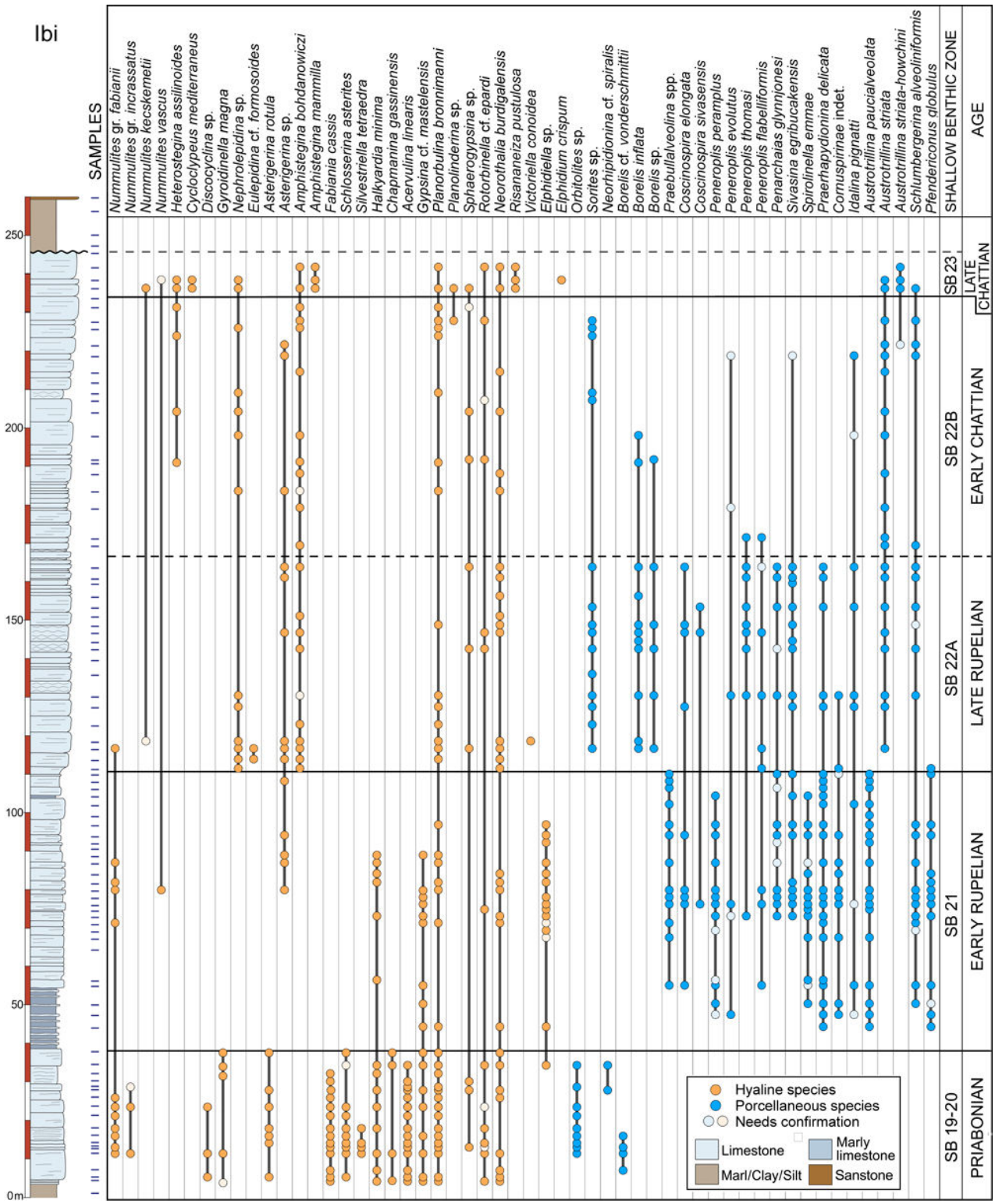


Figure 5: Biostratigraphic distribution of foraminiferal taxa in the Ibi section.

La Font Roja succession

The stratigraphic section measured at FR has a thickness of 250 metres (Figs. 1-2, 3B). The succession is faulted, although the faults show only minor displacements. The base of the succession is marked by metre-thick breccias made up of carbonate intraclasts containing coral fragments and lepidocyclinids. The uppermost breccia bed shows an undulated bedding and conforms to an underlying irregular palaeotopography (Fig. 4G-H). Above this, the succession consists of centimetre- to metre-thick massive limestones with packstone to grainstone textures, dominated by hyaline Foraminifera. Other common skeletal components include porcellaneous Foraminifera, agglutinated Foraminifera (including encrusting forms), planktic Foraminifera, and fragments of rhodophytes, echinoids, bivalves, gastropods, bryozoans, and serpulids. Porcellaneous Foraminifera are particularly abundant between metres

80 and 137, where they locally dominate the facies (Fig. 3B). Entire echinoid tests occur locally and are commonly associated with siliciclastic-influenced deposits (Fig. 4J). Coral fragments, as well as rare colonies in growth position, are found between metres 5 and 115, and again between metres 142 and 152 (Fig. 4I). Two samples, collected at metres 98 and 248 respectively, yielded rare, reworked fragments of *Microcodium* (Fig. 4K). The most abundant non-skeletal components identified are silt- to sand-sized quartz grains and peloids. Significant siliciclastic input, resulting in sandy limestones, occurs between metres 182 and 201, and 245 and 249. At metre 114, there is a layer with wackestone texture with intraclasts, most of which contain foraminiferal fragments (Fig. 4L-M). Samples from La Font Roja section are numbered as FR-x and SA-x (Fig. 2).

Biostratigraphy

We follow the Shallow Benthic biozonation (SB zones), based on larger Foraminifera, stablished for the Paleocene-Eocene (SB zones 1-20; Serra-Kiel *et al.*, 1998a, 1998b) and for the Oligocene-Miocene (21-26; Cahuzac & Poignant, 1997, 1998). See further details on the SB zonation in Pignatti and Papazzoni (2017) and Papazzoni *et al.* (2017). Based on the assemblages of larger Foraminifera identified in the samples, different Shallow Benthic (SB) biozones were identified, corresponding to the Priabonian (SB 19-20), lower Rupelian (SB 21), upper Rupelian-lower Chattian (SB 22A-22B), and upper Chattian (SB 23) (Figs. 5-6).

In the Ibi section, the Priabonian is represented by 35 m of limestones overlying marls without larger Foraminifera. The Oligocene starts with 16 m of marly limestone interbedded with thin limestone beds, followed by 55 m of limestones of lower Rupelian age. The next 125 m consist of limestones and marly limestones of upper Rupelian and lower Chattian age. The Rupelian/Chattian boundary (SB 22A-22B) is not distinguished by any major change in the foraminiferal assemblages (see below). The upper Chattian is truncated by an erosional surface and reduced to about 10 m of limestones in the Ibi section. To complement this limited exposure of the upper Chattian in the Ibi section, we studied a nearby section (*La Font Roja*, FR), located 9 km ESE, which comprises 250 m of monotonous upper Chattian limestones, bounded at the base by a karstic breccia and topped by a major fault. The fault at the top of the section separates it from another block with more than 100 m of similar monotonous upper Chattian limestones, which are difficult to correlate with those of the section studied. Therefore, the latest Chattian and the Oligocene-Miocene boundaries are not included in this study.

Reworked foraminiferal tests were observed in several samples, but rarely mixing species from different biozones. In samples Ibi-116 and Ibi-117 (the last samples with Eocene assemblages, at 35 and 38 m in the Ibi section; Figs. 2, 5), well-preserved specimens of *Chapmanina* occur together with eroded ones. In the Ibi section, *Orbitolites* occurs in several samples from the first 40 m, associated with other Eocene genera. However, a small fragment (0.45 mm) of *Orbitolites* was found in sample Ibi-124, approximately 27 m above the Eocene/Oligocene boundary. Similarly, in sample Ibi-10 (238 m), characterised by late Chattian (SB 23) species, some intraclasts contain *Borelis inflata* and *Praerhapydionina delicata*, 74 m above their last occurrence in the section. In the FR section, a layer with intraclasts containing fragments of hyaline larger Foraminifera was observed (sample FR-89, at 114m; Fig. 3B). Foraminiferal tests showing a low degree of abrasion are common throughout the succession, which could be related either to winnowing or limited reworking. In addition, *Microcodium* is recorded in several layers of the Ibi section (Figs. 3B, 4D), indicating short-term emersion and subaerial exposure. Reworking was considered when characterizing the biozones and do not have major implications for the biostratigraphic interpretation.

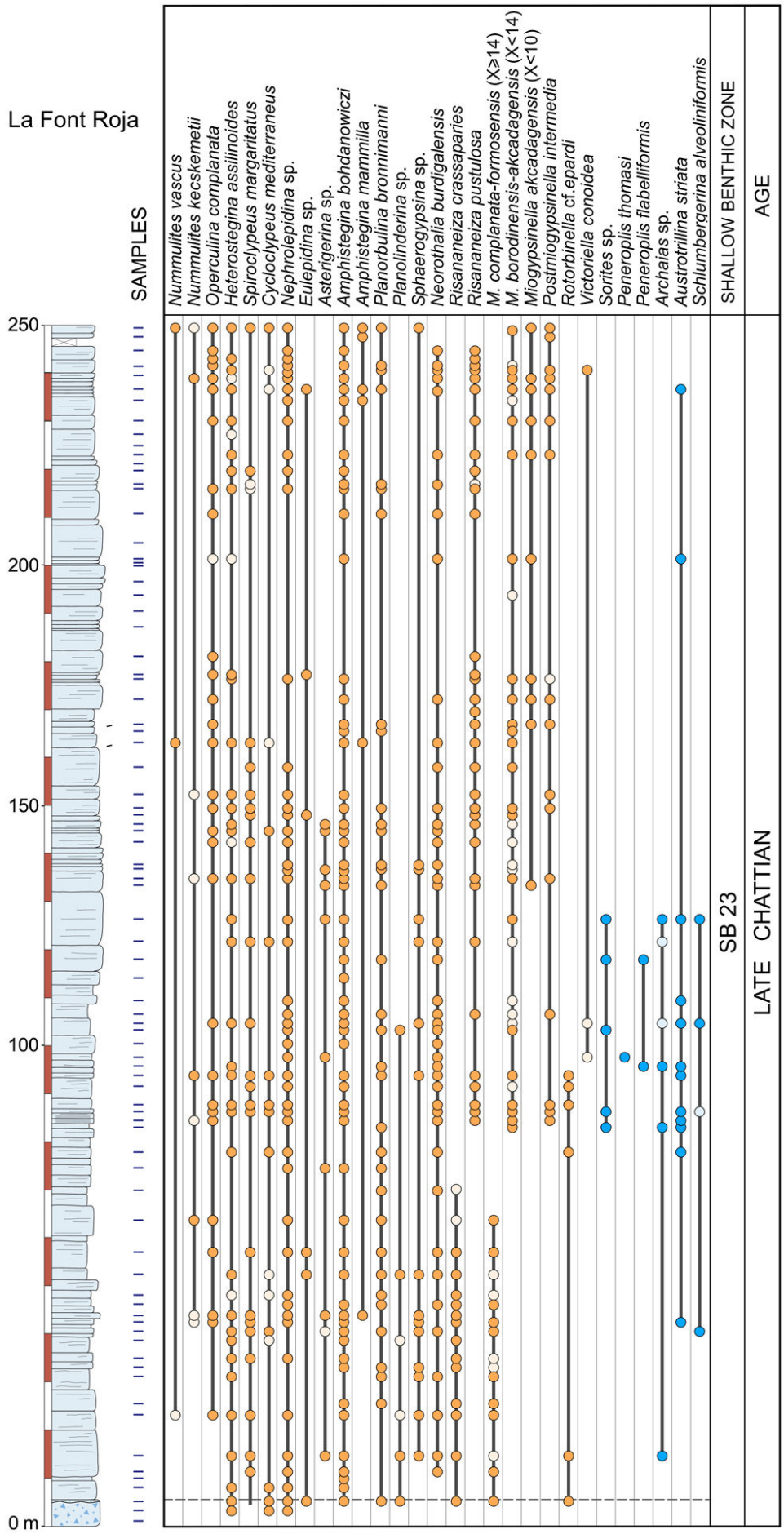
The biostratigraphic interpretation (Figs. 5-6) is based on the following larger foraminiferal assemblages:

Priabonian, SB 19-20

This biozone is recognised at the base of the Ibi section (Fig. 5) and is characterised by the following association of larger Foraminifera: *Nummulites fabianii*, *Nummulites* ex gr. *N. incrassatus*, *Acervulina linearis*, *Gypsina mastelensis*, *Gypsina* sp., *Asterigerina rotula*, *Discocyclina* spp., *Fabiania cassis*, *Planorbulina bronnimanni*, *Sphaerogypsina globulus*, *Halkyardia minima*, *Gyroidinella magna*, *Schlosserina asterites*, *Chapmanina gassinensis*, *Silvestriella tetraedra*, *Neorotalia burdigalensis*, *Rotorbinella epardi*, *Borelis vonderschmittii*, *Orbitolites* cf. *cotentinensis*, and *Neorhipidionina* cf. *spiralis* (Figs. 7-8, 10, 12).

Early Rupelian, SB 21

The biozone was identified in the lower part of the Ibi section (Fig. 5) and is distinguished by the presence of *Nummulites fichteli*, *N. vascus*, *Gypsina* cf. *mastelensis*, *Gypsina* sp., *Halkyardia minima*, *Neorotalia burdigalensis*, *Rotorbinella* cf. *epardi*, *Asterigerina* sp., *Planorbulina bronnimanni*, *Austrotrillina paucialveolata*, *Praebullalveolina minuta*, *P. oligocenica*, *Sivasina egribucakensis*, *Penarchaias glynnjonesi*, *Coscinospira sivasensis*, *C. elongata*, *Praerhapydionina delicata*, *Spirolinella emmae*, *Peneroplis evolutus*, *P. peramplus*, *P. thomasi*, *P. flabelliformis*, *Idalina pignattii*, *Schlumbergerina alveoliniformis*, and *Pfendericonus globulus* (Figs. 9-11, 13).



◀ **Figure 6:** Biostratigraphic distribution of foraminiferal taxa in La Font Roja section.

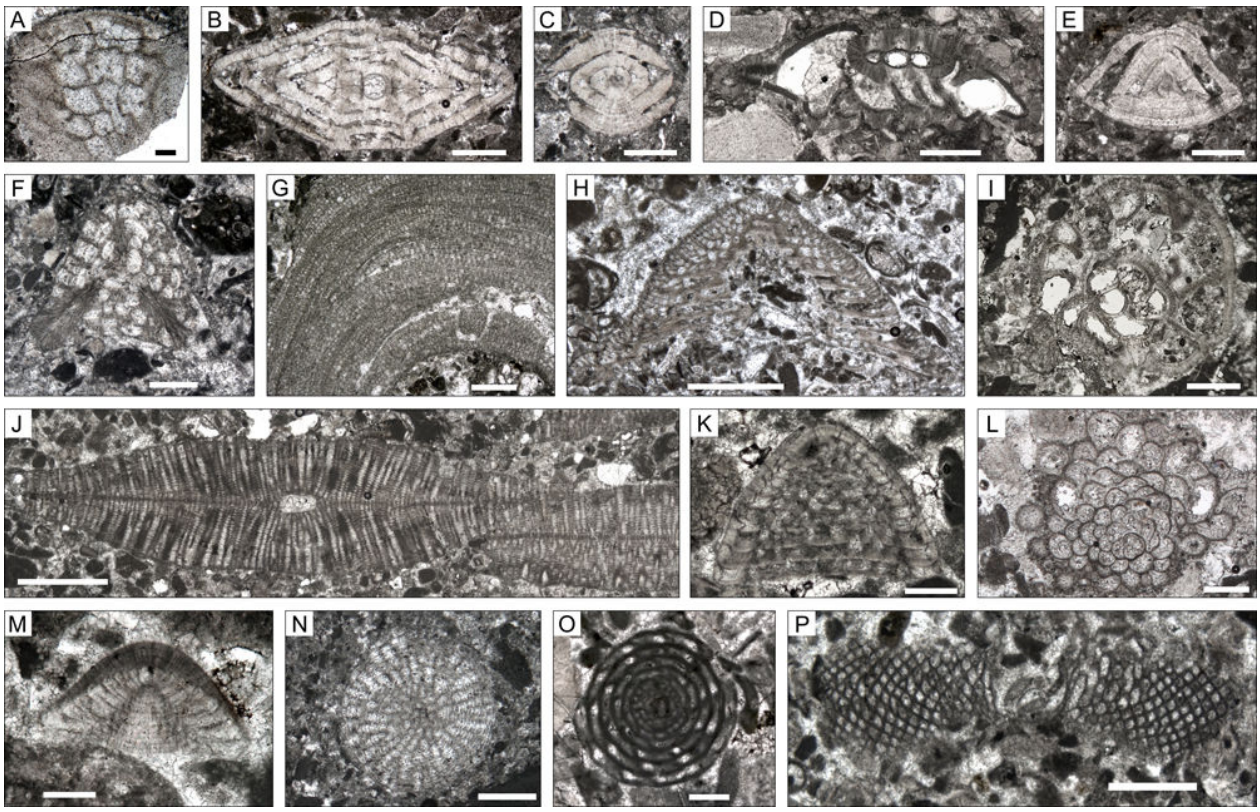


Figure 7: Priabonian larger Foraminifera association from the Ibi section. **A)** *Nummulites* ex gr. *N. fabianii* (PREVER in FABIANI), tangential section showing reticulate septal filaments, sample Ibi-111; **B)** *N. fabianii*, axial section (*P* = 235 µm), sample Ibi-109. **C)** *Nummulites* ex gr. *N. incrassatus* (HARPE), sample Ibi-111. **D)** *Schlosserina asterites* (GÜMBEL), subaxial section, sample Ibi-111. **E)** *Asterigerina rotula* (KAUFMANN), subaxial section, sample Ibi-107. **F)** *Silvestriella tetraedra* (GÜMBEL), oblique section, sample Ibi-106. **G)** *Acervulina linearis* HANZAWA, subaxial section, sample Ibi-107. **H)** *Fabiania casis* (OPPENHEIM), subaxial section, sample Ibi-106. **I)** *Gyroidinella magna* LE CALVEZ, equatorial section, sample Ibi-104. **J)** *Discocyclina* sp., axial section, sample Ibi-104. **K)** *Chapmanina gassinensis* (SILVESTRI), subaxial section, sample Ibi-104. **L)** *Planorbulina bronnimanni* BIGNOT & DECROUEZ, equatorial section, sample Ibi-116. **M)** *Halkyardia minima* (LIEBUS, 1911), axial section, sample Ibi-104. **N)** *Sphaerogypsina globulus* (REUSS), sample Ibi-113A. **O)** *Borelis vonderschmitti* (SCHWEIGHAUSER), subequatorial section, sample Ibi-108. **P)** *Orbitolites* cf. *O. cotentinensis* LEHMANN, sample Ibi-110. Scale bars: B-D, F-G, I, N, P = 500 µm; J = 1 mm; rest = 200 µm.

This assemblage also includes an indeterminate pseudo-involute Spiroloculinidae (Fig. 11H-K), which occurs in samples Ibi-118 to Ibi-5, corresponding to the lower-middle Rupelian (SB 21 and the basal part of SB 22A). It resembles *Elazigella altineri* from the Thanetian of western Turkey (SIREL, 1999, 2015), the type species of Subfamily Elasigellinae (MIKHALEVICH, 2008), but differs by the apparent lack of apertural teeth and by the occasional presence of involute chambers (Fig. 11K). The scarcity of specimens and the lack of equatorial sections prevent a more detailed characterization of this form.

Late Rupelian-Early Chattian, SB 22A-22B

This biozone is recognised in the upper part of the Ibi section (Fig. 5) and is characterised by the occurrence of *Nummulites fichteli*, *N. kecskemetii*, *Heterostegina assilinoides*, *Nephrolepidina* spp., *Eulepidina* cf. *formosoides*, *Asterigerina* sp., *Planorbulina* sp., *Planolinderina* sp., *Amphistegina bohdanowiczi*, *Neorotalia burdigalensis*, *Rotorbinella* cf. *epardi*, *Victoriella conoidea*, *Austrotrillina striata*, *Sorites* sp., *Borelis inflata*, *Borelis* sp. 1, *Praerhapydionina delicata*, *Peneroplis evolutus*, *P. thomasi*, *P. flabelliformis*, *Penarchaias glynnjonesi*, *Coscinospira elongata*, *C. sivasensis*, *Sivasina egribucakensis*, *Idalina pignatti*, *Schlumbergerina alveoliniformis*, *Pfendericonus globulus*, and Spiroloculinidae indet. (Figs. 8-13).

Late Chattian SB 23, Ibi section

In the Ibi section (Fig. 5), this biozone is characterised by the following association of larger Foraminifera: *Nummulites kecskemetii*, *Nummulites* sp., *Heterostegina assilinoides*, *Cycloclypeus mediterraneus*, *Nephrolepidina* spp., *Planorbulina bronnimanni*, *Planolinderina* sp., *Biarritzina* sp., *Neorotalia burdigalensis*, *Risananeiza crassaparies*, *Elphidium* cf. *crispum*, *Austrotrillina striata*, *Austrotrillina* ex gr. *striata-howchini*, and *Schlumbergerina alveoliniformis* (Figs. 8-10, 13-15).

Late Chattian SB 23, FR section

In FR, the SB 23 is distinguished by the presence of *Nummulites vascus*, *Nummulites kecskemetii*, *Heterostegina assilinoides*, *Spiroclypeus margaritatus*, *Cycloclypeus mediterraneus*, *Operculina complanata*, *Nephrolepidina* cf. *morgani*, *Nephrolepidina* sp., *Eulepidina* sp., *Miogypsinella complanata*, *M. formosensis*, *Miogypsinella borodinensis*, *M. akcadagensis*, *Postmiogypsinella intermedia*, *Asterigerina* sp., *Amphistegina bohdanowiczi*, *A. mammilla*, *Sphaerogypsina* sp., *Biar-*

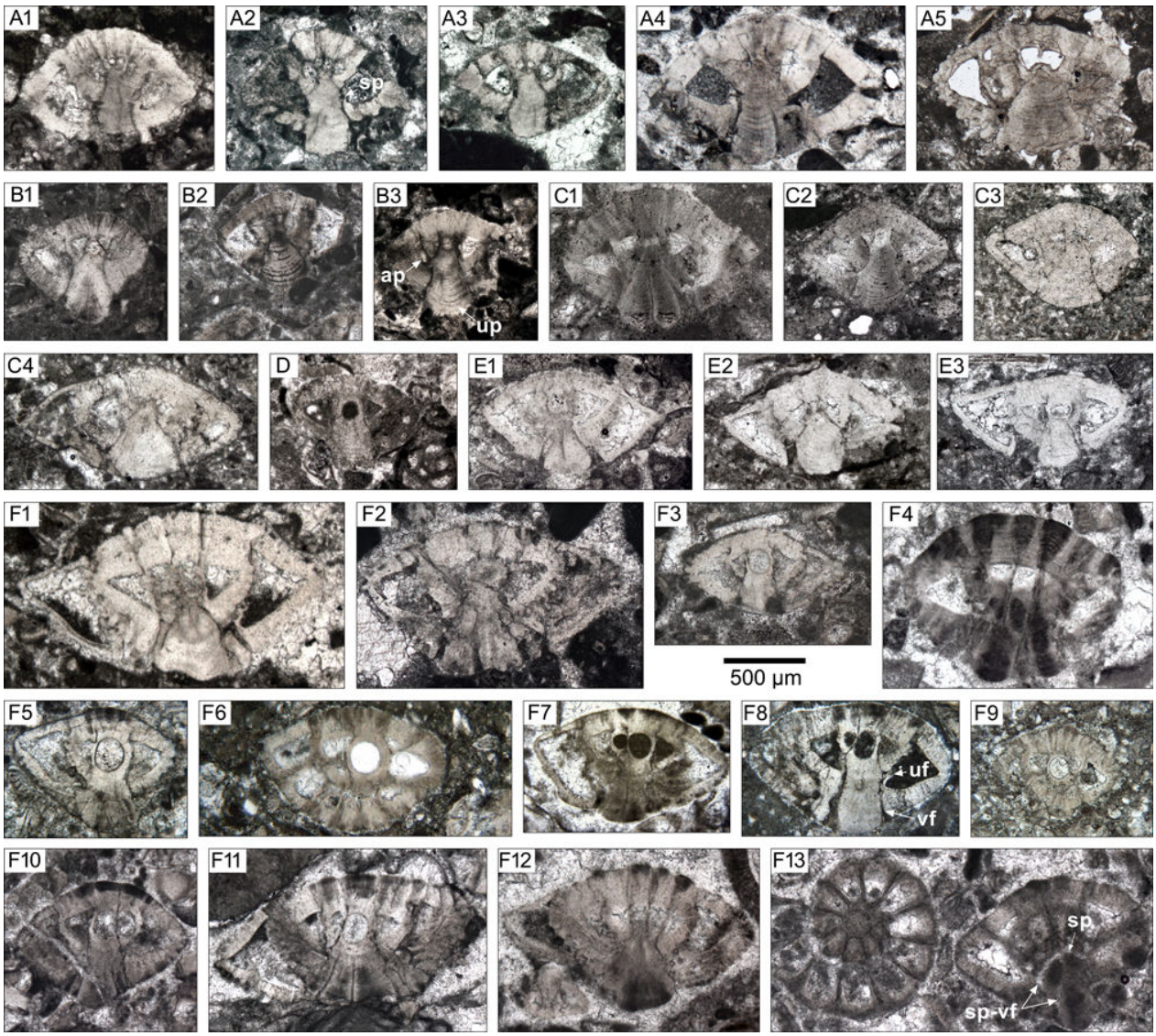


Figure 8: *Neorotalia burdigalensis* (ORBIGNY) from the Ibi and La Font Roja sections, Eocene and Oligocene forms at the same scale. **A)** Priabonian (SB 19-20) specimens, Ibi section; **B)** Lower Rupelian (SB 21) specimens, Ibi section; **C)** Upper Rupelian (SB 22A) specimens, Ibi section; **D)** Lower Chattian (SB 22B) specimens, Ibi section; **E)** Lower-upper Chattian (SB 23) specimens, Ibi section; **F)** Upper Chattian (SB 23) specimens, La Font Roja section, F1-F6) SB 23A; F7-F13) SB 23B. Samples: A1) Ibi-101, A2-A3) Ibi-102, A4) Ibi-103; A5) Ibi-104; B1) Ibi-127, B2) Ibi-MN-7, B3) Ibi-MN-9; C1-C2) Ibi-2, C3) SA-58, C4) SA-60; D) SA-63; E1-E2) Ibi-9, E3) Ibi-20;F1) FR-65, F2) FR-70, F3) FR-74, F4) FR-77, F5) FR-4, F6) FR-6; F7) FR-7, F8) FR-9, F9) FR-10, F10) FR-82, F11) FR-84, F12) FR-91, F13) FR-96. Note that some specimens (A4, A5, C1, C4?, F1, F2, F4) are microspheric forms. See Fig. 2 for the stratigraphic location of samples. **ap**: aperture, **sp**: spiral canal, **uf**: umbilical flap, **up**: umbilical pile, **vf**: adaxial ventral furrows.

ritzina sp., *Planorbulina bronnimanni*, *Planolinderina* sp., *Risananeiza crassaparies*, *R. pustulosa*, *Neorotalia burdigalensis*, *Rotorbinella* sp., *Sorites* sp., *Peneroplis thomasi*, *P. flabelliformis*, *Archaias* sp., *Austrotrillina striata*, *Austrotrillina* ex gr. *striata-howchini*, *A. howchini*, and *Schlumbergerina alveoliniformis* (Figs. 6, 8-12, 14-16).

5. Micropalaeontology

More than 80 different species or Foraminifera have been distinguished in the studied sections: 25 species were identified from the Eocene and about 60 from the Oligocene. Some agglutinated Foraminifera, peneroplids, victoriellids, orthophragmines or lepidocyclinids could not be identified at the species level, so the total number of species in the assemblages is actually higher. All taxa were identified in random thin sections, which in most cases do not allow for detailed descriptions. Due to the high number of foraminiferal taxa identified, including agglutinated, porcellaneous and hyaline species of Priabonian, Rupelian, and Chattian age, we summarise here the results for those most relevant to biostratigraphy or palaeobiogeography. Taxa requiring taxonomic revision are discussed in detail in the *Systematic Palaeontology* section.

The suprageneric classification mainly follows LOEBLICH and TAPPAN (1987a), taking into account that the former is outdated in some aspects (*e.g.*, the inclusion of orthophragmines, Discocyclinidae and Orbitoclypeidae within the Nummulitoidea based on the supposed presence of canal systems is incorrect). See Appendix for full species names.

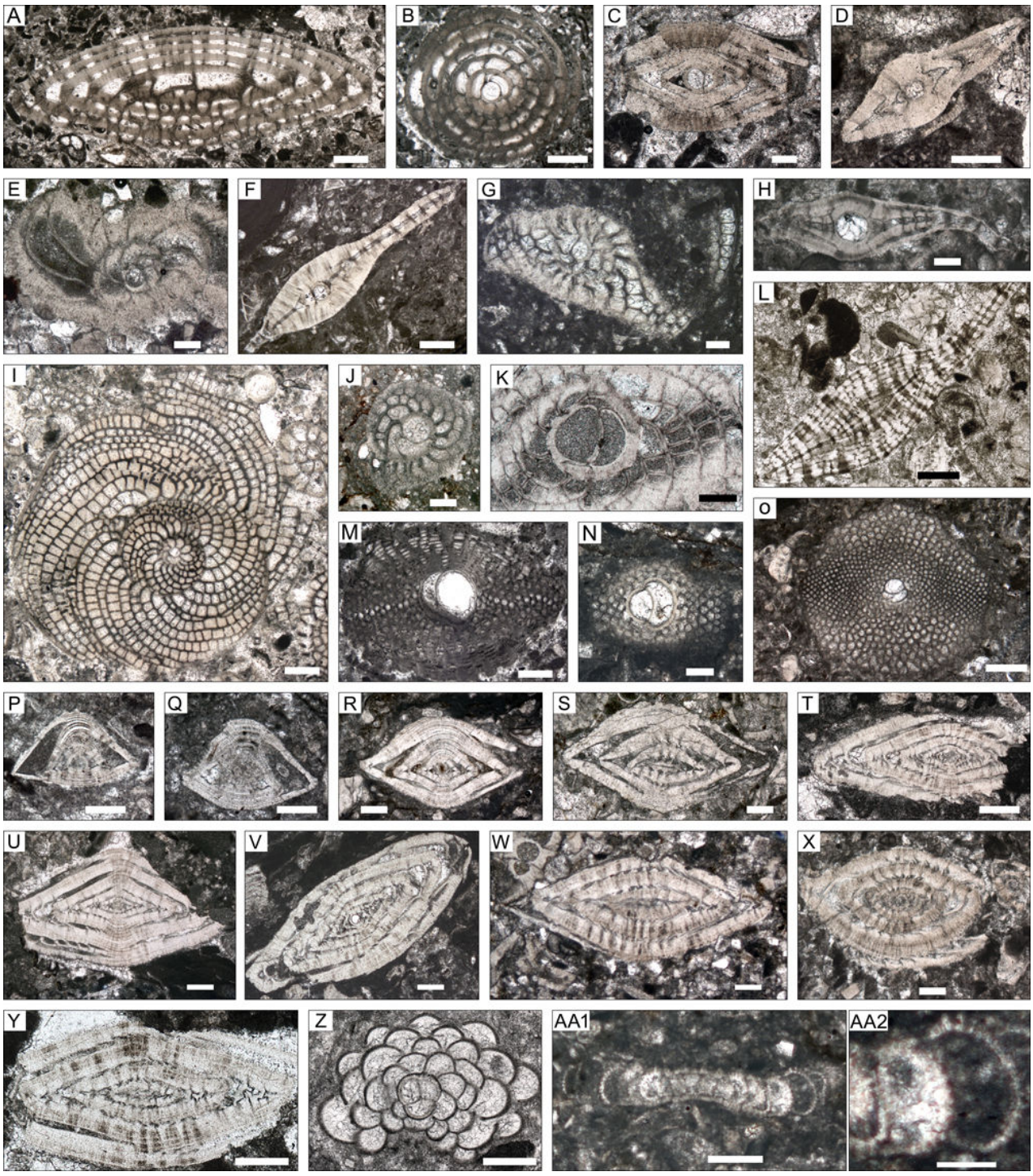


Figure 9: Oligocene hyaline larger Foraminifera. **A-B)** *Nummulites fichteli* MICHELOTTI, A) subaxial-oblique section, MN-8; B) equatorial section (*P* = 240 µm), sample MN-2. **C)** *Nummulites vascus* JOLY & LEYMERIE, axial section, sample MN-7. **D)** *Nummulites kecskemetii* LESS, axial section, Ibi-9. **E)** *Operculina complanata* DEFRANCE, equatorial section, sample FR-29. **F-G)** *Cycloclypeus mediterraneus* MATTEUCCI & SCHIAVINOTTO, F) axial section, sample Ibi-9; G) equatorial-oblique section, sample AA-2. **H-J)** *Heterostegina assilinoides* BLANCKENHORN, H) axial section, sample FR-80; I) equatorial section, sample FR-97; J) equatorial section, sample FR-27. **K-L)** *Spiroclypeus margaritatus* (SCHLUMBERGER), K) equatorial section, sample FR-22; L) subaxial section, sample FR-1. **M)** *Eulepidina* cf. *formosoides* (DOUVILLÉ), sample Ibi-2. **N)** *Nephrolepidina* sp., equatorial section, sample FR-62. **O)** *Nephrolepidina* cf. *morgani* (LEMOINE & R. DOUVILLÉ), equatorial section, sample FR-80. **P-Q)** *Asterigerina* sp., P) axial section, sample FR-72; Q) subaxial section, sample MN-22. **R-S)** *Amphistegina bohdanowiczi* BIEDA, R) axial section, sample Ibi-9; S) subaxial section, sample FR-27. **T-Y)** *Amphistegina mammilla* (FICHTEL & MOLL), T-U) sample Ibi-10, V sample AA-3, W) sample FR-50, X) sample FR-72, Y) sample Ibi-10. **Z)** *Planorbulina* sp., equatorial section, sample Ibi-20. **AA)** *Planolinderina* sp., subaxial section (AA1) and detail (AA2) showing the two apertures characteristic of the genus, sample FR-62. Scale bars: A-B, I, F, L, M, O = 500 µm; AA2 = 50 µm; rest = 200 µm.

Idalina pignattii

A few specimens of *Idalina* (Family Haeuerinidae, Subfamily Miliolinellinae) were observed in samples from the Rupelian and lower Chattian (Ibi section). They match *Idalina pignattii* GALLARDO-GARCÍA and SERRA-KIEL from Oman (in SERRA-KIEL *et al.*, 2016) in test size and shape, quinqueloculine-biloculine growth pattern, and apertural structure (compare Fig. 11W with Fig. 13.13 and 13.15 in SERRA-KIEL *et al.*, 2016). The diameter of the proloculus, *P* = 88-102 µm (N = 2) (Fig. 11W-Y), also falls within the 70-100 µm range given in the species diagnoses (SERRA-KIEL *et al.*, 2016). However, the adscription of this species to the genus *Idalina* remains uncertain. The diagnosis of *Idalina* includes a trematophorate aperture in adult growth stages (GRIMSDALE, 1952; LOEBLICH & TAPPAN, 1987a), a feature not clearly visible in any of the specimens of *I. pignattii* figured in the original description by SERRA-KIEL *et al.* (2016), nor in our material. SERRA-KIEL *et al.* (2016) reported a biostratigraphic range of SB 21-22 for *I. pignattii*. In the Prebetic, this species occurs within this range (early and late Rupelian) but also in SB 22B, extending its range to the early Chattian (Fig. 5). ESCANDELL and COLOM (1962) described a new species, "*Idalina laminata*", from the Oligocene of Mallorca, similar to *I. pignattii*. However, their illustrations lack magnification and, according to SERRA-KIEL *et al.* (2016), the original material is lost. Furthermore, no reference to the type locality (other than "beds of the Oligocene transgression" in Mallorca) is made in the original description (ESCANDELL & COLOM, 1962, p. 127).

Peneroplis peramplus and *Spirolinella emmae*

These two species (Superfamily Soritoidea, Family Peneroplidae) were described in detail from samples of the Ibi section in a previous work (FERRÀNDEZ-CAÑADELL, 2024). *Peneroplis peramplus* (Fig. 11O) is an evolute annular species characterised by a large bilocular megalospheric embryo, with a protoconch measuring approximately 240 µm and a deuteroconch up to 400 µm. The genus *Spirolinella*, with the type species *S. emmae* (Fig. 11V), is similar to *Spirolina* but differs by its slender test, thinner walls, and its distinctive complex aperture, petaloid to stellate in shape, with distally protruding lips forming capsular cavities radially arranged, each with an aperture at the distal end. Based on current knowledge, these two forms are exclusive to SB 21 (lower Rupelian) and are considered endemic to the Prebetic (FERRÀNDEZ-CAÑADELL, 2024).

Archaias

The genus *Archaias* (Superfamily Soritoidea**,** Family Soritidae) has been identified in a few samples from the FR section (Figs. 6, 12A-D). The available material, although scarce and fragmentary, shows involute growth and the presence of endoskeletal pillars, but does not allow identification at the species level. *Archaias* originated in the Eocene (middle Eocene of the Caribbean region, according to ROBINSON and WRIGHT, 1993). In the Mediterranean region up to the Middle East it ranges up to the upper Oligocene (lower Chattian), as reviewed by SEIGLIE *et al.* (1977), HOTTINGER (2007), and BASSI *et al.* (2007). Oligocene species include *A. hensoni*, *A. kirkukensis*, and two Rupelian species, *A. diyarbakirensis* and *A. minimus*, originally assigned to the genus *Praearchaias* (SIREL, 1997, 2003; SIREL *et al.*, 2013; HAKYEMEZ *et al.*, 2016), which was later regarded as a synonym of *Archaias* (HOTTINGER, 2007). A further species, *A. asmaricus* differs in test architecture, which is similar to *Peneroplis thomasi* in the shape of chambers, and likely belongs to another genus (BASSI *et al.*, 2007). A review of the literature reveals a lack of consensus regarding both the species assignment and their stratigraphic range. HENSON (1950) reported *A. operculiniformis* from the lower Oligocene and *A. kirkukensis* and *Archaias* cf. *aduncus* from the upper Oligocene of Iraq. From the Zagros Basin in Iran, HABIBI (2016a) reported *A. operculiniformis* from the middle Rupelian, *A. kirkukensis* from the middle Rupelian-middle Chattian, and *A. hensoni* from the Chattian. Later works reported *A. operculiniformis* from the lower Rupelian (YAZDI-MOGHADAM *et al.*, 2023a) or *Archaias* sp. from the Rupelian and *A. kirkukensis* and *A. asmaricus* from the Chattian (HABIBI, 2018; HABIBI & BOVER-ARNAL, 2018; HABIBI *et al.*, 2024). ALLAHKARAMPOUR DILL *et al.* (2020) provided a biostratigraphical distribution of the species of *Archaias* in the Asmari Fm. in Iran, calibrated with Sr isotope stratigraphy. They concluded that *A. operculiniformis* occurs in the Rupelian and *A. hensoni* and *A asmaricus* in the Chattian. From the Oligocene of Turkey, SIREL (2003, 2013), followed by HAKYEMEZ *et al.* (2016), reported "*Praearchaias*" *minimus* and "*P.*" *diyarbakirensis* restricted to SB 21, and *A. kirkukensis* and *A. asmaricus* ranging from SB 21 to SB22. From this interval (Rupelian-early Chattian), GEDIK (2014, 2015) reported *A. kirkukensis* and *A. hensoni*, whereas KAYĞILI and AKSOY (2019) recognised only *A. kirkukensis*. From Oman and Yemen (Socotra), SERRA-KIEL *et al.* (2016) reported two species ranging from the Bartonian to the Rupelian (SB 17-21), which they assigned to *A. operculiniformis* and *A. diyarbakirensis*.

Considering this biostratigraphic distribution, the specimens from FR section probably belong to either *A. hensonii* or *A. kirkukensis*. The main difference between these two species lies in the number of rows of pillars: one row in *A. hensonii* and two or more rows in *A. kirkukensis* (BASSI *et al.*, 2007). This character is only properly visible in centred axial sections and could not be distinguished in our specimens.

Orbitolites

Orbitolites (Superfamily Soritoidea, Family Soritidae) occurs in several samples from the lower (Priabonian) part of the Ibi section (Fig. 5). Most specimens are fragmentary oblique sections; the largest preserved test measures approximately

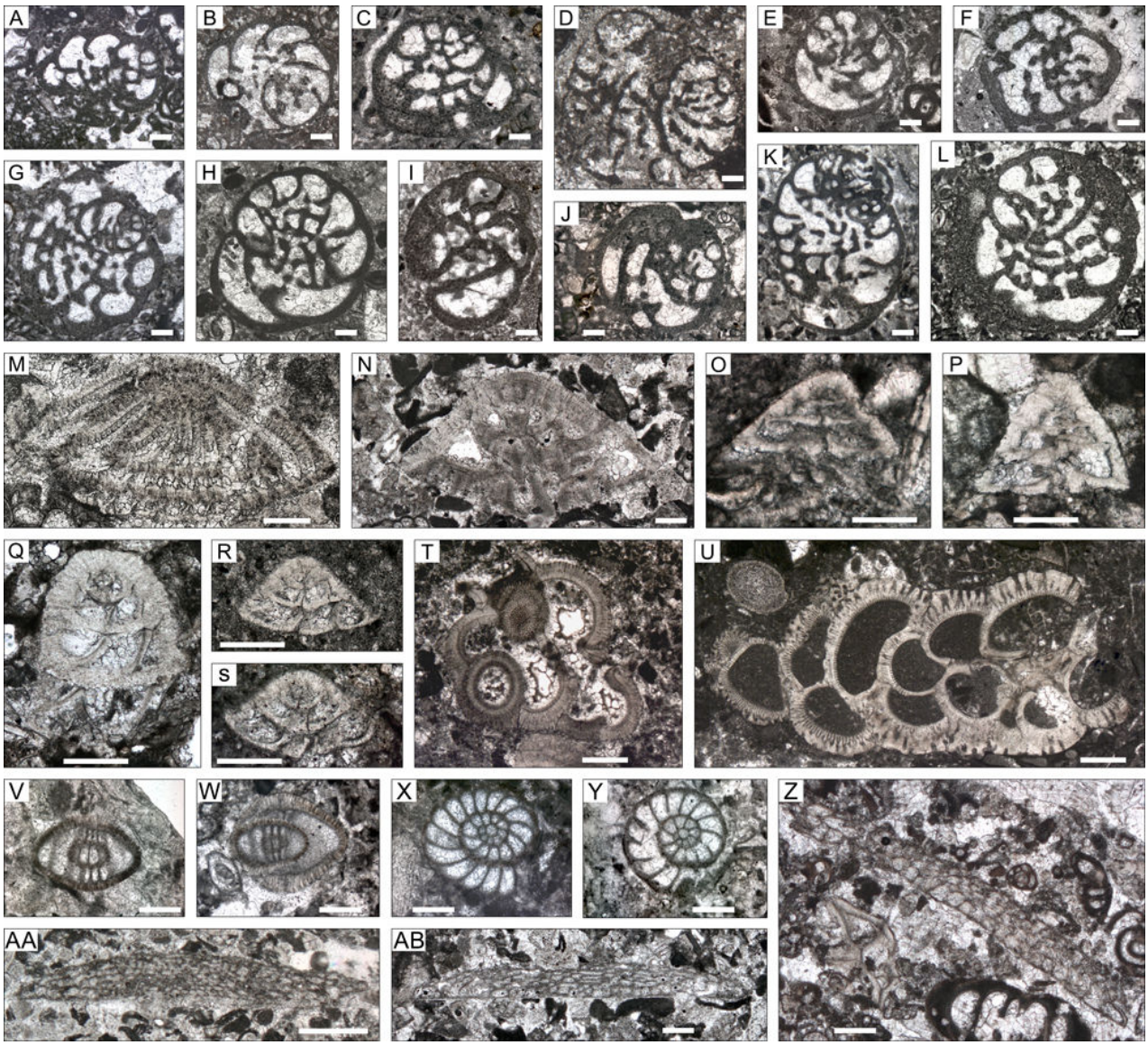


Figure 10: Oligocene larger Foraminifera from the Ibi and La Font Roja sections. **A-L)** *Pfendericonus globulus* SIREL & DECEVILER, lower Rupelian (SB 21); samples: A, G, L) Ibi-MN-6, B) Ibi-119, C) Ibi-121, D) Ibi-125, E, F) Ibi-126, H) Ibi-MN-8, I) Ibi-MN-20, J,K) Ibi-127. **M)** *Elphidium* cf. *E. crispum* (LINNAEUS), subaxial-peripheral section, sample Ibi-10. **N)** Rotalid indet., subaxial section, sample Ibi-116. **O-S)** *Rotorbinella* cf. *epardi* FERRÀNDEZ-CAÑADELL & BAUMGARTNER-MORA; samples: O) FR-81 (SB 23), P, Q) Ibi-101 (SB 20), R) Ibi-40 (SB 22A), S) Ibi-41 (SB 22A). **T)** *Victoriella conoidea* (RUTTEN), subaxial section, sample MN-23. **U)** *Rupertina* sp., subaxial section, sample FR-113. **V-Y)** *Elphidiella* sp., subaxial (V, W) and equatorial (X, Y) sections; samples: V) Ibi-128, W) Ibi-130, X) Ibi-MN-4, Y) Ibi-129. **Z-AB)** *Gypsina* cf. *G. mastelensis* BURSCH, axial section; samples: Z) Ibi-MN-6 (early Rupelian), AA, AB) Ibi-116 (Priabonian). Scale bars: M, T-U, AA = 500 µm; rest = 200 µm.

4 mm in diameter. An equatorial section (Fig. 7P) shows a bilocular megalospheric embryo similar in size and morphology to that of *O. cotentinensis*, which has been reported from the Bartonian and Priabonian (SB 17-20) of France (LEHMANN, 1961), Oman (SERRA-KIEL *et al.*, 2016), and Crimea (ZAKREVSKAYA, 2023). Other Priabonian occurrences of *Orbitolites* have been documented from the Ebro Basin in north-eastern Spain (TRAVÉ *et al.*, 1996), northern Italy (BARBIN, 1986, not shown in a figure; PAPAZZONI & SIROTTI, 1995, not shown in a figure), northern Hungary (VITALIS-ZILAHY, 1967), north-western Turkey (SIMMONS *et al.*, 2020; SIREL *et al.*, 2020a), and offshore India (COTTON *et al.*, 2019).

Sorites

Another soritid genus, *Sorites*, is relatively common in the Oligocene of the Prebetic (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2018), although it is never abundant. It occurs in the upper part (SB 22A-22B) of the Ibi section and in the middle part of the FR section (SB 23) (Figs. 6, 11A-C). Despite the large number of thin sections prepared from the richest samples from the Ibi and FR sections, as well as from the Benitatxell Range (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017, 2018), no centred sections were obtained to adequately characterise the species and compare it with known taxa. The Prebetic specimens are characterised by the axial section of septula, which are

Figure 11: Oligocene porcellaneous larger Foraminifera from the Ibi and La Font Roja sections. **A**-**C)**. *Sorites* sp. A, B) axial and subaxial sections of megalospheric specimens; C) equatorial section of a megalospheric specimen; samples: A) Ibi-6; B, C) SA-57. **D)** *Coscinospira sivasensis* SIREL & ÖZGEN-ERDEM, equatorial section, sample Ibi-7. **E)** *Coscinospira elongata* SIREL & ÖZGEN-ERDEM, subaxial section, sample Ibi-MN-7. **F)** *Praebullalveolina minuta* SIREL & ÖZGEN-ERDEM, sample Ibi-MN-17. **G)** *Praebullalveolina oligocenica* SIREL & ÖZGEN-ERDEM, sample Ibi-MN-17. **H-K)** Spiroloculinidae indet., axial and subaxial sections. Note the semi-involute test, with evolute chambers and involute walls in H-J and the involute chambers in K; samples: H) Ibi-MN-21, I) Ibi-120, J) Ibi-MN-6, K) Ibi-MN-14. **L)** *Peneroplis flabelliformis* SIREL & ÖZGEN-ERDEM, equatorial section; sample Ibi-5. **M)** *Peneroplis* cf. *evolutus* HENSON, equatorial-oblique section, sample Ibi-130. **N)** *Peneroplis thomasi* HENSON, axial section, sample Ibi-6. **O)** *Peneroplis peramplus* FERRÀNDEZ-CAÑADELL, oblique section, sample Ibi-130. **P)** *Penarchaias glynnjonesi* (HENSON) (left) and *Peneroplis peramplus* paratype MGB 94151 LP2.1 (right), sample Ibi-MN-6. **Q)** *Penarchaias glynnjonesi*, axial section, note the apertures in the alar prolongations; sample Ibi-MN-6. **R-T)** *Sivasina egribucakensis* SIREL & ÖZGEN-ERDEM, R) subaxial section showing the dendritine aperture; S) axial section, megalospheric form; T) axial section, microspheric form; samples: R) Ibi-6; S) Ibi-127; T) Ibi-127. **U)** *Praerhapydionina delicata* HENSON, axial-oblique section, megalospheric form; sample Ibi-129. **V)** *Spirolinella emmae* FERRÀNDEZ-CAÑADELL, subaxial section (paratype MGB 94153 LPb.1); sample Ibi-120. **W-Y)** *Idalina pignattii* GALLARDO-GARCÍA & SERRA-KIEL, megalospheric forms; samples: W) SA-53, X) Ibi-121, Y) Ibi-43. **Z)** *Schlumbergerina* cf. *alveoliniformis* (BRADY), axial section, sample SA-53. Scale bars: C, T = 500 µm; rest = 200 µm.

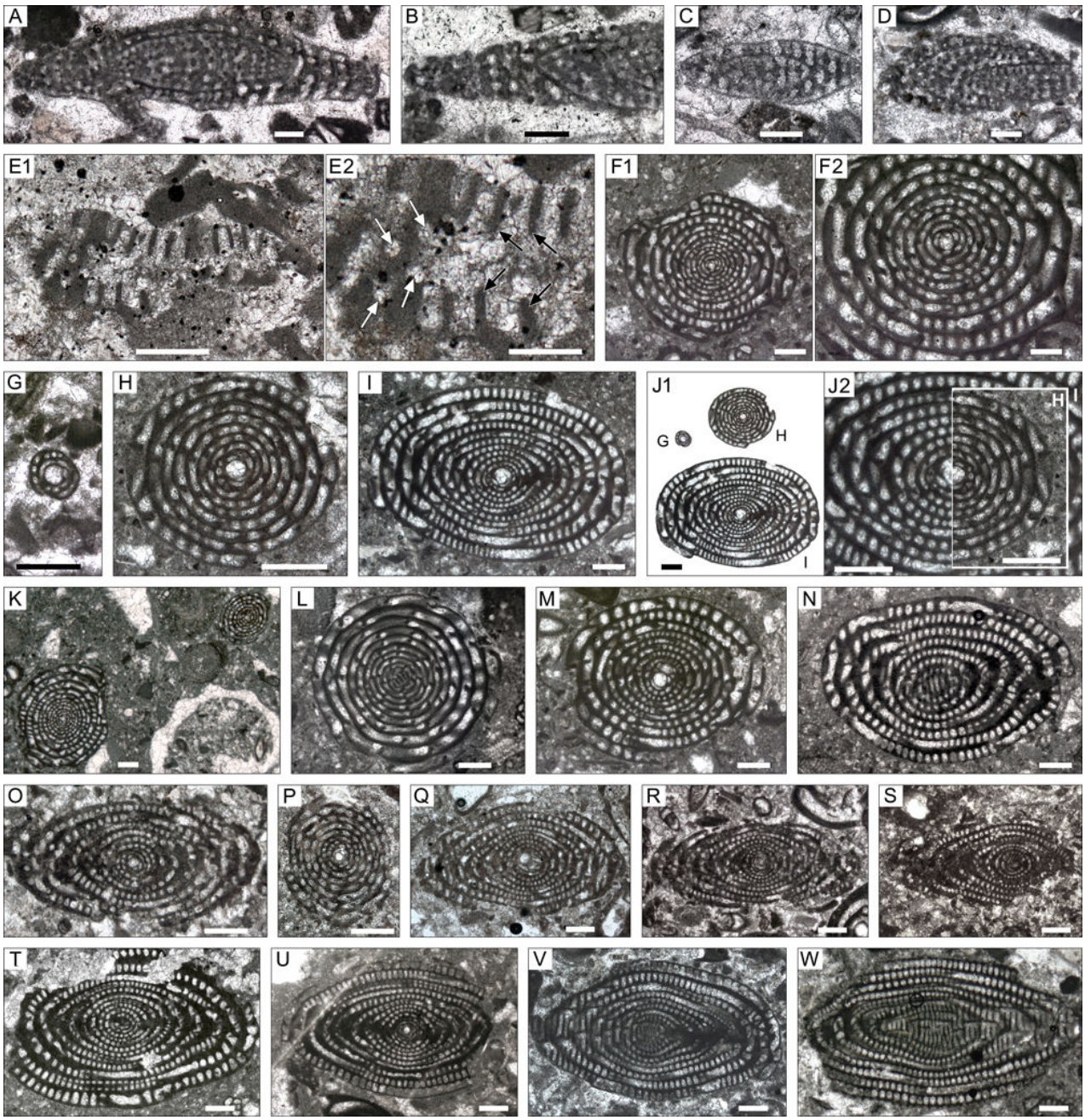


Figure 12: Oligocene porcellaneous larger Foraminifera from the Ibi and La Font Roja sections. **A-D)** *Archaias* sp., subaxial sections; A-B) sample FR-91, C) sample FR-83, D) sample FR-78. **E)** *Neorhipidionina* cf. *N. spiralis* HOTTINGER, subaxial-tangential section (E1) and detail (E2), sample Ibi-116. Note the septula (black arrows) and the foramina (white arrows), with median foramina alternating with the marginal ones. **F-N)** *Borelis inflata* (ADAMS); G-I) megalospheric specimens in different ontogenetic stages from the same sample, SA-57; J1) comparison of specimens in G-I at the same scale, J2) photocomposition to compare specimens in Figure 12H-I (right half of H superposed on I), note the close correspondence of whorls, chambers and chamberlets; K) two megalospheric specimens of different ontogenetic stage in the same thin section, sample Ibi-6; L) subequatorial section, sample Ibi-40. M) oblique section, sample SA-57; N) subaxial section, sample Ibi-6. **O-W)** *Borelis* sp. 1, with morphological characters intermediate between *B. inflata* (ADAMS), *B. merici* SIREL & GÜNDÜZ and *B. pygmaea* HANZAWA. Note the fusiform test (elongation index between 1.7 and 2.6), the subsphaerical initial whorls, the columellar thickening and the absence of Y-shaped septula; O-S) sample SA-60, T) sample Ibi-6, U) sample Ibi-5, V) sample SA-57, W) sample SA-52. Scale bars: E2, F2 = 100 µm; rest = 200 µm.

thicker in the median plane and become thinner towards the lateral walls, similar to those of *Sorites variabilis* (*sensu* HOTTINGER *et al.*, 1994, Pl. 84, figs. 9-10). However, the megalospheric embryo resembles that of *S. orbiculus* (*sensu* HOTTINGER *et al.*, 1994), with a proloculus diameter of 76-96 µm (measured in two axial sections), followed by a wide flexostyle. These specimens also show similarities to the few Oligocene occurrences reported from the Mediterranean region (see Pl. 5, fig. 6 in ZUFFARDI-COMERCI, 1930; Fig. 4A in BRANDANO *et al.*, 2009; Fig. 2c in POMAR *et al.*, 2014).

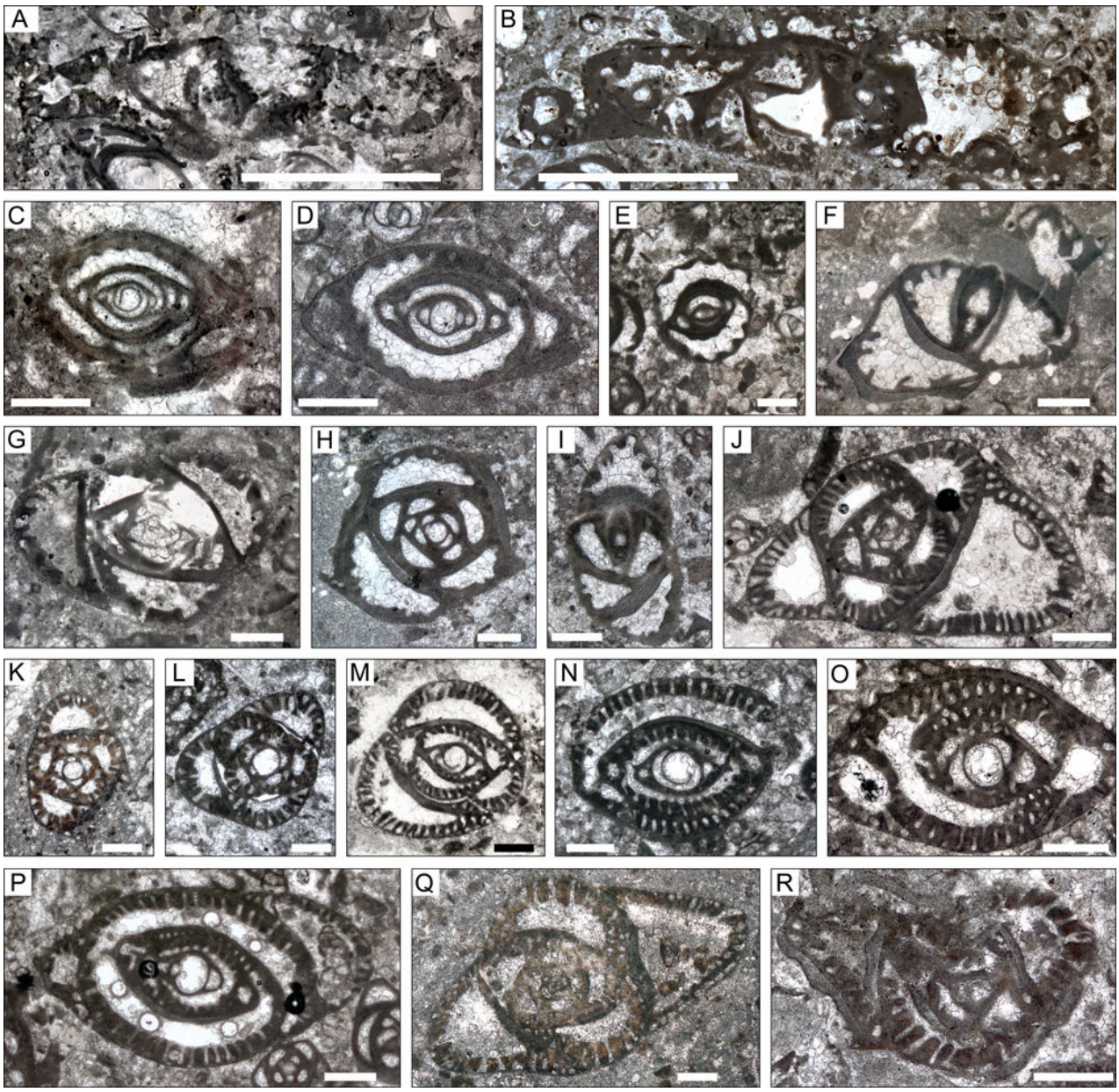


Figure 13: *Austrotrillina* species and morphotypes from the Ibi section. **A-I)** *Austrotrillina paucialveolata* ADAMS. A, B) microspheric forms from the basal lower Rupelian. C-I) specimens showing bilocular and trilocular growth and the variability of the exoskeleton, from a simple undulate inner surface of the wall (C-E) to protrusions variable in size and shape and irregularly distributed (F-I). Note the flexostyle in C and H. **J-R)**. *Austrotrillina striata* TODD & POST, with exoskeletal patterns of asmariensis-type in J-M (SB 21-22A), and of striata-type in N-R (SB 22A). Note bi-, tri- and quinquelocular types of growth and the flexostyle in L, M, N, and P. Samples: A-B, G) Ibi-121; C) Ibi-120; D) Ibi-MN-19; E) Ibi-129; F, H) Ibi-126; I) Ibi-MN-6; J, L-P) SA-53; K) SA-57; Q) Ibi-43; R) Ibi-7. Scale bars: A-B = 1 mm; C-R = 200 µm.

Praerhapydionina

Praerhapydionina delicata (Superfamily Soritoidea, Family Soritidae) from the Ibi section was described in detail in a previous work (FERRÀNDEZ-CAÑADELL, 2024). The most significant feature discussed there is the presence of a pseudokeriotheca-like texture on the walls, which may serve as a useful criterion for identifying the genus and clarifying its alleged wide geographical distribution, reported from the Caribbean to Indonesia (HOTTINGER, 2007). In the Ibi section, *P. delicata* occurs in the Rupelian (SB 21-22A) (Figs. 5, 11U), and its last occurrence may represent a potential marker for the Rupelian/Chattian (SB 22A-22B) boundary (see the discussion on biostratigraphy below).

Neorhipidionina

The Eocene genus *Neorhipidionina* (Superfamily Alveolinoidea, Family Rhapydioninidae) is characterised by a planispiral-involute nepionic stage that transitions to an uncoiled, evolute stage with fan-shaped adult chambers of elongate-oval axial section. The chambers are subdivided by radial septula perpendicular to the lateral walls, leaving an annular passage in the median part where the foramina are located. Initially, the foramina are arranged in a single row, increasing to two or three rows in adult chambers. The foramina of the

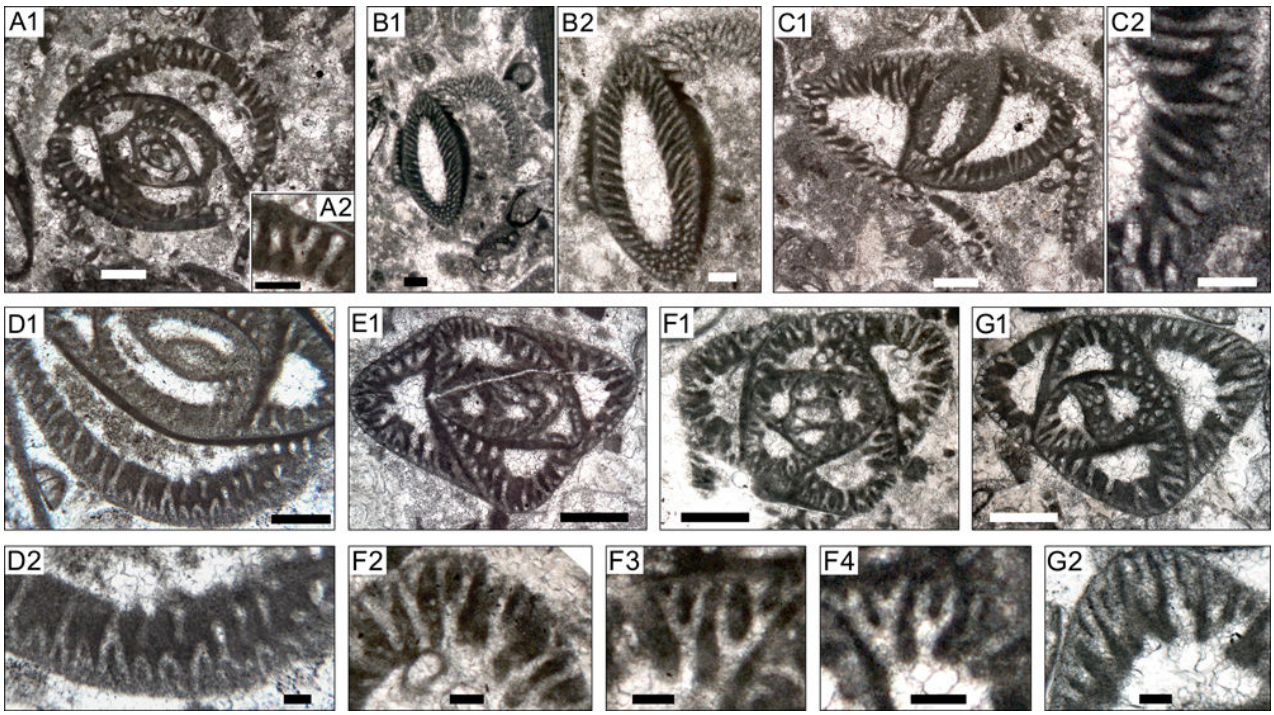


Figure 14: *Austrotrillina* with bifurcated alveoli. **A)** *Austrotrillina striata* TODD & POST, axial-oblique section (A1) and detail (a2) showing ocasional bifurcated alveoli, sample SA-60, Ibi section. **B-C)** Specimens (B1, C1) and details (B2, C2) with exoskeletal patterns transitional between *striata* and *howchini* morphotypes from the basal late Chattian (basal SB 23) of the Ibi section, samples: B) Ibi-9, C) Ibi-15; the latter, could be considered a true *A. howchini* (SCHLUMBERGER). **D-G)** *Austrotrillina howchini* (SCHLUMBERGER), D) equatorial-oblique section (D1) and detail (D2) from La Font Roja section, sample FR-7 (SB 23); E-G specimens (E1, F1, G1) and details (F2-F4, G2) from Serra de l'Ombria (section under study, about 30 km SW from Ibi); note the regular bifurcate alveoli. Scale bars: details A2, B2, C2, T2 = 100 µm; D2, F2-F4, G2 = 50 µm; rest = 200 µm. Scale bar = 0.5 mm.

additional median row (median foramina) alternate with those of the other two rows (marginal apertures), positioned between the septula (HOTTINGER, 2007; SERRA-KIEL *et al.*, 2016; NAFARIEH *et al.*, 2019). Two specimens from the lower part of the Ibi section (samples Ibi-113A and Ibi-116, Fig. 5) show these characters. Both are peripheral axial sections showing the characteristic elongate-oval chamber shape and radial septula with a central, unsubdivided passage. One specimen (Fig. 12E) also shows marginal foramina between septula and median apertures alternating with the marginal ones. This specimen (Fig. 12E) therefore shows virtually all the diagnostic characters of *Neorhipidionina* according to the original definition of the genus (HOTTINGER, 2007, p. 9). Based on the size and shape of the chambers, these specimens are most similar to *N. spiralis. Neorhipidionina urensis* exhibits uncoiled stages with an oval outline, whereas *N. williamsoni* has a larger test. However, the main difference between *N. spiralis* and *N. williamsoni* lies in the size of the protoconch, which was not observed in our specimens. The known range of the genus is Bartonian-Priabonian, SB 17-20 (HENSON, 1948; HOTTINGER, 2007; SERRA-KIEL *et al.*, 2016; COTTON *et al.*, 2019; NAFARIEH *et al.*, 2019; CHANGAEI *et al.*, 2022), which is consistent with the Priabonian age assigned to the lower part of the Ibi section.

Praebullalveolina

Praebullalveolina oligocenica and *P. minuta* (Superfamily Alveolinoidea, Family Alveolinidae) were defined by SIREL and ÖZGEN-ERDEM (in SIREL *et al.*, 2013) from the early Rupelian, SB 21, in the Sivas Basin of central Turkey. Both species were identified in the lower part of the Ibi section (Fig. 11F-G). They are difficult to distinguish in partial random sections and are, therefore, grouped together as *Praebullalveolina* spp. in the biostratigraphic plot (Fig. 5). They occur in porcellaneous foraminiferal facies associated with *Austrotrillina paucialveolata*, *Idalina pignattii*, *Coscinospira elongata*, *C. sivasensis*, *Peneroplis evolutus*, *P. peramplus*, *Spirolinella emmae*, *Penarchaias glynnjonesi*, *Sivasina egribucakensis*, *Praerhapydionina delicata*, and *Pfendericonus globulus*, interpreted as early Rupelian, SB 21. *Praebullalveolina oligocenica* was reported from the Rupelian (without differentiating between SB 21 and 22B) of Oman and Socotra Island (Yemen) by SERRA-KIEL *et al.* (2016). The association, including *P. delicata*, *C. elongata*, and *C. sivasensis*, suggests an early Rupelian (SB 21) age. This species was also reported as "*Praebullalveolina* sp." from the lowermost Oligocene of Priabona (northern Italy) by BARBIN *et al.* (1997).

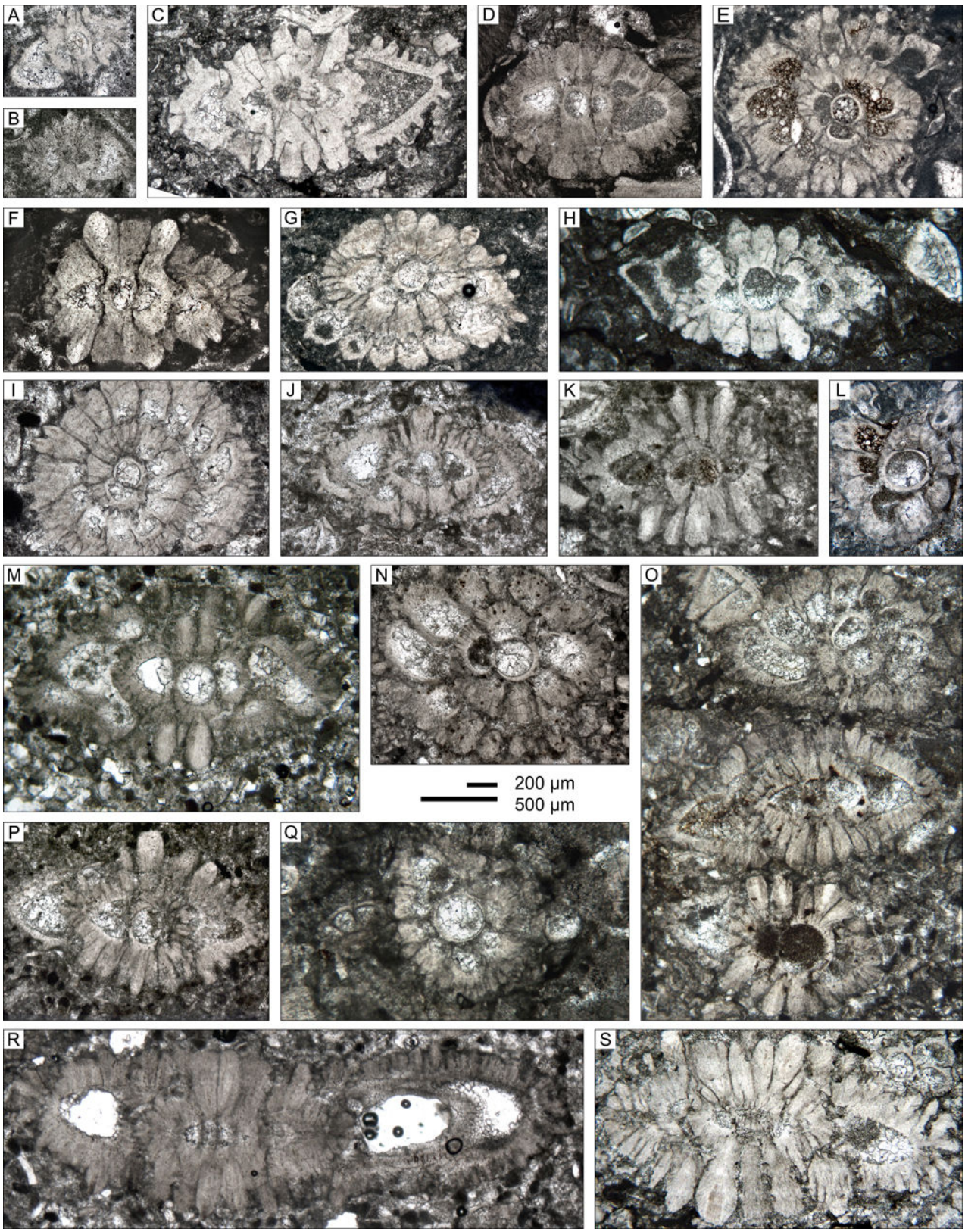


Figure 15: *Risananeiza* from the Ibi and FR sections. **A-J)** *Risananeiza crassaparies* BENEDETTI & BRIGUGLIO, megalospheric forms. A-D) specimens from the basal SB 23A, Ibi section; E-J) specimens from SB 23A, lower part of the FR section; **K-Q)** *Risananeiza pustulosa* BOUKHARY *et al.*, megalospheric forms, SB 23B, FR section; Note the large proloculus in O (*P* = 318 µm) and Q (*P* = 320 µm). **R-S)** *Risananeiza pustulosa*, microspheric forms, SB 23B, FR section. All specimens at the same magnification. Samples: A) Ibi-9, B) Ibi-15, C) Ibi-20, D) AA-3, E) FR-62, F) FR-65, G) FR-67, H) FR-68, I) FR-69, J) FR-71; K) FR-87, L) FR-98, M) FR-103, N) FR-105, O) FR-13, P) FR-106, Q) FR-15; R) FR-103, S) FR-15. The scale bars apply to all photos.

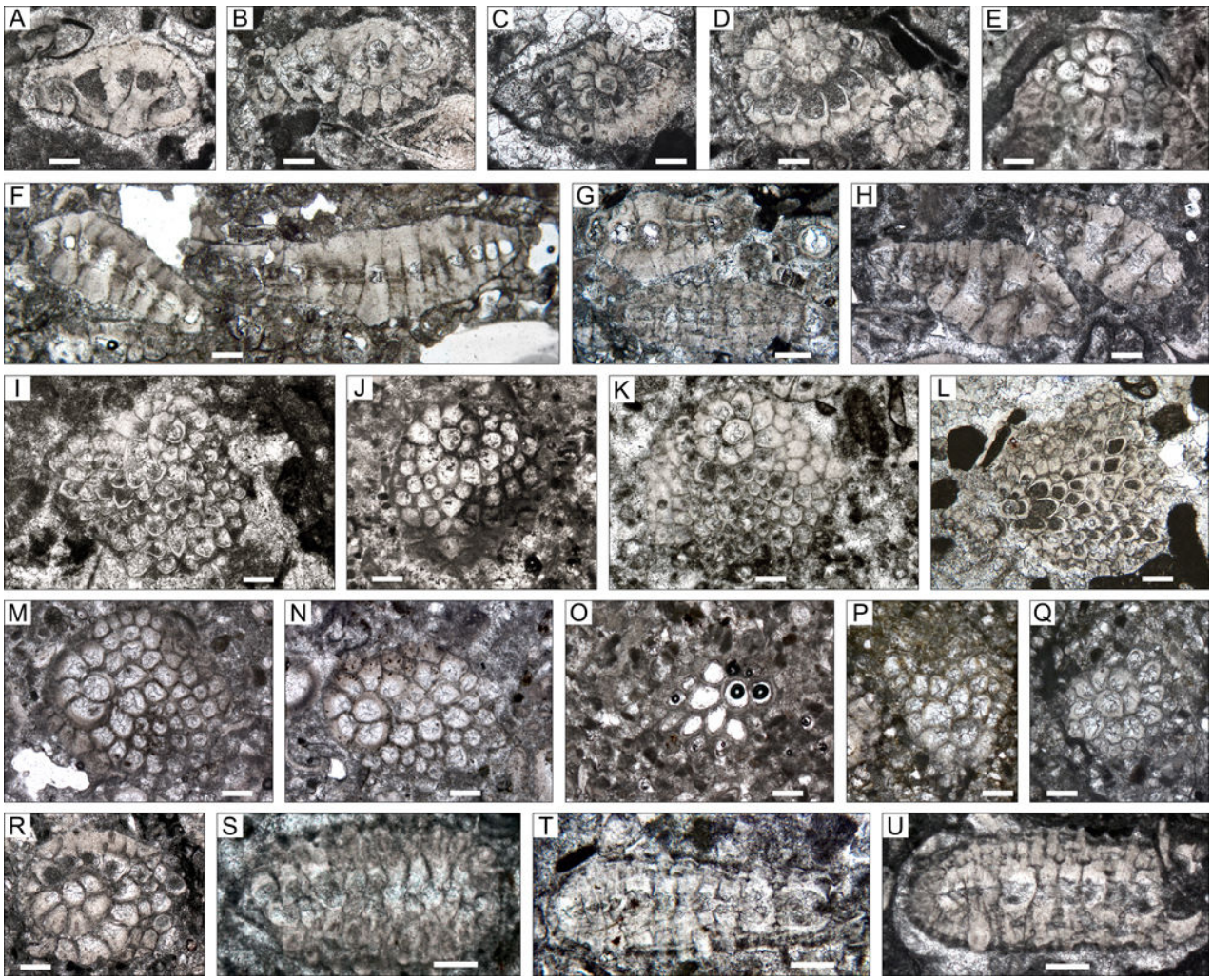
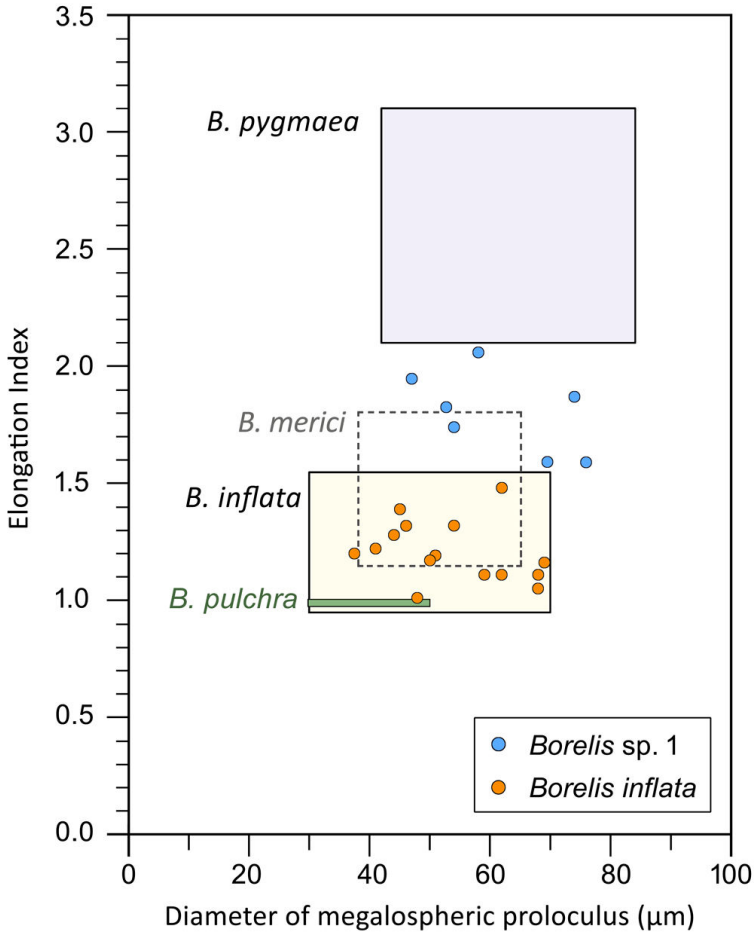


Figure 16: Miogypsinids from the upper Chattian (SBZ 23) from the La Font Roja section. **A-B)** *Miogypsinella* sp., axial section, sample FR-70. **C-D)** *Miogypsinella* cf. *M. formosensis* (YABE & HANZAWA), subequatorial section, sample FR-70. **E)** *Miogypsinella* cf. *M. borodinensis* HANZAWA, subequatorial section, sample FR-82. **F)** *Miogypsinella* sp., axial and subaxial sections, sample FR-88. **G)** *Miogypsinella* sp., axial section (top) and *Postmiogypsinella intermedia* SIREL & GEDIK, subaxial section (bottom), sample FR-98. **H)** *Miogypsinella* sp., subaxial sections, sample FR-102. **I)** *Miogypsinella* cf. *M. formosensis*, sample FR-1. **J)** *Miogypsinella borodinensis/M. akcadagensis* (GEDIK & SIREL), sample FR-2. **K)** *Miogypsinella formosensis/borodensis*, sample FR-5. **L)** *Miogypsinella* cf. *formosensis*, equatorial section, sample FR-22. **M)** *Miogypsinella* cf. *M. borodinensis*, equatorial section, sample FR-102. **N-P)** *Miogypsinella* cf. *M. akcadagensis*, equatorial sections; samples: N) FR-102, O) FR-103, P) FR-104. **Q-R)** *Miogypsinella* cf. *M. borodinensis*, equatorial sections; samples: Q) FR-104, R) FR-118. **S-U)** *Postmiogypsinella* cf. *M. intermedia*, S) subaxial-oblique section, megalospheric specimen, sample FR-79; T-U) microspheric specimens, axial sections, samples: T) FR-87, U) FR-98. Scale bars = 200 µm.

Borelis

Borelis (Family Alveolinidae) occurs in both the Eocene and Oligocene parts of the Ibi section. Only four specimens of *Borelis* were recovered from the lowermost part of the Ibi section (Fig. 5). They exhibit a subspherical test measuring 0.65 to 0.83 mm in diameter (mean = 0.77 mm, N = 4). A subequatorial section (Fig. 7O) shows a proloculus approximately 48 µm in diameter, followed by two (?) streptospiral whorls and five planispiral whorls, the last whorl containing 12 chambers. These features correspond to the Eocene species *B. vonderschmitti* (*e.g.*, BENEDETTI, 2010; SIREL *et al.*, 2020a).

Most *Borelis* specimens from the Oligocene part of the section (Fig. 12F-N) exhibit the following features: proloculus diameter between 30 and 85 µm (typically 50-60 µm), 7-9 chambers per whorl at a test diameter of 1 mm (N = 3), 25-29 chamberlets per 1 mm length (N = 3), an elongation index (*EI* = test length/width) mostly between 1.2-1.6, Y-shaped septula completely absent, and a thin basal layer with columellar thickening reduced or absent. These characters correspond to the diagnostic features of *B. inflata* (*EI* = 0.95-1.56 according to ADAMS, 1965; HOTTINGER, 1974; BASSI *et al.*, 2021b). The *EI* values in the specimens from Ibi match those reported for *B. inflata* specimens from the Rupelian of Sicily (1.13-1.27; BENEDETTI, 2010) and eastern Turkey (1.22-1.35; SIREL, 2003).



◀ **Figure 17:** Plot of elongation index and megalospheric proloculus diameter (µm) for *Borelis* from the Ibi and La Font Roja sections (see data in Table 1), with ranges for Oligocene species (squares) based on the Fig. 1 in BASSI *et al.* (2021b). The ranges of proloculus diameter were extended, for *B. merici* SIREL & GÜNDÜZ, from 1.35-1.56 to 1.3-1.8 µm to include data in SIREL (2003), and for *Borelis pulchra* (ORBIGNY) from 25-30 to 25-50 µm to include data in COLE (1957) on *Borelis primitivus*, considered a synonym of *B. pulchra* by BASSI *et al.* (2021b). Note that part of the specimens from Ibi and La Font Roja sections (orange circles) fit well within the range of *B. inflata* (ADAMS), whereas some specimens (blue circles) fall between the ranges of *B. in flata/B. merici* and *B. pygmaea* HANZAWA, and are here referred to as *Borelis* sp. 1.

A second group of Oligocene specimens exhibits columellar thickening and a notably higher *EI* of 1.7-2.2, possibly reaching 2.6 in incomplete forms (Fig. 12O-W). These *EI* values are larger than those documented for *B. merici* (1.3-1.8; SIREL & GÜNDÜZ, 1981; SIREL, 2003) and *B. philippinensis* (1.3-1.8; BASSI *et al.*, 2021b), but smaller than those for *B. pygmaea* (2.3-2.5 according to SIREL, 2003; 2.2-3.2 according to BASSI *et al.*, 2021b). They also differ from *B. philippinensis* by lacking Y-shaped septula. Because these specimens do not fit the diagnosis of any known species, they are referred to here as *Borelis* sp. 1. The limited number of available centred sections prevents a formal, detailed characterization of a potential new species. These forms may be related to the specimens reported from the Malatya Basin as *B. merici* by GEDIK (2017), which exhibit an *EI* of 1.79-2.71. A graphic plotting elongation index (*EI*) against proloculus diameter (*P*) confirms that most specimens fall within the variability *of B. inflata*, whereas those assigned to *Borelis* sp. 1 occupy intermediate values between *B. inflata*/*B. merici* and *B. pygmaea* (Fig. 17; Table 1).

Table 1: Measurements in *Borelis* specimens from the Ibi section. **P**: Diameter of the megalospheric proloculus, **L**: Test lenght, **D**: Test diameter, **EI**: Elongation index. (See plot in Fig. 17).

Species	Sample	*P* (µm)	*L* (µm)	*D* (µm)	*EI* (L/D)
Borelis inflata	SA-60	68.0	552	524	1.05
		45.0	843	606	1.39
		37.4	631	527	1.20
		69.0	565	489	1.16
	Ibi-57	62.0	660	592	1.11
		54.0	637	481	1.32
		59.0	168	151	1.11
		48.0	416	410	1.01
		62.0	1,587	1,074	1.48
	Ibi-6	44.0	1,339	1,046	1.28
		46.0	1,256	950	1.32
		51.0	574	483	1.19
		50.0	1,138	974	1.17
	Ibi-5	68.0	336	303	1.11
	SA-52	41.0	365	298	1.22
Borelis sp. 1	SA-60	54.0	1,015	583	1.74
		76.0	1,606	839	1.91
		47.0	1,210	622	1.95
		74.0	1,496	798	1.87
		58.0	1,493	726	2.06
	Ibi-58	69.5	1,234	774	1.59
	Ibi-5	52.8	1,732	950	1.82
	Ibi-52	76.0	624	393	1.59

The samples from the Ibi section also include several small subspherical forms (Fig. 12G-K). To assess whether these represent juveniles or a smaller species such as *B. pulchra*, we overlaid images of small and large specimens from the same samples (Fig. 12J1-J2). As no significant differences were observed apart from test size (they show similar size, shape and number of chambers and chamberlets), we interpret the small tests as juvenile forms of *B. inflata*. On the other hand, the occurrence of *Borelis pulchra* in the Oligocene (BASSI *et al.*, 2021b) is questionable (see also BOUDAGHER-FADEL & PRICE, 2021). This species was originally defined from recent material from Cuba (ORBIGNY, 1839) and, according to HOTTINGER (1974), is known only from modern sands in the Caribbean (Florida, Bahamas, Cuba, Jamaica) and from Ascension Island in the Atlantic. BASSI *et al.* (2021b) placed in synonymy with *B. pulchra* four fossil species, *B. primitivus*, *B. parvula*, *B. boninensis*, and *B. globosa*, and extended its stratigraphic range down to the Priabonian and its geographic distribution to the Pacific (Philippines, Ogasawara Islands, Eniwetok, Saipan, Australia). However, the adscription of these fossil species to *B. pulchra* is questionable for several reasons: (1) most characters used to define *Borelis* species cannot be applied to small forms with sphaerical tests < 1 mm (*e.g.*, number of chambers per whorl at 1 mm test diameter, number of chamberlets per 1 mm chamber length, or elongation index, since elongated forms may initially have a sphaerical shape); (2) contradiction in the definition of *B. pulchra* by BASSI *et al.* (2021b) as having a proloculus of 25-30 µm, whereas including as a synonym *B. primitivus*, defined as having a proloculus of 50 µm (COLE, 1957); (3) gaps in the stratigraphic record (*e.g.*, the alleged occurrence of *B. pulchra* in the Pliocene is based on an arbitrary reinterpretation of an unfigured mention of *B. melo* by MATSUMARU (2011); and (4) geographic inconsistency, with recent forms in the Caribbean and Atlantic and fossil forms in the Pacific (interpreted as homoplassic by BOUDAGHER-FADEL & PRICE, 2021). The small specimens from the Prebetic fit the diagnosis of *B. pulchra* by BASSI *et al.* (2021b), but also match juvenile individuals of other species, including the Eocene *B. vonderschmitti*. These small forms from the Prebetic are, therefore, interpreted as juvenile individuals of the two recognised species: *B. inflata* and *Borelis* sp. 1.

Amphistegina

Two species of *Amphistegina* (Superfamily Asterigerinoidea, Family Amphisteginidae) were identified in the sections studied: *Amphistegina bohdanowiczi* and *A. mammilla*. Both species were described in detail by FERRÀNDEZ-CAÑADELL and BOVER-ARNAL (2017; see also RÖGL & BRANDSTÄTTER, 1993). *Amphistegina bohdanowiczi* (Fig. 9R-S) is very similar to *Asterigerina rotula*, from which it probably originated by developing a lenticular test with involute chambers. It occurs throughout the Oligocene (SB 21-23) and has also been reported from the Lower Miocene (*e.g.*, RÖGL & BRANDSTÄTTER, 1993). In the Ibi section its first occurrence (FO) was observed in the middle part, corresponding to the SB 22A. Its absence in the lower part may be due to the shallow-water facies of SB 21 layers, dominated by porcellaneous Foraminifera where hyaline species are scarce.

The test of *A. mammilla* (Fig. 9T-Y), with its symmetrical lenticular-rhomboidal outline and umbonal bosses on both sides, resembles that of some *Nummulites*, particularly *N. vascus*, with which it has sometimes been confused (*e.g.*, STOKLOSA & SIMO, 2008). Chattian *A. mammilla* has been reported as *A. hauerina* (a synonym of *A. mammilla*; RÖGL & BRANDSTÄTTER, 1993; FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017) from Palestine (HENSON, 1936) and the Aquitaine Basin (SZTRÁKOS & STEURBAUT, 2017), and as *A. lessonii* from Malta (FELIX, 1973).

HABIBI and BOVER-ARNAL (2018) reported *Amphistegina mammilla* (as *A. mammilla*, *A.* cf. *mammilla*, and *N. vascus* in their Fig. 7a, 7k, and 7d, respectively) from the Rupelian and lowermost Chattian of the Asmari Formation in Iran. However, its association with *Nummulites vascus*, *Heterostegina assilinoides*, and *Eulepidina elephantina* suggests a late Chattian (SB 23) age. Their interpretation of the Rupelian/Chattian boundary coincides with a marked shift to shallower facies, where hyaline associations are replaced by porcellaneous forms and miogypsinids. WIELANDT-SCHUSTER (2004) also reported *Amphistegina* cf. *mammilla* from the Rupelian of the Mesohellenic Basin (Greece). Although no specimens were illustrated, the association with *Eulepidina elephantina*, *Heterostegina assilinoides*, and *Cycloclypeus droogeri* suggests a late Chattian age. The report of *A. mammilla* from the Rupelian of Zagros (Iran) by AMIRSHAHKARAMI (2013) corresponds to *A. bohdanowiczi* (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017).

Lepidocyclinids

Nephrolepidina and *Eulepidina* (Superfamily Asterigerinoidea, Family Lepidocyclinidae) are widely used in Oligocene biostratigraphy. Both genera were identified in samples from the two sections studied, but species-level determination was not possible due to the lack of loose specimens, which are necessary for a statistically significant biometrical study based on centred equatorial sections. One specimen was tentatively assigned to *N.* cf. *morgani* (Fig. 9O) because it closely matches the specimens illustrated by BENEDETTI and SCHIAVINOTTO (2023, Figs. 7-8). The diameter of the deuteroconch in *Eulepidina* from non-centred sections in the lowermost part of the basal upper Rupelian of the Ibi section (730-845 µm, Fig. 9M) agrees with the values of topotypes of *E. formosoides* (363-1285 µm, mean = 772 µm) reported by HECK and DROOGER (1984), as well as with values from other localities in Turkey

and Iran (*e.g.*, Özcan *et al.*, 2010a; Akbar-Baskalayeh *et al.*, 2020; Yazdi-Moghadam *et al.*, 2025).

Nummulitids

In the Ibi and FR sections, nummulitids (Superfamily Nummulitoidea, Family Nummulitidae) are represented by species of *Nummulites*, *Heterostegina*, *Spiroclypeus*, and *Cycloclypeus. Nummulites* is scarce in the two studied sections. Specimens belonging to the *N. fabianii* group (*N. fabianii*, *N. fichteli*), the *N. incrassatus* group (*N. incrassatus*, *N. vascus*), and the operculiniform *N. kecskemetii* were identified. We follow the classification of reticulate *Nummulites* proposed by Özcan *et al.* (2009a), which has been adopted by several authors (Özcan *et al.*, 2010a, 2010b, 2019; Less *et al.*, 2011; Akbar-Baskalayeh *et al.*, 2020; Hadi *et al.*, 2023). According to this classification, *Nummulites fabianii* is characterised by having umbo, weak granules, heavy reticulation, and a proloculus diameter of 200-300 µm. The specimens of reticulate *Nummulites* from the lower part of the Ibi section exhibit these features (Fig. 7A-B). The proloculus could only be measured in one axial section, with an equatorial diameter of 235 µm. This species is associated with *Nummulites* of the *N. incrassatus* group, which have a small proloculus (< 50 µm; Fig. 7C), along with *Acervulina linearis*, *Asterigerina rotula*, *Discocyclina* spp., *Fabiania cassis*, *Halkyardia minima*, *Gyroidinella magna*, *Schlosserina asterites*, *Chapmanina gassinensis*, *Silvestriella tetraedra*, *Rotorbinella epardi*, *Borelis vonderschmittii*, and *Orbitolites* cf. *cotentinensis.*

In upper levels of the Ibi section, *N. vascus* and *N. kecskemetii*, together with *Nummulites* of the group of *N. fabianii* occur. Within the latter, most specimens are characterised by a larger, smooth reticulate test (Fig. 9A-B). Measurements taken from an equatorial section (Fig. 9B) yielded the following values: *P* = 238 µm, outer diameter of the first two whorls = 1.135 µm, 18 post-embryonic chambers in the first two whorls, and an index of spiral opening = 26.4. These parameters fall within the variability of *N. fichteli* (*e.g.*, Özcan *et al.*, 2010a).

Nummulites vascus (Fig. 9C) is characterised by a radiate, biconvex test with an indistinct central knob and an acute margin. The protoconch, measured in subaxial sections, yielded *P* values of 122-153 µm (N = 5), which are lower than those reported for *N. vascus* by Less *et al.* (2011) and Sirel *et al.* (2020a), possibly because the sections are not centred.

Nummulites kecskemetii is characterised by its very small proloculus (usually 60-90 µm in diameter), operculinid spiral, narrow chambers, and curved septa, almost at right angle in the proximal half and at 10°-15° where joining the spiral wall (Less, 1991). It is rare in the studied sections and was recognised only in axial sections (Fig. 9D) as a small operculinid nummulitid, with *P* values of 47-96 µm (N = 3). Its biostratigraphic range spans the entire Chattian (SB 22A-23) (Less, 1991; Báldi *et al.*, 1999; Wielandt-Schuster *et al.*, 2004; Özcan *et al.*, 2009a, 2010a; Parente & Less, 2019).

Heterostegina assilinoides and *Spiroclypeus margaritatus* from the Prebetic upper Chattian were previously described (the latter as "*S. blanckenhorni*") by Ferràndez-Cañadell and Bover-Arnal (2017). No significant morphological or biometrical differences were observed in the specimens from the Ibi and FR sections. *Heterostegina assilinoides* (Fig. 9H-J) occurs in the upper part of the Ibi section and throughout the FR section (Figs. 5-6). The estimated *P* values 162-247 µm (mean = 201.2 µm, N = 8) are similar to those reported for specimens from Benitatxell in the eastern Prebetic (210-338 µm, mean = 268 µm; Ferràndez-Cañadell & Bover-Arnal, 2017) and within the variability documented in the literature (Henson, 1937; Özcan *et al.*, 2009a, 2010a; Benedetti *et al.*, 2018). *Spiroclypeus margaritatus* occurs in the uppermost part of the Ibi section and throughout the FR section (Fig. 9K-L), with *P* values of 296-356 µm (mean = 328.75 µm, N = 4). This species, often reported as *S. blanckenhorni* (a junior synonym) in the Mediterranean region, is not related to the Priabonian species (Özcan *et al.*, 2009b; Less *et al.*, 2018). It occurs in the upper Chattian (SB 23) across the entire Tethys realm, from the Mediterranean to the Pacific (Cole, 1969; Cahuzac & Poignant, 1997; Ehrenberg *et al.*, 2007; Less *et al.*, 2018), and also occurs in the lower Aquitanian of central Turkey (Özcan *et al.*, 2009b).

Cycloclypeus is very scarce in our samples (Fig. 9F-G). It occurs at the top of the Ibi section and throughout the FR section (Figs. 5-6). The test exhibits a central swelling of flattened lenticular shape, and the external surface is smooth, lacking granules. The diameter of the megalospheric protoconch (*P* = 114-192 µm, mean = 151 µm, N = 11) corresponds to *C. mediterraneus* (120-160 µm) and differs from the smaller protoconch of *C. droogeri* (< 120 µm) and the very small embryo of *C. eidae* (60-90 µm) (Matteucci & Schiavinotto, 1985; Özcan & Less, 2009). It also differs from the larger proloculus of *C. pseudocarpenteri* (*P* = 195-375 µm) described from the lower Chattian (SB 22B) of eastern Turkey (Özcan *et al.*, 2010a). No significant differences were observed between specimens from the Ibi section (*P* = 162-182 µm, mean = 164 µm) and those from the FR section (*P* = 128-192 µm, mean = 143.6 µm). Similar specimens assigned to *C. mediterraneus* have been reported from the Prebetic and southern Spain (Laagland, 1990; Renema, 2015; Ferràndez-Cañadell & Bover-Arnal, 2017) and central Italy (Matteucci & Schiavinotto, 1977, 1985; Renema, 2015).

Rotorbinella

Rotorbinella is a small conical rotalid (Family Rotaliidae, Subfamily Rotaliinae) with the simplest canal system. It is a polyphyletic genus with a discontinuous biostratigraphic record, including

species known from the Cenomanian, Coniacian-Santonian, Paleocene-Ilerdian, and Miocene-Recent intervals, reflecting recurrent origins and extinctions (FERRÀNDEZ-CAÑADELL *et al.*, 2023a). *Rotorbinella epardi* was originally defined from material of the Helvetic Alps, later recognised in other western basins of the Tethys, and considered a characteristic species for the Priabonian, SB 19-20 (FERRÀNDEZ-CAÑADELL *et al.*, 2023b). In the Prebetic, it occurs in the Priabonian of the lowermost part of the Ibi section (Figs. 5, 10P-Q). A similar form, here referred to as *Rotorbinella* cf. *epardi* also occurs throughout the Oligocene (Fig. 10O, R-S). The limited material prevents a conclusive species determination, but it is likely that the biostratigraphic range of *R. epardi* extends upward into the upper Chattian, as previously suggested by FERRÀNDEZ-CAÑADELL *et al.* (2023b).

Miogypsinella and *Postmiogypsinella*

Western Neothethys miogypsinids (Superfamily Rotalioidea, Family Miogypsinidae) without lateral chamberlets, classically assigned to *Miogypsinoides*, actually belong to the genus *Miogypsinella* HANZAWA, which is characterised by an initial, low trochospiral coil and thinner lateral walls (SIREL, 2015; GEDIK, 2020). Similarly, some reports of *Miogypsina* from the Chattian of the Mediterranean region may correspond to *Postmiogypsinella* SIREL & GEDIK. This reinterpretation could explain certain age misinterpretations (*e.g.*, the interpretation of the uppermost part of the Ibi section as Burdigalian by GEEL, 1995).

Four species of *Miogypsinella* (= *Miogypsinoides* auct.) have been differentiated based on the number of spiral chambers (factor *X*), with varying limits according to different authors as well as different ranges of variability and biostratigraphic ranges (*e.g.*, GEDIK & SIREL, 2009; SIREL & GEDIK, 2011; SIREL & IŞIK, 2011; GEDIK, 2014, 2020; HAKYEMEZ *et al.*, 2016). Since our study was carried out entirely on random thin sections (Fig. 16), the exact number of spiral chambers and their variability could rarely be observed. To address this limitation, we adopted a threshold of 14 spiral chambers to differentiate *M. complanata* and *M. formosensis* (with more than 14 spiral chambers, X > 14) from *M. borodensis* and *M. akcadagensis* (with 14 or fewer spiral chambers, X ≤14). Some specimens with fewer than 10 spiral chambers were identified as *M. akcadagensis* (Figs. 6, 16N-P). As a result, a distinct biostratigraphic distribution was observed for the two groups (Fig. 6): specimens with X > 14 occur in the lower part of the FR section, whereas those with X ≤14 occur in the middle-upper part, associated with *Postmiogypsinella*. No miogypsinids were found in the uppermost samples from the Ibi section (last 12 m; Fig. 5), which are interpreted as late Chattian in age based on the presence of *Risananeiza pustulosa*, *Amphistegina mammilla*, and *Cycloclypeus mediterraneus.*

Elphidium and *Elphidiella*

Elphidiella (Family Elphidiellidae) differs from *Elphidium* (Family Elphidiidae) by lacking retral processes and having multiple interioareal apertures and a rounded periphery (*e.g.*, CONSORTI *et al.*, 2018). In our samples *Elphidiella* sp. occurs in the uppermost Eocene and the lower Rupelian (SB 21) (Figs. 5, 10V-X). This species is likely the same reported as "*Elphidium* sp. 1" from the lower Rupelian of the Asmari Formation in the Sepidar Anticline (Zagros Basin, Iran) by HABIBI (2016a, Pl. 2, figs. 3, 18).

Elphidium crispum is a relatively common species in Middle Miocene or younger rocks (*e.g.*, HANSEN *et al.*, 1987; CAHUZAC & POIGNANT, 2004). According to YAZDI-MOGHADAM *et al.* (2021), its earliest occurrence in Central Iran is in the Burdigalian (SBZ 25). *Elphidium* cf. *crispum* was found in a single sample from the lowermost upper Chattian of the Ibi section (Fig. 10M). The occurrence of *Elphidium crispum* in the lowermost upper Chattian (SB 23) in the Prebetic is in accordance with the biostratigraphic study by SZTRÁKOS and STEURBAUT (2017) in western Aquitaine Basin. SIREL and GEDIK (2011) included "*Elphidium* sp." in the assemblage characterizing the upper Chattian of Malatya Basin (eastern Turkey), although they did not provide illustrations.

6. Systematic palaeontology (C. FERRÀNDEZ-CAÑADELL)

The record along a succession spanning the early Rupelian to the late Chattian has revealed new features in two genera, *Austrotrillina* and *Risananeiza*, which have implications for their systematics. Consequently, these two genera are discussed in more detail in this section. Two other genera with Eocene and Oligocene representatives, *Pfendericonus* and *Neorotalia*, also require clarification and are, therefore, also included in this section.

The genus *Austrotrillina.* Structure and diagnostic criteria

The extensive literature on *Austrotrillina* reveals diverse and often contradictory systematic interpretations and biostratigraphic ranges for its species. Based on observations of morphological features and evolutionary trends along the sections studied, together with a critical assessment of the literature, a comprehensive review of the genus is made here.

In the literature five species of *Austrotrillina* are currently accepted: the Eocene *A. eocaenica* HOTTINGER, and the Oligocene-Miocene species *A. paucialveolata* GRIMSDALE, *A. asmariensis* ADAMS, *A. striata* TODD and POST, *A. brunni* MARIE, and *A. howchini* (SCHLUMBERGER). Among the Oligo-Miocene species, *A. paucialveolata* and *A. howchini* are clearly differentiated by their exoskeleton: simple and irregular or scattered in the former (and in *A. eocaenica*), and regular and complex with bifurcated alveoli in the latter. There is a

considerable confusion with the other three species, *A. asmariensis*, *A. striata*, and *A. brunni*, with different species definitions and diagnostic features, partly resulting from insufficient original descriptions. Characters such as size of alveoli, spacing between alveoli, thickness of the walls between alveoli, test shape, growth type (biloculer/trilocular/quinquelocular), and diameter of the megalospheric proloculus are highly variable and, to some extent, subject to subjective interpretation. Consequently, these species do not exhibit clear patterns in their biostratigraphic ranges, nor even in their order of appearance in the geological record across different regions.

ADAMS (1968) carried out a first revision of the genus, checking type material, redefining species, and erecting a new one, *A. asmariensis*. A key conclusion of his review was the difficulty in distinguishing species due to variability and the presence of intermediate forms. The genus *Austrotrillina* was recently revised by BASSI *et al.* (2021a), who recognised only four species and concluded that *A. eocaenica* is the ancestor of the group, from which two species originated in the Rupelian, *A. brunni* and *A. striata* (including *A. paucialveolata*), with a fourth species, *A. howchini*, appearing in the Burdigalian.

The observations of *Austrotrillina* along the Ibi and FR sections, spanning from the lowest Rupelian to the upper Chattian, revealed architectural features and evolutionary patterns that enabled a revision and reinterpretation of the genus taxonomy (Figs. 13-14, 18-19).

First, there is confusion regarding both the architecture, mainly the structure of the wall, and the terminology used to describe it (alveoli, alcoves, parapores), which needs clarification. In their revision of *Austrotrillina*, BASSI *et al.* (2021a) described the wall structure not as an *exoskeleton* but as a *wall texture*, consisting "of a tectum and a parakeriotheca with subsutural alcoves" (BASSI *et al.* (2021a, p. 15). Therefore, they considered the cavities in the wall to be *parapores*, not *alveoli*: "The alveole recesses are of varying depth and end blind beneath the tectum. Consequently, they are parapores *sensu* HOTTINGER (2006)" (BASSI *et al.*, 2021a, p. 6). However, HOTTINGER (2006) emphasised the distinction between *exosqueletal structures* (including alveoli) and *wall textures* (keriotheca, pseudokeriotheca, parapores), noting the simultaneous presence of both in some genera. He clearly stated (HOTTINGER, 2006, p. 6) that "Alveoles must be distinguished from parapores or parakeriothecal cavities that are an adjunct of wall texture" and highlighted that "Among the porcellaneous Foraminifera with alveoles, *Austrotrillina* is a prominent group". The present work follows HOTTINGER (2006) in considering that the terms "parapores" and "parakeriotheca" (wall texture) should not be applied to *Austrotrillina*. A special case is *A. howchini*, in which the alveoli are bifurcated, with morphotypes progressively more complex structures and levels of bifurcation. BASSI *et al.* (2021a) studied in detail (using microCT) the most complex forms of the genus, specimens of *A. howchini* with three orders of bifurcation in alveoli, where the wall structure becomes homogeneous, lacking recognizable beams or rafters, and closely resembling pseudokeriothecal wall textures. Whereas this type of structure might be interpreted as pseudokeriothecal wall with parapores (even illustrating a particular origin of keriothecal wall from increasing alveolar complexity), this terminology cannot be applied to the simple cavities in the in the walls of the other species of *Austrotrillina*, which are true alveoli (*i.e.*, exoskeleton), not parapores (*i.e.*, wall texture). This is evident in *A. eocaenica* and *A. paucialveolata*, where cavities in the wall can reach 100 µm in width (Fig. 13F) or appear as smooth, shallow depressions on the inner wall surface (Fig. 13C-E). The same applies to the *asmariensis*, *striata*, and *brunni* morphotypes, as well as the simplest forms of *A. howchini* with a single level of bifurcation in alveoli.

Second, BASSI *et al.* (2021a) considered, and used as a diagnostic character, that beams are present only in *A. howchini* and *A. eocaenica*, and therefore absent in their concept of *A. brunni* (including *A. asmariensis*) and *A. striata* (including *A. paucialveolata*). This interpretation is incorrect, because beams are conspicuous in all regular morphotypes (*striata*, *asmariensis*, *brunni*), as well as in simple *howchini* (Fig. 18B-D, G). An exception occurs in the complex forms of *A. howchini* (with two or three bifurcation levels in alveoli), where beams become less discernible or disappear entirely. BASSI *et al.* (2021a) did not provide thin-section photographs of these complex forms, relying exclusively on processed microCT images.

Third, HOTTINGER (2007) introduced the presence of so-called "alcoves" as an architectural diagnostic character in *Austrotrillina*, defined as blind cavities formed by beams merging with the basal layer in the chamber suture. Subsequent authors followed HOTTINGER (2007), adding the presence of alcoves into the description of *Austrotrillina* species (*e.g.*, BASSI *et al.*, 2021a, for *A. eocaenica* and *A. howchini*; SERRA-KIEL *et al.*, 2016, for *A. eocaenica*, *A. brunni*, and *A. striata*). However, there are no blind cavities in the test of *Austrotrillina;* the supposed alcoves are simply alveoli observed in tangential section. The few illustrated "alcoves" in *Austrotrillina* in the literature (HOTTINGER, 2007; SERRA-KIEL *et al.*, 2016; BASSI *et al.*, 2021a) are always shown in tangential section. Sections normal to the chamber wall show that the exoskeleton (beams) only reaches the basal layer at the chamber junction, forming a cavity that remains open to the chamber lumen, that is, an alveolus (Fig. 18E-H). As noted by HOTTINGER (2007), these alveoli in the marginal part of chambers (suture) are somewhat larger and quadrangular (Fig. 18C-D, G). The confusion

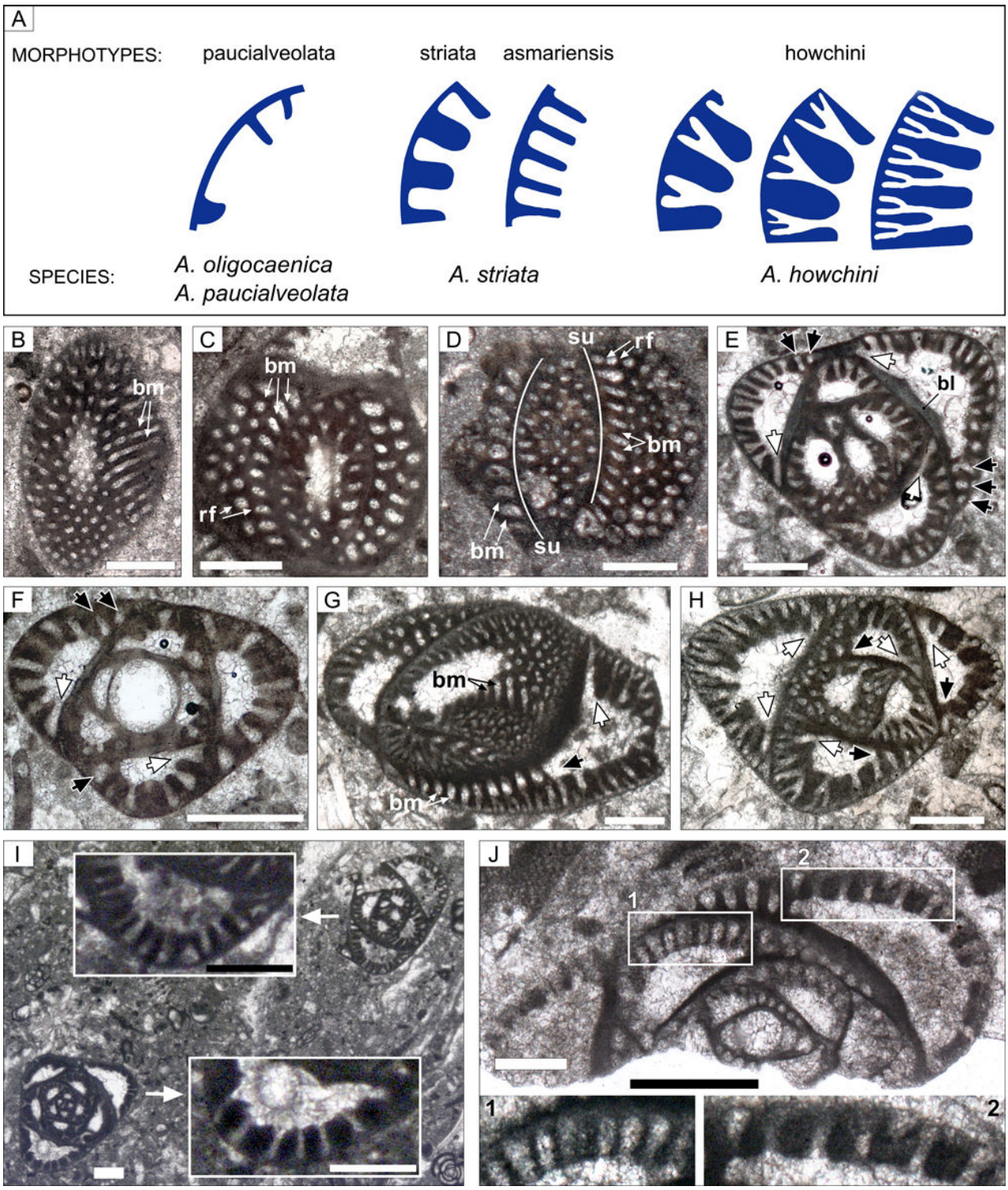


Figure 18: Architecture of the test of *Austrotrillina*. **A)** Different morphotypes of the exoskeleton of *Austrillina* and the species bearing each morphotype. **B-J)** Architecture of the test and morphotypes in *Austrotrillina*. **B-D)** Tangential sections showing the two exoskeletal elements that form the alveoli, beams (*bm*), normal to the chamber sutures, and rafters (*rf*) normal to sutures (*su*); note the larger size of alveoli beside sutures; samples: B) Ibi-9, C SA-57, D) Ibi-43. **E-H)** Sections showing the exoskeletal features in the different morphotypes: asmariensis-type (E), striata-type (F) and howchini-type (G-H). All the cavities in the wall are formed by open cavities, *i.e.*, alveoli. The alleged presence of alcoves (*i.e.*, blind cavities within the walls) are actually misinterpreted oblique or tangential sections of alveoli (black arrows); when the section is normal to the wall it is clear that all the cavities are open (white arrows). Note the bifurcation of alveoli in G and H; samples: E-F) SA-60, G-H) SU-2 (Serra de l'Ombria, section under study). **I)** Microphotograph of a thin section and details (white squares) showing the occurrence of the two morphotypes of exoskeleton in the same sample (SA-57), asmariensis-type (top) and striata-type (bottom). **J)** Equatorial-oblique section and details showing the two morphotypes of alveoli in the same specimen, asmariensis-type in the inner chambers (1) and striata-type in the external chambers (2); sample FR-83. Scale bars = 200 µm.

may have arisen because, in the marginal (polar) zones of the test, the walls of two adjacent chambers meet at a closed angle along a curved suture, so that part of the section is always tangential. It is only in this tangential part of the section where the supposed alcoves are seen, whereas at the opposite end of the chamber the cavities appear as open alveolus (Fig. 18E-H). This can also be seen in the section of *A. howchini* in ADAMS (1968, Pl. 3, fig. 6), and in Figure 9D and 9H in BASSI *et al.* (2021a), where "alcoves" appear only on one side of the chamber, whereas on the other side the alveolus is clearly open to the chamber lumen. The conclusion is that there are no alcoves in *Austrotrillina* and, therefore, they cannot be considered a valid diagnostic character.

Fourth, according to BASSI *et al.* (2021a), *A. howchini* would be the only species lacking a flexostyle. However, in the original description of the species, based on material from Australia, SCHLUMBERGER (1893, p. 119) clearly stated that "on remarque au centre la mégasphère avec son canal", which he also illustrated in his Fig. 1. Furthermore, in his description of *A. howchini*, ADAMS (1968, p. 86) wrote: "Test comprising a subglobular proloculus (...) followed by a tube-like second chamber". The flexostyle is visible in his figured specimens (see Pl. 2, fig. 4 in ADAMS, 1968). Therefore, the absence of a flexostyle cannot be considered a diagnostic feature for *A. howchini*.

Fifth, the diameter of the megalospheric proloculus in the *asmariensis*, *striata*, and *brunni* morphotypes is so variable that it can hardly be used as a diagnostic character for distinguishing species. ADAMS (1968) noted the extreme variability in proloculus diameter (*P*) in *A. asmariensis*, reporting values ranging from 70 to 250 µm, with middle Oligocene specimens having the largest proloculi in the genus. According to his data (ADAMS, 1968), the range of *P* in *A. paucialveolata* (80-130 µm) falls within that in *A. asmariensis* (70-250 µm), *A. striata* (50-130 µm), and *A. howchini* (70-150 µm). In their diagnosis of *A. brunni*, BASSI *et al.* (2021a) included a proloculus diameter ranging from 100 to 250 µm. However, they included in the synonymy list all the specimens assigned to *A. brunni* by SERRA-KIEL *et al.* (2016), who described the species as having a proloculus diameter of 60-100 µm. These two ranges are mutually exclusive. If combined, the total range would be 60-250 µm, similar to that of *A. asmariensis* according to ADAMS (1968) and nearly encompassing the known range of the genus.

In the sections studied, particularly in the Ibi section, the evolution of *Austrotrillina* through the Oligocene can be traced from the lowermost Rupelian to the upper Chattian. The specimens from the lower Rupelian (SB 21) are all of the *A. paucialveolata* type, which is replaced in the upper Rupelian and through the lower to the upper Chattian (SB 22A-23) by *asmariensis/striata/brunni* forms.

Tests with *asmariensis* and *striata*/*brunni* exoskeletal morphotypes occur together in the same samples (Fig. 18I) and even within the same specimen (Fig. 18J). The upper samples with *Austrotrillina* in the Ibi section (basal SB 23) exhibit exoskeletons transitional between *striata* and *howchini* morphotypes, showing incipient bifurcation of alveoli (Fig. 14B-C). Occasional specimens with regular bifurcation of alveoli appear in the middle upper Chattian in the FR section (Fig. 14A). The evidence indicates a progressive phylogenetic change in exoskeleton pattern from the *asmariensis*-type to the *striata*-type, reflected in the ontogeny, and subsequently evolving toward the *howchini*-type. That is, the different exoskeletal patterns represent stages in a continuous, gradual evolutionary trend. Because *asmariensis* and *striata/brunni* exoskeletal types occur together (same stratigraphic layers and even within the same test), they cannot be used to define species.

Based on this review of the main diagnostic characteristics and the terminology to be used in descriptions, along with the observations made on the studied material and data from the literature, the currently accepted species are reviewed below.

Austrotrillina paucialveolata and *A. eocaenica*

The exoskeleton in *Austrotrillina paucialveolata* is highly variable, ranging from a simple rounded thickening of the wall (producing an undulate internal surface in sections perpendicular to the wall) to alveoli that are irregular in size, shape, and distribution (Fig. 13A-I). As stated by ADAMS (1968) in his emended diagnosis of the species, alveoli are restricted to the last few chambers. *Austrotrillina paucialveolata* is very similar to *A. eocaenica*, differing by its smaller test, smaller megalospheric proloculus, and a thinner basal layer (HOTTINGER, 2007; SERRA-KIEL *et al.*, 2016).

Reported values of *P* in the literature are 80-130 µm (ADAMS, 1968), 80-100 µm (HOTTINGER, 2007) or 60-70 µm (SERRA-KIEL *et al.*, 2016) for *A. paucialveolata;* and 240-320 µm (HOTTINGER, 2007; "24-32 µm" in BASSI *et al.*, 2021a) or 190-235 µm (SERRA-KIEL *et al.*, 2016) for *A. eocaenica*. Specimens of *A. paucialveolata* from the Ibi section are consistent with these values, with a P_{mean} = 83 µm (range = 40-140 µm, N = 16), showing an increase from P_{mean} = 75.08 µm in the lowermost samples (Ibi-118 to Ibi121, range = 40-106 µm, N = 6) to a P_{mean} = 117.5 µm in the uppermost sample (Ibi-MN20, range = 120-148 µm, N = 3; Table 2).

BASSI *et al.* (2021a) considered *A. paucialveolata* a junior synonym of *Austrotrillina striata*, stating that "No textural and structural differences were found between *A. striata* and *A. paucialveolata*" (BASSI *et al.*, 2021a, p. 12). In fact, the size and pattern of alveoli in these two species are markedly different (Fig. 13). The evi-

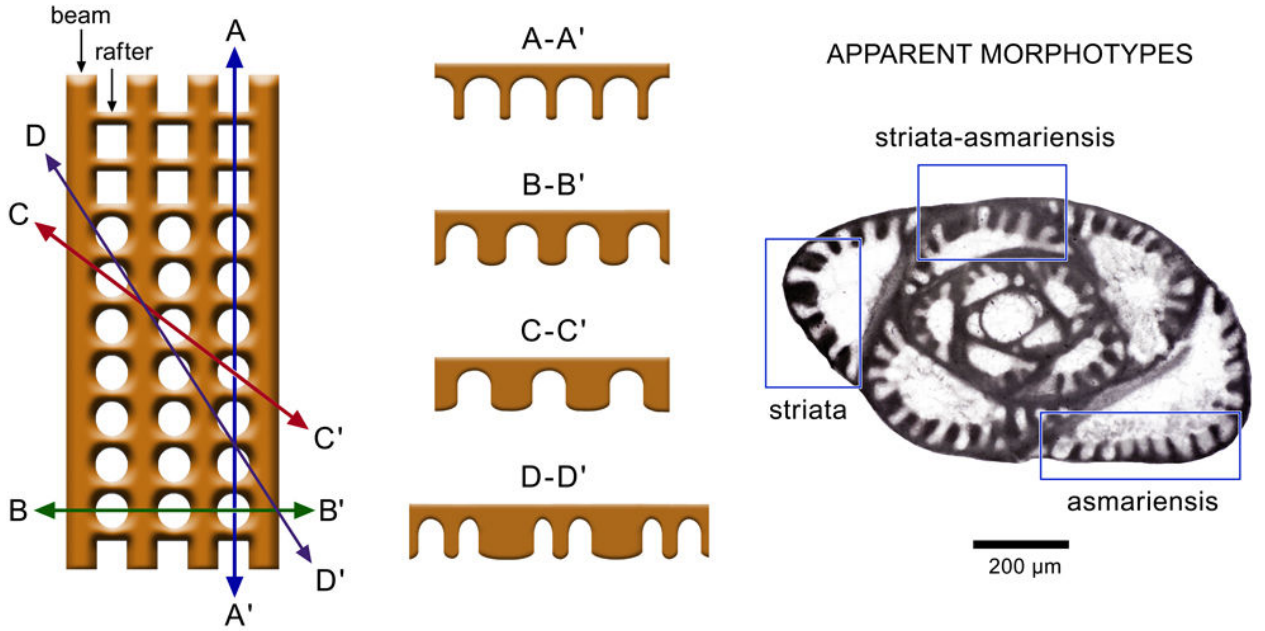


Figure 19: Schematic drawing of the alveolar lateral wall of *Austrotrillina* and the different exoskeletal patterns that will be apparent depending on the direction of the section. The same exoskeleton can appear as asmariensis-type (A-A'), more or less thicker striata-type (B-B', C-C'), or irregular (D-D'). Photo: *A. striata*, Ibi section, sample SA-57 (SB 22A, upper Rupelian).

Table 2: Measurements of megalospheric proloculus diameter (*P*) in *Austrotrillina* from the Ibi and FR sections

Species	Section	Sample	meter in section	*P* (µm)	Mean	N	range	std. dev.
A. striata	FR	FR-83	96	128	–	1	–	–
	Ibi	AA-3	238	167	–	1	–	–
		Ibi-9	236	135	–	1	–	–
		Ibi-11	227.5	67	–	1	–	–
		SA-68	218.5	133, 156	109.25	2	133-156	83.07
		SA-63	188	49	–	1	–	–
		SA-62	179	62	–	1	–	–
		Ibi-45	171	83	–	1	–	–
		SA-60	163.5	57, 64, 66, 73, 82, 89, 106, 109, 110, 111, 118, 122, 129, 131, 132, 136, 138, 141, 144, 144, 144, 144, 144, 149, 151, 156, 160	120.37	27	57-160	34.69
		SA-59	161	59, 116	87.50	2	59-116	57.00
		SA-57	148	52, 60, 66, 70, 98, 100, 104	78.57	7	52-104	32.18
		Ibi-41	146.5	86	–	1	–	–
		Ibi-6	142	48, 63, 64, 78, 94, 104, 120	81.57	7	48-120	35.44
		Ibi-5	130	61, 65, 66, 68, 70, 74, 74, 76, 77, 81	71.20	10	61-81	19.38
		Ibi-2, SA-52	116.5	45		1		
		SA-53	127	94, 111, 118, 121	111.00	4	94-121	48.98
A. paucialveolata		MN-20	110	120, 128, 148	132.00	3	120-148	65.57
		Ibi-MN-19	108	82	–	1	–	–
		Ibi-130	96.5	68	–	1	–	–
		Ibi-129	94	72	–	1	–	–
		MN-6	78	58, 70, 73	66.84	3	58-73	32.56
		Ibi-126	76	67	–	1	–	–
		Ibi-121	55	84	–	1	–	–
		Ibi-120	50	40, 56, 86, 106	71.88	4	40-106	39.79
		Ibi-118	44.5	79	–	1		

dence supports treating *A. paucialveolata* as a valid species. It is the only *Austrotrillina* species occurring in the lower Rupelian in the Ibi section and is easy to distinguish from other Oligocene-Miocene species (*A. striata*, "*A. asmariensis*", "*A. brunni*", *A. howchini*) by its irregular and rudimentary exoskeleton, which is restricted to the peripheral chambers (Figs. 13-14). In the Ibi section, a general trend towards more abundant trilocular forms and a more developed and regular exoskeleton can be observed throughout the lower Rupelian (Fig. 13). *Austrotrillina paucialveolata* was reported from the Rupelian of Mallorca as "*Quinqueloculina laberynthi*ca n. sp." by ESCANDELL

and COLOM (1962, p. 127; Fig. 16.1-16), and as "*Austrotrillina howchini*" by HOTTINGER (1963, Pl. 1, figs. 1-2).

Austrotrillina striata, *A. asmariensis*, and *A. brunni*

The exoskeleton in these forms is regular, with alveoli formed by the intersection of two exoskeletal elements, beams and rafters (Figs. 13J-R, 18B-D, I-J), also noted by SIREL *et al.* (2013). Beams are larger, protruding farther into the chamber lumen, and oriented roughly normal to the sutures. Rafters are smaller and perpendicular to beams. Alveoli are rounded and roughly arranged in rows following the beams. At the sutures, alveoli are larger and quadrangular in outline (Fig. 18C-D), bounded only by beams that merge with the basal layer. These cavities along the sutures correspond to the "alcoves" described by HOTTINGER (2007) and BASSI *et al.* (2021a). However, as discussed above, they remain open to the chamber lumen (white arrows in Fig. 18E-H) and are, therefore, alveoli.

The initial chambers lack an exoskeleton, a feature that is more pronounced in microspheric forms. The ontogenetic stage at which the exoskeleton appears in the different morphotypes could not be determined from our material, although the number of chambers without an exoskeleton is clearly lower than in *A. paucialveolata* (compare Fig. 13A-I with Fig. 13J-R).

The diameter of the alveoli and, more importantly, the thickness of the walls that delimit them are variable. According to ADAMS (1968, p. 82), alveoli may be fine as in *A. asmariensis* or coarse as in *A. striata*, however, he did not provide measurements for alveolar diameter in these two forms. Measurements in our material show that the diameter of the alveoli is similar in both morphotypes (approximately 20-30 µm). The variation between morphotypes lies in the spatial distribution of the alveoli, which is controlled by the thickness of the walls separating them. Therefore, these two morphotypes differ primarily in the thickness of the walls between alveoli, rather than alveolar diameter (Fig. 18). Walls between alveoli are thin in the "*asmariensis*" type and thick in the "*striata*" morphotype, resulting in more or less tightly distributed alveoli. This character has traditionally been used as the main criterion for distinguishing species (*asmariensis* vs. *striata*). Although these two morphotypes appear well differentiated, variability produces intermediate forms that are difficult to assign to either morphotype, even using biometric criteria. Intermediate forms between *asmariensis* and *striata* morphotypes, as well as between *paucialveolata* and *asmariensis*, and between *asmariensis* and *howchini* morphotypes have been reported (*e.g.*, ADAMS, 1968; BELFORD, 1984; RIERA *et al.*, 2019; HAIG *et al.*, 2020). Moreover, some variability in wall thickness between alveoli (and in alveolar diameter or spacing of alveoli, as noted by ADAMS, 1968), may result from section orientation: because beams are thicker than rafters, sections across successive rafters show thinner walls than sections across successive beams (Fig. 19). Therefore, different morphotypes of alveoli (*asmariensis*, *striata* or combinations of both) may appear in differently oriented sections of the same specimen (Fig. 19). In the Ibi section both morphotypes, *asmariensis* and *striata*, occur in the same sample (*i.e.*, population) (Fig. 18I). Furthermore, both morphotypes are present within the same test, as shown in the specimen in Figure 18E-H, where there appears to be a transition from the "*asmariensis*" type to the "*striata*" type during ontogeny. Consequently, the alveolar pattern is not a reliable diagnostic feature for differentiating or characterizing species, and *Austrotrillina asmariensis* ADAMS should be regarded as a junior synonym of *A. striata* TODD & POST. This conclusion is consistent with ADAMS' (1968, p. 85) observation: "Although typical specimens of *A. asmariensis* and *A. striata* (...) look very different, the geographical and stratigraphic distributions of the two are such that it is difficult to avoid the conclusion that we are really dealing with one species and that the differences between them are not of fundamental importance".

A third species, *A. brunni*, has been arbitrarily characterised (*i.e.*, not on the basis of observations of the type material) by the presence of a large megalospheric proloculus, a smaller and more frequent trilocular test, and rounded margins in equatorial section (*e.g.*, SIREL, 2003; SERRA-KIEL *et al.*, 2016). However, no solid morphological, biometric, or biostratigraphic criterion clearly separates *A. brunni* from *A. striata*. The supposed absence of alcoves, used by BASSI *et al.* (2021a) as a diagnostic character of *A. brunni*, is not a valid criterion because, as discussed above, alcoves are not present in the test of *Austrotrillina*. The proloculus diameter values reported for "*A. brunni*" by SERRA-KIEL *et al.* (2016) and BASSI *et al.* (2021a), 60-100 µm and 100-250 µm, respectively, are mutually exclusive. In MARIE's (1955) original description of *A. brunni*, no details on the proloculus were provided. The measurements of the proloculus diameter in *Austrotrillina* carried out in the present study (Table 2) show a general increase in both *A. paucialveolata* and *A. striata*, but also a high degree of variability that prevents discrimination, on this basis alone, among *A. striata*, *A. asmariensis*, and *A. brunni*. Furthermore, according to ADAMS (1968, p. 85), who examined MARIE's original photographs of *A. brunni*, some specimens show alveoli that bifurcate toward their outer ends, a feature that ADAMS interpreted as corresponding to intermediate forms between "the *A. striata/asmariensis* group and the true *A. howchini*". Several authors have assigned the same biostratigraphic range to "*A. asmariensis*", "*A. striata*", and "*A. brunni*", or have reported their co-occurrence within the same beds (*e.g.*, SIREL, 2003, 2015; GEDIK, 2015; SERRA-KIEL *et al.*, 2016; BASSI *et al.*, 2021a), occasionally alongside *A. paucialveolata* as well

(*e.g.*, ADAMS, 1968, p. 90). The co-occurrence and stratigraphic succession of these "species" (*paucialveolata*, *asmariensis*, *striata*, *brunni*, *howchini*) have been reported or interpreted in many different combinations (*e.g.*, ADAMS, 1970; BOUDAGHER-FADEL & BANNER, 1999; GEDIK, 2015; BOUDAGHER-FADEL, 2018; RIERA *et al.*, 2019; BASSI *et al.*, 2021a), with the only consistent point being that *A. howchini* is considered the youngest form. Intermediate specimens between all morphotypes (*paucialveolata/asmariensis*, *asmariensis/striata*, *asmariensis/howchini*, *striata/howchini*, and *brunni/howchini*) have been documented (*e.g.*, ADAMS, 1968; RIERA *et al.*, 2019; HAIG *et al.*, 2020).

Given the lack of clear discriminatory characteristics, the presence of intermediate forms, the co-occurrence of different types of exoskeleton in the same horizons or in the same specimen, and the appearance of morphotypes in different biostratigraphic order in different areas, the three forms (*asmariensis*, *striata*, and *brunni*) are here merged into a single species, *A. striata* TODD (following the priority of the oldest name and the emended description of the topotypes by ADAMS, 1968). The terms *asmariensis*, *brunni*, and *striata*, would then refer to different morphotypes of the species *A. striata*, which appear to descend from *A. paucialveolata* and diachronically evolved into *A. howchini* ("the end point in the evolution of the genus", ADAMS, 1968, p. 93). This interpretation is consistent with the observations of HAIG *et al.* (2020), who also used the term *morphotype* to describe the different forms, including transitional morphotypes between *A. paucialveolata* and *A. asmariensis*, between *A. asmariensis* and *A. howchini*, as well as as well as forms with different orders of alveolar bifurcation within *A. howchini*.

Taking this morphological and biostratigraphical variability of morphotypes into account, only four species can be distinguished within the genus *Austrotrillina*:

- *Austrotrillina eocaenica* HOTTINGER: with simple and irregular alveoli in the last chambers, *P* = 190-320 µm, middle-late Eocene.
- *Austrotrillina paucialveolata* GRIMSDALE: with simple and irregular alveoli, limited to the last chambers or beginning in the 3rd or 4th chamber, *P* = 40-140 µm, Rupelian.
- *Austrotrillina striata* TODD & POST: with regular simple alveoli starting in earlier chambers and showing two main morphotypes according to the thickness of the walls between alveoli, thin in the asmariensis-type and thick in the striata-type. *P* = 50-250 µm, Rupelian-Serravallian.
- *Austrotrillina howchini* (SCHLUMBERGER): with bifurcated alveoli, showing 1 to 3 orders of bifurcation. *P* = 70-150 µm, late Chattian-Langhian.

Because different morphotypes traditionally considered as three separated species are here merged into a single species, *A. striata*, an emended diagnosis is provided for this taxon.

Phylum Foraminifera ORBIGNY, 1826

Class Tubothalamea PAWLOWSKI *et al.*, 2013

Order Miliolida DELAGE & HÉROUARD, 1896

Superfamily Milioloidea EHRENBERG, 1839

Family Austrotrillinidae LOEBLICH & TAPPAN, 1986

Genus *Austrotrillina* PARR, 1942

Type species: *Trillina howchini* SCHLUMBERGER, 1893.

Austrotrillina striata TODD & POST, 1954, emended

(Figs. 13J-U, 14A4, 18B-J)

1954 *Austrotrillina striata*; TODD & POST, p. 555, Pl. 198, fig. 9.
1955 *Austrotrillina brunni* sp.; MARIE, p. 203, Pl. 9, figs. 4-8.
1968 *Austrotrillina striata* TODD and POST; ADAMS, p. 92, Pl. 3, figs. 7-9; Pl. 4, figs. 1-13; Pl. 5, figs. 2-3, 6-8; Pl. 6, fig. 9.
1968 *Austrotrillina asmariensis* sp. nov.; ADAMS, p. 82, Pl. 1, figs. 1-12.

See the supplementary data in BASSI *et al.* (2021a) for a comprehensive synonymy list for *A. striata*, *A. asmariensis*, and *A. brunni*, which should be included here as synonymies of *A. striata*, excluding most references to specimens assigned to *A. paucialveolata*, which is here considered a valid species (GRIMSDALE, 1952, Pl. 20, figs. 7-10; SERRA-KIEL *et al.*, 2016, Figs. 14.8-12, 15.9-20; BOUDAGHER-FADEL, 2018, Pl. 6.9, figs. 15-17 and Pl. 6.10, figs. 1-2; and YAZDI-MOGHADAM *et al.*, 2018, Fig. 8H-I).

Type material: In the original description of *A. striata*, TODD and POST (1954) illustrated only a single specimen in external view from wells in Bikini Atoll. ADAMS (1968) studied topotypes and provided a detailed description. A topotype was also illustrated by BOUDAGHER-FADEL (2018, Pl. 7.1, fig. 6).

Emended diagnosis: An *Austrotrillina* species with simple (non-bifurcated) and regularly distributed alveoli.

Description: Growth biloculine, triloculine or quinqueloculine. Initial chambers without exoskeleton, later chambers with exoskeleton with beams and rafters and alveoli. The number of chambers without exoskeleton is variable, likely lower in stratigraphically upper populations. The diameter of alveoli is about 20-30 µm. The spacing and thickness of the walls between alveoli is variable, but two main morphotypes can be distinguished (Fig. 18A): an *asmariensis-type*, with thin alveolar walls and alveoli densely packed, and a *striata-type*, with thick alveolar walls and, therefore, more widely spaced alveoli. Different morphotypes can occur together in the same stratigraphic layer (Fig. 18I) or in the ontogeny of

a single specimen (*e.g.*, Fig. 18J, with asmariensis-type alveoli in the initial chambers and striata-type in the later ones). Subspherical proloculus with flexostyle. Diameter of the proloculus very variable, between 40 and 250 µm, with a general but irregular increase through time.

Remarks: In the definition of the species, TODD and POST (1954, p. 556) described the aperture of *A. striata* as "rather large, elongate, without a thickened rim or any internal tooth, but when the cribrate plate is absent, there appear to be numerous, small inward-projecting teeth from the outer border". These "teeth" likely correspond to elements of the exoskeleton exposed on a broken or abraded apertural face. The original interpretation of the type species as belonging to *Trillina*, within the group of "Miliolidées trematophorées" of MUNIER CHALMAS (PARR, 1942), probably contributed to the widespread assumption that the aperture of *Austrotrillina* is cribrate. In his description of the type species, *A. howchini*, SCHLUMBERGER (1893) described the aperture as being covered by a perforate plate. PARR (1942) re-examined the type material and concluded that SCHLUMBERGER's statement was a misinterpretation of the internal structures, although in his diagnosis of the new genus *Austrotrillina* he still noted the aperture as "doubtfully cribrate" (PARR, 1942, p. 361). The specimen illustrated in ADAMS (1968, Pl. 1, fig. 12) shows a narrow interiomarginal slit, consistent with the description by TODD and POST (1954). No evidence has been found in the literature for a cribrate aperture in any species of *Austrotrillina*.

Differential diagnosis: *A. eocaenica* and *A. paucialveolata* exhibit a different exoskeletal pattern, characterised by irregular and much wider alveoli. *Austrotrillina brunni* was inadequately defined, based solely on test size and rounded shape, with only five non-centred sections and no data on proloculus diameter. It has subsequently been interpreted subjectively by different authors, resulting in contradictory criteria (*e.g.*, proloculus diameter of 100-250 µm according to BASSI *et al.*, 2021a, or 60-100 µm according to SERRA-KIEL *et al.*, 2016). The alveolar pattern and the presence of occasional bifurcate alveoli in the type material (ADAMS, 1968) suggests that *A. brunni* represents an advanced (*i.e.*, stratigraphically higher) morphotype of *A. striata*, consistent with the occurrence of "*Miogypsina complanata*" at the type level (MARIE, 1955). *Austrotrillina howchini* differs in having a more complex, keriothecal-like exoskeleton with bifurcate alveoli (with one to three orders of bifurcation) and thicker chamber walls.

Austrotrillina howchini (SCHLUMBERGER, 1893)

(Fig. 14D-G)

1893 *Trillina howchini* SCHLUMB. n. sp.; SCHLUMBERGER, p. 119-120, Figs. 1-2, Pl. 3, fig. 6.
1942 *Austrotrillina howchini* (SCHLUMBERGER); PARR, p. 361, Fig. 1.
1968 *Austrotrillina howchini* (SCHLUMBERGER); ADAMS, p. 86, Pl. 2, figs. 1-7; Pl. 5, fig. 5; Pl. 6, figs. 1-5, 7.
1973 *Austrotrillina howchini* (SCHLUMBERGER); ADAMS & BELFORD, p. 13, Pl. 3, fig. 7.
1973 *Austrotrillina howchini* (SCHLUMBERGER); ADAMS, Pl. 2, fig. 5.
1973 *Austrotrillina howchini* (SCHLUMBERGER); BINNEKAMP, p. 9, Pl. 1, figs. 1-4.
1974 *Austrotrillina howchini* (SCHLUMBERGER); ADAMS & BELFORD, p. 487, Pl. 73, fig. 7.
1984 *Austrotrillina howchini* (SCHLUMBERGER); BELFORD, Pl. 6, fig. 19.
2013 *Austrotrillina howchini* (SCHLUMBERGER); AMIRSHAHKARAMI, Pl. 6, fig. 12; Pl. 8, figs. 5-6.
2014 *Austrotrillina howchini* (partim.); NOVAK, Fig. 2A, D-F.
2014 *Austrotrillina asmariensis* ADAMS; GEDIK, Pl. 4, fig. 1.
2015 *Austrotrillina asmariensis* ADAMS; GEDIK, Pl. 1, fig. 14.
2018 *Austrotrillina howchini* (SCHLUMBERGER); BOUDAGHER-FADEL, Pl. 7.1, figs. 1-3, 12.
2020 *Austrotrillina howchini* (SCHLUMBERGER); HAIG *et al.*, Fig. 8F-H.
2020 *Austrotrillina asmariensis* ADAMS; GEDIK, Fig. 14N.
2021a *Austrotrillina howchini* (SCHLUMBERGER); BASSI *et al.*, p. 12, Figs. 7-9.

Type material: SCHLUMBERGER (1893), Pl. 3, fig. 6.; PARR (1942), p. 361, Fig. 1.

Diagnosis: An *Austrotrillina* species with regularly bifurcated alveoli. The bifurcation can be absent in the first chambers, and can be simple or with different, up to three orders of bifurcation.

Remarks: *Austrotrillina howchini* is considered a valid species, characterised by the presence of regularly bifurcated of alveoli. In most specimens reported in the literature, alveoli are bifurcated once, forming two subalveoli, but two (*e.g.*, Fig. 1 in PARR, 1942) or up to three successive bifurcations (*e.g.*, Fig. 7 in BASSI *et al.*, 2021a) may occur in each alveolus, producing between one and four orders of alveoli and subalveoli.

According to BASSI *et al.* (2021a, 2024), *A. howchini* is a Miocene species, first appearing in the latest Aquitanian of Kenya, Tanzania, and Indonesia, and disappearing in the latest Langhian-early Serravallian in the central and northern Central Indo-Pacific. In material from the Prebetic, some specimens of *A. striata* from the middle-upper Chattian (uppermost SB 22B and lower SB 23) exhibit occasional bifurcated alveoli (Fig. 14B-C), although rare, sporadic bifurcate alveoli were also observed in specimens from the middle Rupelian (Fig. 14A). These specimens are interpreted as transitional forms leading to *A. howchini*. Some specimens from the FR section (from the first layers containing *Risananeiza pustulosa*, in the middle part of SB 23) already display regular alveolar bifurcation and can be assigned to *A. howchini* (Fig. 14D). *Austrotrillina howchini* was previously reported from the Betic Cordillera by

HOTTINGER (1963), although these specimens correspond to *A. paucialveolata* rather than *A. striata*, as stated by BASSI *et al.* (2021a). Fully developed *A. howchini* occurs elsewhere in the Prebetic, for example in the Serra de l'Ombria, Elda, 38 km SW Ibi (section under study; Fig. 14E-G).

ADAMS (1968) observed bifurcate alveoli in the peripheral chambers of the type material of *A. brunni* (originally illustrated by MARIE and re-illustrated by ADAMS, 1968, Pl. 6, figs. 6, 8). He interpreted this material as a "very probably transition form" between *A. striata* and *A. howchini*. The age of this material, from the Pentalofon Formation in Greece, has been variably interpreted as "Oligocène supérieur ou même Aquitanien basal" (MARIE, 1955), Lower Miocene (WIELAND-SCHUSTER, 2004), or upper Rupelian-Chattian (NP 24-NP25, see FERRIÈRE *et al.*, 2013). According to MARIE (in BRUNN *et al.*, 1955), this *Austrotrillina* is associated with *Miogypsina complanata*, indicating a late Chattian age (SB 23).

Subclass Textulariana MIKHALEVICH, 1980

Order Textulariida LANKESTER, 1885

Suborder Textulariina DELAGE & HÉROUARD, 1896

Superfamily Chrysalidinoidea NEAGU, 1968

Family Chrysalidinidae NEAGU, 1968

Genus *Pfendericonus* HOTTINGER & DROBNE, 1980

Type species: *Pfendericonus makarskae* (SOEST, 1942)

Pfendericonus globulus SIREL & DEVECILER, 2020, in SIREL *et al.*, 2020a

(Fig. 10A-L)

1962 *Valvulina* cf. *italica*; ESCANDELL & COLOM, Fig. 23.1-4.
1997 *Pfendericonus?* sp.; SIREL, p. 171, Pl. 4, figs. 1-5, 13.
2016a Valvulinid sp.; HABIBI, Pl. 2, fig. 13 ["12" in the figure caption].
2016b *Coskinolina* sp.; HABIBI, Pl. 2, fig. 9.
2020a *Pfendericonus globulus*; SIREL & DEVECILER in SIREL *et al.*, p. 12, Figs. 5B, 6E-F, 11A-J.

Description: The test shape is globular, usually lacking the final rectilinear uniserial stage found in other species of *Pfendericonus*, only observed in one specimen (Fig. 10K). The wall is thick and with pseudokeriothecal texture. The endoskeleton consists of few pillars in the central part, roughly aligned between adjacent chambers (Fig. 10G-H, L). The megalospheric form shows a bilocular embryo with a subspherical protoconch, followed by a second chamber of similar size. The protoconch, measured in three megalospheric specimens (Fig. 10A, J showed diameters of 123, 148 and 155 µm (mean = 143.3 µm), somewhat smaller than the values of 155-175 µm reported in Priabonian (SB 19-20) and Oligocene (SB 21) specimens by SIREL and DEVECILER (in SIREL *et al.*, 2020a). On the other hand, there is incoherence in the values of *P* reported from the Priabonian specimens, 250 µm in SIREL (1997) and 155-175 µm in SIREL *et al.* (2020a).

Distribution and age: *Pfendericonus globulus* occurs in the lower part of the Ibi section associated with *Austrotrillina paucialveolata*, *Idalina pignatii*, *Coscinospira elongata*, *C. sivasensis*, *Peneroplis evolutus*, *P. peramplus*, *Spirolinella emmae*, *Penarchaias glynnjonesi*, *Sivasina egribucakensis*, *Praerhapydionina delicata*, *Praebullalveolina minuta*, and *P. oligocenica*. This assemblage corresponds to the lower Rupelian (SB 21).

Remarks: The specimens from Ibi are morphologically similar to those reported by SIREL (1997) and SIREL *et al.* (2020a) from the Priabonian and lower Oligocene (SB 21) of southern Turkey, which SIREL and DEVECILER (in SIREL *et al.*, 2020a) assigned to a new species, *Pfendericonus globulus*. SCHLAGINTWEIT (2022) considered *P. globulus* a junior synonym of *P. mindanaoensis* MATSUMARU, from the Selandian of the Philippines. *Pfendericonus mindanaoensis* was defined based on only three non-centred sections (Pl. 4, figs. 8-9 in MATSUMARU, 2017), to which SCHLAGINTWEIT (2022) added two specimens previously reported by MATSUMARU as *Chrysalidina* sp., in which no endoskeleton is observable (Pl. 4, figs. 10-11 in MATSUMARU, 2017). The available data on *P. mindanaoensis* are insufficient to characterise the species, as key characters, such as proloculus diameter or dimorphism are unknown. In addition, its test is smaller and its architecture simpler than those of the Priabonian-Oligocene form. Based on these observations, *P. globulus* is considered a valid species, to which the Rupelian specimens from the Prebetic are assigned. One specimen from Ibi exhibits a smaller proloculus of 68 µm (Fig. 10G). Judging from the illustrations, one of the specimens shown in SIREL *et al.* (2020a, Fig. 11F) appears to have a similarly small proloculus. The specimens reported by ESCANDELL and COLOM (1962, Fig. 23.1-4) from the Rupelian of Mallorca as *Valvulina* cf. *italica* CUSHMAN likely belong to *P. globulus*. The occurrence of *P. globulus* from the Rupelian-early Chattian of south-western Iran, reported as "valvulinid sp. 1" (HABIBI, 2016a, Pl. 2, fig. 13) or as "*Coskinolina* sp." (HABIBI, 2016b, Pl. 2, fig. 9), needs confirmation.

The Priabonian and Rupelian specimens from Turkey (SIREL, 1997; SIREL *et al.*, 2020a), and particularly the Oligocene specimens of *P. globulus* from the Prebetic, are smaller, exhibit a shorter uniserial stage, and have a simpler structure (fewer pillars) than the lower-middle Eocene *P. makarskae* (SOEST, 1942; HOTTINGER & DROBNE, 1980; VECCHIO & HOTTINGER, 2007; KAYĞILI, 2016). SERRA-KIEL *et al.* (2016) reported occurrences of *Pfendericonus* from the Bartonian-Priabonian of Oman and Socotra. They assigned these specimens to *P.* aff. *makarskae*, considered a possible new species similar to *P. makarskae*, but distinguished by a larger test (up to 2.3 mm in diameter), thicker test wall, and fewer pillars. This form

also possesses a large protoconch, measuring 215-360 µm in diameter.

Subclass Rotaliana Mikhalevich, 1980

Order Rotaliida Lankester, 1885

Superfamily Calcarinoidea Schwager, 1876

Family Calcarinidae Orbigny, 1826

Subfamily Pararotaliinae Reiss, 1963

Genus *Neorotalia* Bermúdez, 1952

Type species: *Rotalia mexicana* Nuttall, 1928

Neorotalia burdigalensis (Orbigny, 1852)

(Fig. 8A-F)

1826 *Rotalia burdigalensis* n. sp.; Orbigny, p. 273, n 21, nom. nud.
1852 *Rotalia burdigalen*sis; Orbigny, p. 157; Fig. in Fornasini (1906), Pl. 3, fig. 1.
1886 *Rotalia lithothamnica* n. sp.; Uhlig, p. 195-196, Pl. 5, figs. 9-11.
1957 *Rotalia lithothamnica* Uhlig var. *schoragbjurensis* var. n.; Saakyan-Gezalyan, p. 51-52, Pl. 9, figs. 1-3
1967 *Rotalia viennoti*; Adams & Bourgeois, p. 32, Pl. 4, fig. 1.
1974 *Rotalia lithothamnica schoragbjurensis* Sahakyan-Gezalyan; Akopian, p. 306, Pl. 157, figs. 1-3.
?1993 *Pararotalia* sp.; Matsumaru *et al.*, p. 12, Fig. 2.5-6.
1998 *Neorotalia burdigalensis* (Orbigny); Poignant, p. 118, Pl. 1, figs. 18-19.
2003 *Neorotalia lithothamnica* Uhlig; Sirel, p. 304, Pl. 8, figs. 1-5.
2003 *Neorotalia pinarensis* (Cushman & Bermudez); Sirel, p. 304, Pl. 8, figs. 6-8.
2008 *Rotalia viennotti*; Rikhtehgarzadeh *et al.*, Pl. 1, fig. 5.
2009 *Pararotalia lithothamnica* (Uhlig); Bubík, Fig. 1S
2009 *Neorotalia viennoti* (Greig, 1935); Sadeghi *et al.*, Figs. 7.5, .8, 9.5?
2010 *Neorotalia viennotti* Greig, 1935 (partim.); Amirshahkarami & Taheri, Pl. 5, figs. 1-3, 6.
2011 *Neorotalia lithothamnica* (Uhlig); Yazdi-Moghadam, Pl. 1, figs. 9-10.
2013 *Neorotalia tethyana*, new species; Bou Dagher-Fadel & Price, p. 195, Fig. A1b-d, A2b.
2014 *Neorotalia* sp.; Karevan *et al.*, Fig. 6G
2016b *Neorotalia viennoti* (Greig); Habibi, Pl. 1, fig. 3
2018 *Neorotalia viennoti* (Greig); Habibi, p. 1294, Pl. 2, fig. 8; Pl. 4, figs. 8-9.
2018 *Neorotalia viennoti* (after Greig, 1935); Habibi & Bover-Arnal, Fig. 7f, j.
2018 *Neorotalia* sp.; Yazdi-Moghadam, Fig. 6A-C.

Description: Trochospiral test of lenticular shape; dorsal surface smooth or with low, flat piles; ventral side with a single, rarely compound, large, protruding knob; sometimes with small pustules or short, rounded spines on the periphery. Umbilical flap separating the main chamber lumen from an umbilical spiral canal, with axial ventral furrows around the umbilical plug.

Distribution and age*: Neorotalia burdigalensis* occurs throughout the Ibi and La Font Roja sections, spanning the Priabonian, Rupelian, and Chattian (Figs. 5-6).

Remarks*: Neorotalia burdigalensis* is a common species in the Oligocene and Lower Miocene of the Western and Central Tethys. Oligocene forms are frequently reported in the literature as "*N. viennoti*" or "*N. lithothamnica*" (*e.g.*, Sadeghi *et al.*, 2009; Amirshahkarami & Taheri, 2010; Yazdi-Moghadam, 2011; Habibi, 2016a, 2018; Ferràndez-Cañadell & Bover-Arnal, 2017; Habibi & Bover-Arnal, 2018) or assigned to other genera, such as *Pararotalia* (*e.g.*, Cahuzac & Poignant, 1987) or *Nummulites* (see Fig. 7 in Al Menoufy *et al.*, 2024). Following revision of the type material, *N. lithothamnica* was considered a junior synonym of *N. burdigalensis* by Poignant and Pujol (1978). This synonymy was later formally established by Poignant (1998), who revised the type material of *Rotalia burdigalensis* Orbigny and designated a lectotype. Her description of the material matches that of *N. lithothamnica* by Uligh (1886) and the morphological features of our material and differs from that of *N. viennoti*. *Neorotalia tethyana* (Bou Dagher-Fadel & Price, 2013) is also most likely a junior subjective synonym of *N. burdigalensis*.

In the sections studied, *Neorotalia* occurs in Eocene and Oligocene samples and is characterised by a trochospiral test with a smooth dorsal surface and a single large, protruding knob on the umbilical side, occasionally accompanied by small pustules or short rounded spines, mainly along the periphery. These features correspond to the description of "*N. lithothamnica*" by Uhlig (1886) as well as those of the Oligocene *R. lithothamnica* var. *schoragbjurensis* by Saakyan-Gezalyan (1957) and Akopian (1974) which are considered here as belonging to the same species, *N. burdigalensis*. In contrast, the test of *N. viennoti* is flatter and less trochospiral, entirely covered with small pustules on both dorsal and ventral sides and along the periphery, and the umbilical side bears several piles rather than the single large umbilical knob characteristic of *N. burdigalensis* (see Hottinger *et al.*, 1991; Hottinger, 2014). No specimens clearly assignable to a second *Neorotalia* species were observed in the examined samples from the Prebetic.

The biostratigraphic ranges reported for both "*N. lithothamnica*" and *N. viennoti* extend from the middle Eocene to the Middle Miocene (Greig, 1935; Reiss & Merling, 1958; Poignant & Pujol, 1976, 1978; Hottinger *et al.*, 1991; Cahuzac & Poignant, 1993, 1996, 1997; Bubík, 2009; Hottinger, 2014; Tomassetti *et al.*, 2016; Sztrakos *et al.*, 2017), despite the clearly different forms assigned to these species by different authors. The range of *N. burdigalensis* appears to extend from the late Eocene (Saakyan-Gezalyan, 1957; Sztrakos *et al.*, 2017) to the Burdigalian (Poignant, 1998). It is common in the Oligocene of Western and Central Tethys, but its geographic distribution may be wider, extending as far as Japan (see Fig. 2.5-6 in Matsumaru *et al.*, 1993), and potentially reaching the American bioprovince, as Poignant (1998) also regarded *R. mexicana* Nuttall as a junior synonym of *N. burdigalensis*.

Neorotalia burdigalensis occurs throughout the Ibi and FR sections, from the Priabonian to the upper Chattian, showing a general increase in test size together with a reduction in trochospirality (Fig. 8A-F). HOTTINGER (2014) noted that a taxonomic reassessment of Eocene-Miocene *Neorotalia* species could reveal potential biostratigraphic applications. A biometrical study of the megalospheric proloculus in specimens from the Ibi-La Font Roja succession, although based on a relatively small number of specimens from random sections, demonstrates a steady increase of *P* values, from 45-60 µm in Eocene specimens to 130-180 µm in upper Chattian specimens (Fig. 20, Table 3). Notably, a marked increase is observed between specimens from biozones SB 22B and 23, with *P* values rising from < 85 µm in the uppermost Rupelian specimens to ≥120 µm in the lowermost Chattian specimens. These observations suggest that proloculus diameter in *N. burdigalensis* may provide a useful criterion for identifying the Rupelian/Chattian boundary (Fig. 20).

SAAKYAN-GEZALYAN (1957; see also AKOPIAN, 1974) reported a rich assemblage of "*Rotalia*" from the late Eocene and Oligocene of Armenia, including "*R. lithothamnica*", in which two subspecies (varieties) were distinguished: the late Eocene "*R. lithothamnica lithothamnica*" and the Oligocene "*R. lithothamnica schoragbjurensis*". He also erected several new species, such as the late Eocene "*Rotalia denseornata*", similar to "*R. lithothamnica*" but with a rough ornamentation. These forms, described solely from external morphology, are likely attributable to *Neorotalia* and may represent ecophenotypes of *N. burdigalensis*. The description by ULIGH (1886) was based on Eocene material from the Polish Carpathians and also included the new species "*Heterostegina carpatica*", now accepted as *Spiroclypeus carpaticus*, which characterises SB 20, late Priabonian (LESS & ÖZCAN, 2008). POIGNANT (1998) noted that *R. burdigalensis* is more common in the Oligocene than in the Miocene. However, according to SZCZECHURA and POŻARYSKA (1974, p. 65), the lineage may extend back to the Paleocene, with small forms that "easily fall into the limits of variability of *Rotalia lithothamnica*" and "seem to be morphologically transitional between typical representatives of *R. lithothamnica* UHLIG and their presumable ancestors, *Pararotalia tuberculifera* (REUSS, 1862)". Many reports of these forms are based solely on external morphology. Examination of internal characters, such as the canal system and proloculus diameter, would provide additional criteria to confirm the generic assignment, better characterise species, and potentially reveal biostratigraphic value within this group.

Table 3: Measurements of the equatorial diameter of protoconch (*P*) in *Neorotalia burdigalensis* (ORBIGNY) along the composite stratigraphic section of Ibi-La Font Roja. (See plot in Fig. 20).

Section	Sample	meter in the composed section	*P* (µm)
FR	FR-96	395	180.7
	FR-95	392.4	159.6
	FR-95	392.4	150.8
	FR-9	372	146.8
		372	147.5
	FR-84	348	155.1
	FR-7	336.3	138
	FR-77	328	144.4
		328	142.2
		328	163.3
		328	154
	FR-6	320	179
	FR-74	302.5	130
	FR-4	296	177
	FR-70	290.5	133.7
	FR-65	265	154
Ibi	Ibi-10	238	128.3
	Ibi-20	236	119.8
	Ibi-9	236	126
	SA-63	188	103.7
	SA-63	188	108
	SA-58	156	79.6
	MN-22 b	114	73.8
	MN-9	84.5	72.7
	Ibi-127	80	82.3
	MN-2	71	58.8
	Ibi-104	12	60
		12	44.3
	Ibi-102	6	46.5
		6	52.4
	Ibi-101 b	5	53.5

Subclass Rotaliana MIKHALEVICH, 1980
Order Rotaliida LANKESTER, 1885
Superfamily Calcarinoidea SCHWAGER, 1876
Family Calcarinidae ORBIGNY, 1826
Subfamily Pararotaliinae REISS, 1963
Genus *Risananeiza* BOUKHARY *et al.*, 2008

Type species: *Risananeiza pustulosa* BOUKHARY *et al.*, 2008

Risananeiza is a marker for the upper Chattian, SB 23 (see BOUKHARY *et al.*, 2008; BENEDETTI & BRIGUGLIO, 2012, and FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017, for further descriptions of the genus). It has been reported from Egypt (BOUKHARY *et al.*, 2008), Italy (RENZ, 1936; BASSI *et al.*, 2007; BENEDETTI & BRIGUGLIO, 2012; BRANDANO *et al.*, 2009; MARINO *et al.*, 2022), Turkey (SANCAY *et al.*, 2006; IŞIK, 2010; IŞIK & HAKYEMEZ, 2011; SIREL & IŞIK, 2011; GEDIK, 2020), southern and

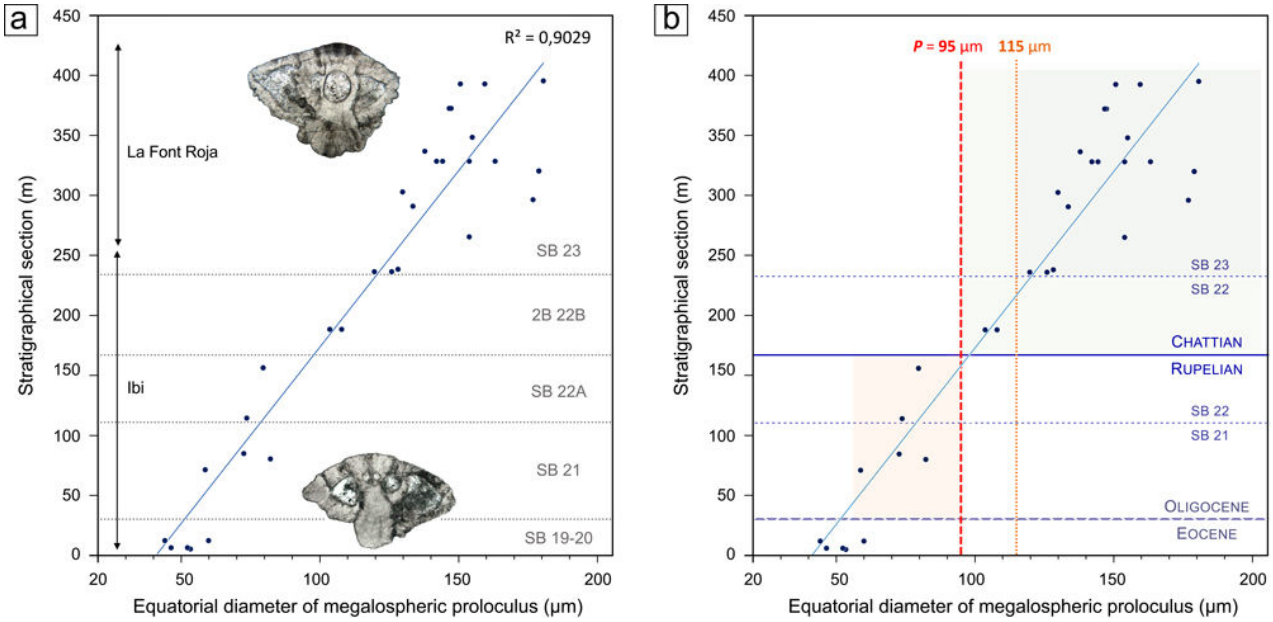


Figure 20: Plot of megalospheric proloculus diameter (*P*) in *Neorotalia burdigalensis* (ORBIGNY) along about 400 m of the composite stratigraphic successions of Ibi and Font Roja. **A)** Note the steady and progressive increase (R^2 = 0.9) in *P*, from the upper Eocene to the upper Chattian, without a noticeable shift between the basal Chattian of the Ibi section and the early Chattian of the La Font Roja section. **B)** The diameter of the proloculus could possibly be used to identify the Rupelian/Chattian (SB 22A/22B) boundary (red line of P = 95 µm) and the lower/upper Chattian (SB 22B/23) boundary (orange line of P = 115 µm). Measurements were made on thin section specimens; see data in Table 3. Illustrated specimens from samples Ibi-102, Priabonian (bottom), and FR-4, upper Chattian (above).

south-eastern Spain (DIDON *et al.*, 1961; FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017; BOLÍVAR FERICHE, 2022; GRANERO *et al.*, 2022), and Iran (RAHAGHI, 1980; DANESHIAN & HOSSEINZADEH, 2010; MAGHFOURI MOGHADAM *et al.*, 2014; SADR, 2017; HOLAKOUEE *et al.*, 2018; SARFI & YAZDI-MOGHADAM, 2024), and often assigned to other genera such as *Neorotalia*, *Pararotalia*, *Rotalia*, or *Bozorgniella*. The report of *R. crassaparies* and *R. pustulosa* from Kurdistan (north-eastern Iraq) by GHAFOR and AHMAD (2019) requires confirmation. The figured specimen (GHAFOR & AHMAD, 2019, Fig. 7g) appears to be a peneroplid, whereas the specimens reported as *Miogypsinoides* sp. in GHAFOR and AHMAD (2021, Pl. 2, figs. f-g) are likely *Risananeiza.*

Two species of *Risananeiza* are currently recognised: *R. pustulosa*, the type species (BOUKHARY *et al.*, 2008), and *R. crassaparies* (BENEDETTI & BRIGUGLIO, 2012). They are primarily distinguished based on the diameter of the megalospheric proloculus and the size of the test, including micro- and megalospheric forms. The ranges of *P* values for the two species largely overlap. The diameter of the proloculus was defined as 90-225 µm for *R. crassaparies* (N = 12, mean = 159 µm, holotype = 173 µm; BENEDETTI & BRIGUGLIO, 2012), and 150-250 µm for *R. pustulosa* (BOUKHARY *et al.*, 2008). The later was extended to 140-286 µm after IŞIK (2010) and FERRÀNDEZ-CAÑADELL and BOVER-ARNAL (2017). The overlapping range of *P* is therefore 140-225 µm. Similarly, the ranges of the megalospheric test diameters overlap, with *R. crassaparies* measuring 1.10-1.81 mm (BENEDETTI & BRIGUGLIO 2012), which falls within the range of 0.925-2.9 mm documented for *R. pustulosa* (BOUKHARY *et al.*, 2008).

All previous studies of the genus reported only one of the two species, both considered to be late Chattian (SB 23) in age. Based on a revision of the microfacies from which the two species have been reported, BENEDETTI *et al.* (2025) concluded that they possibly represent two different eco-morphotypes: *R. pustulosa*, inhabiting the innermost to uppermost middle ramp, and *R. crassaparies* the high-energy zones of the inner and middle ramp.

Together, the two Prebetic sections studied here recorded a long succession of upper Chattian age, with the lower boundary (SB 22B/23) and 12 m of the basal upper Chattian outcrop exposed at the Ibi section, and a continuous 250 m-thick succession at the FR section. Most samples in this succession bear *Risananeiza* tests, which allows the examination of biometrical and morphological trends. A steady increase in *P* values is observed throughout the succession (Fig. 20). Specimens from the Ibi section and the lower part of the FR section fall within the variability of *R. crassaparies*. In the remaining specimens, from the middle and upper parts of the FR section, the minimum *P* values correspond well with those diagnostic for *R. pustulosa*, whereas the maximum values greatly exceed both the 250 µm maximum reported in the original description and the 286 µm maximum reported from the Prebetic in a previous work (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017),

with two specimens reaching proloculus diameters of 318 and 320 µm (Fig. 15O, Q; Table 4).

The data (Fig. 20) indicate a gradual increase in test and proloculus size of *Risananeiza* throughout the upper Chattian, with the early stages corresponding to *R. crassaparies* and the middle-upper stages to *R. pustulosa.* In other words, the two species defined so far actually correspond to different, partial intervals of an *anagenetic species* (in the original sense, *i.e.*, a species evolving gradually, not in the sense commonly used in island biogeography studies, see EMERSON & PATIÑO, 2018a, 2018b). The biometrical boundaries used to define the two species are, therefore, contingent, reflecting only the partial interval of gradual evolution recorded in each study. Although a third species could be defined for specimens with maximum *P* values between 250 and 320 µm, this is not considered necessary or useful. Instead, the diagnosis of the genus and of *R. pustulosa* is emended to include these larger specimens.

Table 4: Measurements of the equatorial diameter of protoconch (*P*) in *Risananeiza* from the Ibi and La Font Roja sections. (See plot in Fig. 21).

Section	Sample	meter in section	*P* (µm)	Mean
FR	FR-17	237	200	–
	FR-23	234	218	–
	FR-20	225	203	–
	FR-15	223	187, 217, 246, 240, 249, 306, 233	239.7
	FR-106	182	198	–
	FR-13	178	237	–
	FR-105	176.5	168, 172, 180, 212, 219, 221, 224, 248, 252, 250	214.6
	FR-104	172.5	156	–
	FR-103	167	226, 253, 259	246.0
	FR-101	163.5	184, 238	211.0
	FR-12	162.5	192	–
	FR-98	149.8	266	–
	FR-96	145	200	–
	FR-87	106.5	178	–
	FR-72	44	167, 195	181.0
	FR-71	42.6	139	–
	FR-70	40.5	128	–
	FR-69	39	181	–
	FR-67	33	174	–
	FR-66	26	152	–
	FR-65	15	162	–
	FR-62	5.5	181	–
IBI	Ibi-15	241.5	84	–
	AA-3	238	153	–
	Ibi-9	236	133	–

Genus *Risananeiza* BOUKHARY *et al.*, 2008, emended

Type species*: Risananeiza pustulosa* BOUKHARY *et al.*, 2008

Emended diagnosis: Test lenticular, planispiral to very low trochospiral, wall calcareous hyaline, with numerous large piles on both sides and heavily granulated lateral surfaces. Dimorphism is pronounced. Chambers higher than wide; sutures strongly incised. Aperture interiomarginal, triangular in shape (Pl. 1, fig. 11 in BOUKHARY *et al.*, 2008). Canal system consisting of intraseptal canals with marginal sutural canals at the lateral walls of the interlocular space, spiral interlocular canals, and axial funnels between the piles in both dorsal and ventral sides; cover plate in the chamber of last whorl (BENEDETTI & BRIGUGLIO, 2012; IŞIK, 2010; SIREL & IŞIK, 2011). Megalospheric proloculus of paraboloid shape, elongated along axial direction, subcircular in equatorial section and elliptical in axial section, with an elongation index (axial diameter/equatorial diameter) of around 1.2.

Remarks: The genus *Risananeiza* was established by BOUKHARY *et al.* (2008) and placed in the Superfamily Rotaliaceae (a synonym of Rotalioidea). It was later assigned to the family Rotaliidae (BENEDETTI & BRIGUGLIO, 2012) and subsequently to the Ornatorotaliidae (BENEDETTI, 2015; BENEDETTI *et al.*, 2025), and within the subfamilies Cuvillierininae (BENEDETTI, 2015) and Pararotaliinae (HAYWARD *et al.*, 2021, in BENEDETTI *et al.*, 2025). According to BENEDETTI *et al.* (2025) the family Ornatorotaliidae, including *Risananeiza*, *Ornatorotalia*, and *Granorotalia*, should be maintained, differing from Pararotaliinae by the presence of open dorsal canals.

The two known species, *R. pustulosa* and *R. crassaparies*, are actually chronosubspecies, each corresponding to a contingent, biometrically defined, partial range within a continuous gradual (anagenetic) increase throughout the late Chattian. They could be formally treated as subspecies, *R. pustulosa pustulosa* and *R. pustulosa crassaparies*, as is done for other anagenetic species, such as in orthophragminae (LESS, 1987) or *Heterostegina* (HERB, 1978; LESS *et al.*, 2008). A third, stratigraphically higher and larger subspecies could also be defined for specimens with maximum *P* values > 250 µm. However, such a classification would introduce unnecessary terminological complexity, and, given the limited occurrences of these forms, could be difficult to apply to specimens outside the Prebetic domain. For these reasons, the two species are maintained, with the understanding that they correspond to arbitrarily defined evolutionary stages of an anagenetic series. The diagnosis of *R. pustulosa* is emended below to include the specimens from the FR section with large proloculi exceeding the range given in previous works (BOUKHARY *et al.*, 2008; FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017), whereas the diagnosis of *R. crassaparies* is retained as originally established (BENEDETTI & BRIGUGLIO, 2012). The two species are thus redefined as follows:

- *Risananeiza crassaparies*: *P* between 90 and 225 µm
- *Risananeiza pustulosa: P* between 150 and 320 µm

Other features, such as the test size and shape of megalospheric and microspheric forms, do not appear to be useful for characterizing or differentiating the two species. The maximum diameter of the microspheric form observed in *R. crassaparies*

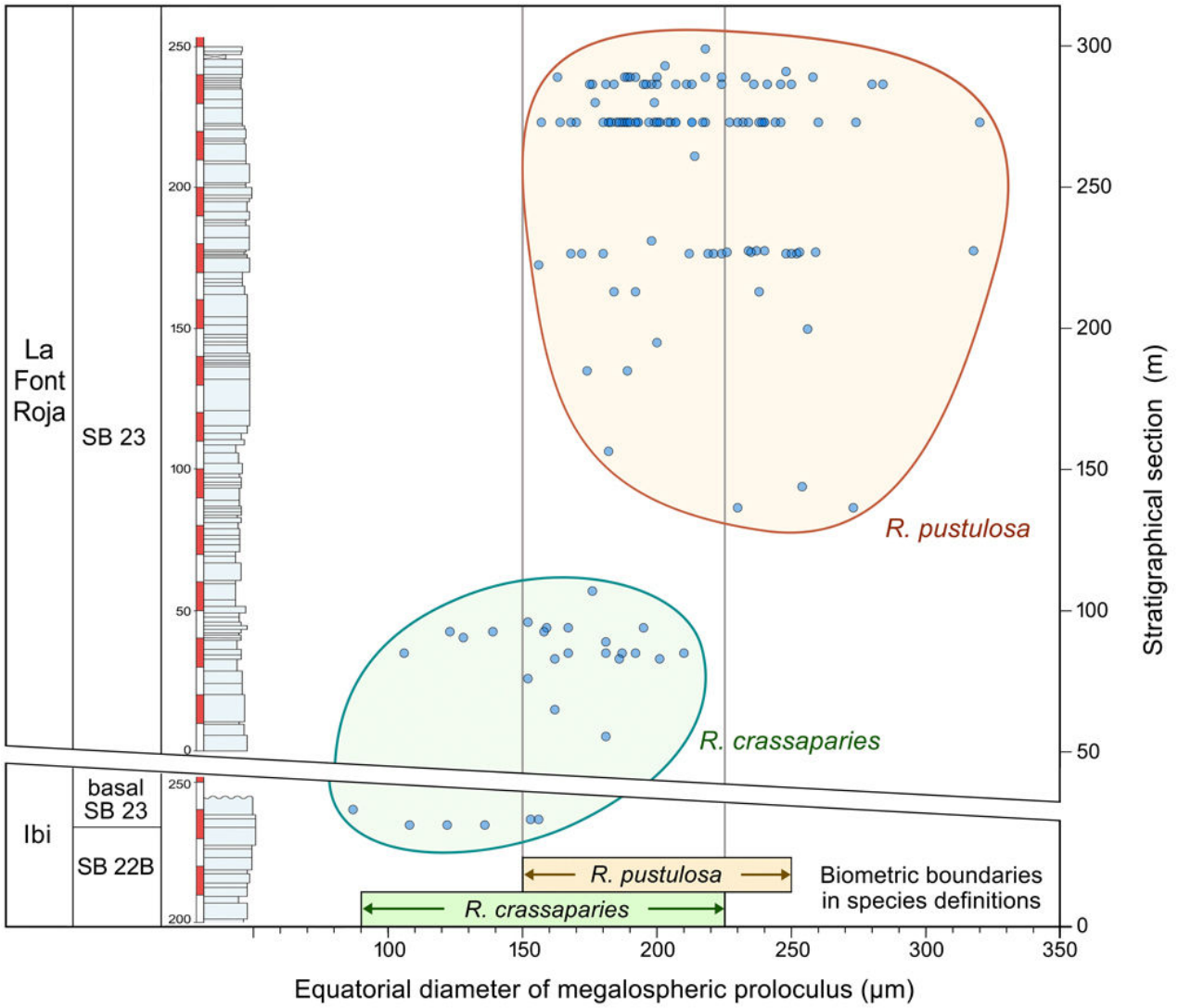


Figure 21: Plot of megalospheric proloculus diameter in upper Chattian *Risananeiza* along ~300 m of the stratigraphic sections of Ibi (uppermost part) and La Font Roja. The biometrical limits of the two known species of *Risananeiza* are shown at the bottom of the figure: 90-225 µm for *R. crassaparies* (BENEDETTI & BRIGUGLIO, 2012), and 150-250 µm for *R. pustulosa* (BOUKHARY *et al.*, 2008). A steady increase in proloculus diameter is observed from the basal upper Chattian (basal SB 23) to the upper Chattian (upper SB 23), excluding the uppermost Chattian. Specimens from the lower interval fall within the range of *R. crassaparies* BENEDETTI & BRIGUGLIO, whereas those from the upper part correspond to *R. pustulosa* BOUKHARY *et al.*. Measurements were made on thin section specimens; see data in Table 4.

is 3.82 mm (BENEDETTI & BRIGUGLIO, 2012), smaller than the average diameter of that in *R. pustulosa* of about 5.375 mm (BOUKHARY *et al.*, 2008). In the material from the Prebetic, the largest observed test, including a few microspheric forms of *R. pustulosa*, measured 3.67 mm (Fig. 15R). Test shape, including thickness/diameter ratio, protrusion of piles and pustules, and axial shape of chambers, are highly variable, and no significant differences were observed between the two species.

According to data from the Ibi and FR sections and data from the literature, it can be concluded that *R. crassaparies* occurs in the lower part of SB 23, whereas *R. pustulosa* (with a *P* range extended up to 320 µm) occurs in the upper part (Fig. 21). The biometrics of *Risananeiza*, thus, allow subdivision of the upper Chattian into two biozones, SB 23A and SB 23B (see below).

Risananeiza crassaparies BENEDETTI & BRIGUGLIO, 2012

(Fig. 15A-J)

2010 *Risananeiza postulosa* BOUKHARY, KUSS & ABDELRAOUF; IŞIK, p. 74-76, Pl. 7, figs. 1-16; Pl. 8, figs. 1-20.
2012 *Risananeiza crassaparies* n. sp.; BENEDETTI & BRIGUGLIO, Figs. 3 a-g, 4 a-e, Pl. 1, figs. 1-13; Pl. 2, figs. 1-15.
2017 *Rotalia* sp.; SADR, Pl. 6, fig. 6.
2020 *Risananeiza crassaparies* BENEDETTI & BRIGUGLIO, 2012; GEDIK, p. 393, Fig. 9 A-G.
2023c *Risananeiza postulosa* BOUKHARY, KUSS & ABDELRAOUF (partim.); YAZDI-MOGHADAM *et al.*, Fig. 11 F-H.
2024 *Risananeiza pustulosa* BOUKHARY, KUSS & ABDELRAOUF; SARFI & YAZDI-MOGHADAM, Fig. 7 I-J.

Type material*:* Holotype (MPUR NS161.1; Fig 3 a-g), and 38 paratypes (9 microspheric and 29 megalospheric specimens, MPUR NS161.2-38; Fig. 4 a-e, Pl. 1, figs. 1-13), deposited in the micropaleontological collection of the Museo di Paleontologia, Dipartimento di Scienze della Terra, Università di Roma 'La Sapienza' (BENEDETTI & BRIGUGLIO, 2012).

Diagnosis: A small species of *Risananeiza* with *P* values between 90 and 225 µm. Microspheric test up to 3.82 mm in diameter (BENEDETTI & BRIGUGLIO, 2012). Megalospheric test up to 2.38 mm.

Remarks: BENEDETTI and BRIGUGLIO (2012) reported the largest megalospheric test diameter as 1.81 mm. However, a few megalospheric specimens from the FR section (samples FR-68 to FR-75) exceeded 2 mm in diameter, with the largest specimen reaching 2.38 mm. The specimens reported as "*R. postulosa*" by IŞIK (2010) show *P* values of 140-220 µm, which fall within the 90-225 µm range of *R. crassaparies*.

The megalospheric specimens assigned to *R. pustulosa* figured in YAZDI-MOGHADAM (2023c, Fig. 11F-H; the first two reproduced in SARFI & YAZDI-MOGHADAM, 2024, Fig. 7I-J) exhibit test diameters of *c*. 1.52, 1.98, and 1.46 mm, with proloculus diameters of 162, 184, and 145 µm, respectively. Based on their relatively small test sizes and the associated miogypsinid species (*M. complanata* and *M. formosensis*), which are characteristic of the lower part of SB 23 (see below), these specimens most likely correspond to *R. crassaparies*. An axial section of *Risananeiza crassaparies* (with *P* about 120 µm) from the top of the Castro Limestone (Salento, southern Italy) was illustrated as "*Neorotalia*" in POMAR *et al.* (2014, Fig. 2c bottom left).

Risananeiza pustulosa
BOUKHARY *et al.*, 2008, emended

(Fig. 15K-S)

1980 *Rotalia viennoti* GREIG; RAHAGHI, Pl. 8, figs. 1(?), 2.
2008 *Risananeiza pustulosa* n. sp.; BOUKHARY, KUSS & ABDELRAOUF, p. 184-186, Pl. 1, figs. 1-18.
2011 *Risananeiza pustulosa* BOUKHARY, KUSS & ABDELRAOUF; SIREL & IŞIK, p. 40-42, Pl. 3, figs. 1-15; Pl. 4, figs. 1-19.
2017 *Risananeiza pustulosa* BOUKHARY, KUSS & ABDELRAOUF; FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, p. 102, Figs. 3J, 14A-N.
2017 *Neorotalia viennoti* (GREIG, 1935); LE COZE in HAYWARD *et al.*, WoRMS Photogallery, album 772, pics 119136, 119137.
2023c *Risananeiza postulosa* BOUKHARY, KUSS & ABDELRAOUF (partim.); YAZDI-MOGHADAM *et al.*, Fig. 11I.

Type material*:* Holotype (Pl. 1, fig. 8) and 40 paratypes (3 microspheric and 47 megalospheric specimens) in 47 thin sections plus 37 additional thin sections deposited at the Geochronology group of the University of Bremen (Germany) and at the stratigraphy group of Ain Shams University Cairo, Egypt (BOUKHARY *et al.*, 2008).

Emended diagnosis: A large species of *Risananeiza* with *P* values between 150 and 320 µm. Microspheric test initially low trochospiral changing to very low trochospiral or planispiral, up to 5.37 mm in diameter (BOUKHARY *et al.*, 2008). Megalospheric test very low trochospiral to planispiral, up to 3 mm in diameter.

Remarks: In the original description by BOUKHARY *et al.* (2008), the protoconch size of *R. pustulosa* was set between 150 and 225 µm. Specimens with larger proloculus diameters, up to 286 µm, were reported by FERRÀNDEZ-CAÑADELL and BOVER-ARNAL (2017). The specimens from the FR section described here show even larger protoconch diameters, reaching up to 320 µm (Fig. 15O, Q; Table 4), whereas still maintaining minimum *P* values above 150 µm. The largest microspheric specimen observed in this section measures 3.67 mm.

The specimens from Iran identified as "*Rotalia viennoti*" by RAHAGHI (1980, Pl. 8, figs. 1-2) show *P* values (measured from the photographs) of *c*. 166 and 276 µm, which correspond to *R. pustulosa*. The specimen with a smaller proloculus could also belong to *R. crassaparies*; RAHAGI did not provide the precise stratigraphical position of the specimens. He reported the species as being associated either with *Spiroclypeus* or "*Miogypsinoides complanatus*" (RAHAGHI, 1980, p. 19 and p. 42, respectively). The specimen illustrated in SADR (2017, Pl. 6, fig. 6) from the Chattian of Central Iran (Qom Formation) clearly belongs to *Risananeiza*, most likely *R. crassaparies* (*P*≈140 µm, measured from the photograph). As noted above, the specimens reported by IŞIK (2010) as "*R. postulosa*", as well as those illustrated as *R. pustulosa* by SARFI and YAZDI-MOGHADAM (2024) and by YAZDI-MOGHADAM *et al.* (2023c, Fig. 11F-H), are likely *R. crassaparies.* However, the megalospheric specimen in Fig. 11I in YAZDI-MOGHADAM (2023c) has a proloculus diameter of *c*. 264 µm, which is consistent with *R. pustulosa*.

7. Discussion

Biostratigraphy

Larger Foraminifera are a useful tool in Paleogene biostratigraphy. Their high abundance and taxonomic diversity during this period, particularly from the late Paleocene to the middle Eocene, enabled the development of a precise biozonation for sedimentary rocks, initially based on *Alveolina* and *Nummulites* species (HOTTINGER *et al.*, 1964; SCHAUB, 1981). Additional groups were incorporated later, such as orthophragmines (LESS, 1987). The synthesis of these biozonations, complemented by other genera, calibrated with planktic foraminiferal and calcareous nannoplankton biozones, as well as with magnetostratigraphy, resulted in the Shallow Benthic (SB) biozonation for the Paleocene-Eocene interval (SERRA-KIEL *et al.*, 1998a, 1998b) and the Oligocene (CAHUZAC &

POIGNANT, 1997, 1998). The SB biozonation has since been continually refined (see PAPAZZONI *et al.*, 2017; PIGNATTI and PAPAZZONI, 2017). However, whereas the SB biozones (often referred to as "SBZ") provide high temporal resolution for the Thanetian-Bartonian interval, those defined for the upper Paleogene are less precise due to the progressive decline in larger foraminiferal diversity (*e.g.*, HOTTINGER, 1998; BOUDAGHER-FADEL, 2018). Some stratigraphic boundaries, such as the middle-upper Priabonian (SB 19-20), are biostratigraphically defined by very few species. Furthermore, key stage boundaries, including the Bartonian-Priabonian and Rupelian-Chattian, are difficult to identify based solely on larger foraminiferal assemblages and are currently placed between sub-biozones SB 18A/18B and SB 22A/22B, respectively. The results of this study increase the number of known taxa in Priabonian and Oligocene assemblages of the Western Tethys and contribute to a more accurate characterization of the Oligocene biozones SB 21-23, as well as improved correlations between palaeobioprovinces.

The Priabonian-Oligocene larger foraminiferal assemblages from the Prebetic include several species not known from other parts of the Western Tethys. Among the porcellaneous forms, a rich assemblage was previously reported from the lower Rupelian (FERRÀNDEZ-CAÑADELL, 2024), including two new species, *Spirolinella emmae* and *Peneroplis peramplus*, which have so far been described only from the Prebetic, and are interpreted as endemic to the region. We report for the first time the occurrence of *Neorhipidionina* cf. *spiralis* in the Priabonian; *Pfendericonus globulus* in the Rupelian; *Idalina pignatti* in the Rupelian-lower Chattian; and *Austrotrillina howchini* and *Archaias* sp. in the upper Chattian of the westernmost Tethys. The latter is rather scarce and could not be identified to species level. Among the hyaline species, the miogypsinids are assigned to the genera *Miogypsinella* and *Postmiogypsinella*. The co-occurrence of the two known species of *Risananeiza*, *R. crassaparies* and *R. pustulosa*, within the same section is documented for the first time, enabling a revision and reinterpretation of the genus. Among the nummulitids, the presence of *N. vascus* and *N. kecskemetii* in the upper Chattian (SB 23) of the Prebetic, previously reported by FERRÀNDEZ-CAÑADELL and BOVER-ARNAL (2017), is confirmed. The oldest documented occurrence of *Elphidium crispum*, previously placed in the Burdigalian (SB 25) of Central Iran, is here reassigned to the upper Chattian (SB 23) in the Ibi section. The lepidocyclinids (*Nephrolepidina* and *Eulepidina*), widely used in Oligocene biostratigraphy, could not be studied in detail owing to the lack of loose specimens required for statistically meaningful biometric analyses. Nonetheless, a few species could be tentatively identified (*Nephrolepidina* cf. *morgani*, *Eulepidina* cf. *formosoides*).

The revision of the foraminiferal assemblages from the Ibi and FR sections allowed us to revise the age of the stratigraphic succession. MARTÍN-MARTÍN *et al.* (2025) and MICLĂUȘ *et al.* (2025) interpreted the uppermost Eocene layers of the Ibi section as Lutetian in age (SB 13 or 14). In fact, these layers correspond to the Priabonian, as previously interpreted by GEEL (2000). HÖNTZSCH *et al.* (2013) interpreted the Ibi section as spanning from the middle Eocene to the middle Oligocene, whereas Geel initially dated the uppermost limestones as Burdigalian (GEEL, 1995) and later reassigned them to the middle Oligocene (GEEL, 2000). Here, we demonstrate that the upper part of the Ibi section encompasses the entire Rupelian, the lower Chattian, and part of the upper Chattian. A summary and discussion of the updated foraminiferal assemblages is provided below.

Upper Eocene (Priabonian)

The upper Eocene (Priabonian) is recognised by the occurrence of *Nummulites fabianii*, which, in the Western Tethys (Mediterranean Region and Turkey), indicates a Priabonian to early Rupelian age, SB 19-21 (*e.g.*, ÖZCAN *et al.*, 2010a, 2010b, 2019; LESS *et al.*, 2011), and by *Borelis vonderschmitti*, which is restricted to the Priabonian. Previous reports of *B. vonderschmitti* from the upper Bartonian were based on its association with *Nummulites* species then considered Bartonian (SB 18 in SERRA-KIEL *et al.*, 1998a), such as *N. biedai* (*e.g.*, BASSI & LORIGA BROGLIO, 1999), but these taxa are now interpreted as lowermost Priabonian, SB 18B-C (*e.g.*, YÜCEL *et al.*, 2020, and references therein). These two species, *N. fabianii* and *B. vonderschmitti*, occur together with other Eocene taxa which, although characteristic components of Priabonian assemblages, have longer biostratigraphic ranges extending back to the Bartonian. These include *Nummulites* cf. *incrassatus*, *Orbitolites* cf. *cotentinensis*, *Neorhipidionina* cf. *spiralis*, *Acervulina linearis*, *Asterigerina rotula*, *Fabiania cassis*, *Chapmanina gassinensis*, *Gyroidinella magna*, *Schlosserina asterites*, *Silvestriella tetraedra*, *Neorotalia burdigalensis*, and *Rotorbinella* cf. *epardi* (*e.g.*, HOTTINGER *et al.*, 1964; HOTTINGER, 1974; DROBNE *et al.*, 1985; BASSI & LORIGA BROGLIO, 1999; SIREL, 2003; ÖZCAN *et al.*, 2010a; LESS & ÖZCAN, 2012; SIREL, 2015; SERRA-KIEL *et al.*, 2016; AKBAR-BASKALAYEH *et al.*, 2020; SIREL *et al.*, 2020a; FERRÀNDEZ-CAÑADELL *et al.*, 2023b; ZAKREVSKAYA, 2023).

We found no reliable criteria to discriminate between SB 19 and 20, which are currently based mainly on species and subspecies of *Heterostegina* (LESS *et al.*, 2008, 2011), *Spiroclypeus* (LESS & ÖZCAN, 2008; ZAKREVSKAYA *et al.*, 2020), and *Virgasterocyclina* (FERRÀNDEZ-CAÑADELL *et al.*, 2023b).

According to the regional study by GEEL (1995, 2000), uplift following the deposition of the upper Eocene carbonates produced angular unconformities, erosional surfaces, and localised karstification. Geel identified eight sedimentary cycles (E1 to E8) in the Eocene series of the region, includ-

ing the Ibi section. He interpreted the upper cycles, E6 to E8, as upper Eocene (post-extinction of *Alveolina* and *Assilina*), with the last cycle (E8), a very thin unit, representing "an abortive one of fossiliferous limestones on top of a hardground" (GEEL, 2000, p. 222). We did not identify the hardground reported by GEEL (2000). The uppermost Eocene in the Ibi section is considerably reworked, indicating a stratigraphic discontinuity. Given our limited data, the SB biozone cannot be discriminated with confidence, and it is likely that part of the Priabonian record was removed by erosion. However, based on both our observations and the interpretations of GEEL (2000), the major stratigraphic gap proposed by MARTÍN-MARTÍN *et al.* (2025) and MICLĂUȘ *et al.* (2025), spanning the early Lutetian to the Rupelian, would be restricted to only a portion of the Priabonian.

Lower Rupelian

The lower Rupelian (SB 21) is currently characterised by the occurrence of *Nummulites* (*N. fichteli*, *N. vascus*) in the absence of lepidocyclinids. In the Prebetic, SB 21 is marked by a small number of hyaline species (*N. fichtelli*, *N. vascus*, *Halkyardia minima*, *Neorotalia burdigalensis*) and a rich assemblage of porcellaneous species, some of which (*Praebullalveolina minuta*, *P. oligocenica*, *Austrotrillina paucialveolata*) are restricted to this biozone (BARBIN *et al.*, 1997; SIREL *et al.*, 2013). The porcellaneous assemblage closely matches that of the Central Tethys (Turkey, Oman, Iraq, Iran), except for *Spirolinella emmae* and *Peneroplis peramplus*, which are regarded as endemic to the Prebetic (FERRÀNDEZ-CAÑADELL, 2024). *Peneroplis flabelliformis* occurs in SB 21-22 in Turkey (SIREL *et al.*, 2013; SIREL, 2015). The presence of *Peneroplis evolutus* and *P. thomasi* in the lower Rupelian has been reported from Turkey and Iran (YAZDI-MOGHADAM, 2011; SIREL, 2015; YAZDI-MOGHADAM *et al.*, 2023a), with a biostratigraphic range extending into the lower Burdigalian (SB 25; YAZDI-MOGHADAM *et al.*, 2021, 2023b, 2025).

Two species, *Idalina pignattii* and *Pfendericonus globulus*, are reported here for the first time from the Western Tethys. The earliest occurrence of *Schlumbergerina alveoliniformis*, previously placed in the late Chattian (SB 23; FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017), is revised downward to the lower Rupelian (SB 21; sample Ibi-120, Ibi section). *Austrotrillina paucialveolata* is a characteristic species of SB 21 in the Prebetic.

Upper Rupelian-lower Chattian

The first occurrence of *Nephrolepidina* and *Eulepidina* is considered to mark the base of SB 22A, upper Rupelian (CAHUZAC & POIGNANT, 1997, 1998). In the Ibi section, the first occurrence of both genera (*Nephrolepidina* sp., *Eulepidina* cf. *formosoides*) coincides with the FO of *Amphistegina bohdanowiczi*, *Borelis inflata*, *Borelis* sp. 1, *Sorites*, and with the replacement of *Austrotrillina paucialveolata* by *A. striata* (Fig. 5). The Rupelian/Chattian boundary corresponds to a major sea-level fall (TA/TB supercycle boundary of HAQ *et al.*, 1987, 1988; Ch1 Megacycle in GRADSTEIN *et al.*, 2020) associated with the Oligocene Glacial Maximum (SIMAEYS, 2004). The boundary has been formally defined based on planktic Foraminifera and calcareous nannofossils (COCCIONI *et al.*, 2018), but it is still not clearly resolved using larger foraminiferal biostratigraphy (SB 22A/22B). In the sections studied, it is expressed by a change in depositional environment, reflected in a shift from dominance of porcellaneous forms to hyaline forms. This shift complicates recognition of the boundary because apparent biostratigraphic events (first or last occurrences) may, instead, reflect local environmental changes. The difficulty of distinguishing the Rupelian/Chattian boundary (SB 22A/22B) based on larger Foraminifera has been noted by other authors (*e.g.*, SIREL *et al.*, 2013). Indeed, several studies of Oligocene larger Foraminifera have reported no clear differences between the associations of SB 22A and 22B (*e.g.*, SIREL *et al.*, 2013; GEDIK, 2015; SERRA-KIEL *et al.*, 2016). Different criteria have been proposed to characterise SB 22B in different basins, such as the first occurrence of *Miogypsinoides* (LESS *et al.*, 2018) or of *Eulepidina dilatata* and *Nummulites kecskemetii* (PARENTE & LESS, 2019). In the assemblage studied, dominated by porcellaneous forms, with hyaline taxa scarce and miogypsinids absent, these criteria cannot be applied, making recognition of the boundary particularly challenging. We tentatively place the boundary at a change within the porcellaneous association, marked by the near-simultaneous last occurrences of several species (*Praerhapydionina delicata*, *Coscinospira* spp., *Peneroplis* spp., *Penarchaias glynnjonesi*, and *Sivasina egribucakensis*), while other taxa persist (*Borelis* spp., *Sorites* sp., *Idalina pignatti*, *Austrotrillina striata*). This change, however, may also reflect palaeoenvironmental change, because several of the taxa that disappear in the Ibi section are known from younger intervals elsewhere. For example, *Peneroplis flabelliformis* occurs at the lower Chattian (SB 22B; SIREL, 2015), and *Sivasina egribucakensis* is reported from the lower Chattian (SIREL *et al.*, 2013; SIREL, 2015) and even from the Lower Miocene (YAZDI-MOGHADAM *et al.*, 2023b; also documented as "*Dendritina rangi*" in AMIRSHAHKARAMI *et al.*, 2010). The last occurrence of *Penarchaias glynnjonesi* is placed either in SB 21 (*e.g.*, SIREL, 2015; YAZDI-MOGHADAM *et al.*, 2018) or SB 22A (SERRA-KIEL *et al.*, 2016). HOTTINGER (2007) did not specify the upper biostratigraphic range of this species. In the Prebetic (Ibi section), the last occurrence of *P. glyjonnesi* coincides with those of *Praerhapydionina delicata* and several other porcellaneous species, including *Coscinospira elongata*, *C. sivasensis*, and *Spirolinella emmae*. The latter is more likely endemic to the Prebetic, whereas *C. elongata* and *C. sivasensis* are restricted to SB 21 in Turkey (SIREL *et al.*, 2013; SIREL, 2015).

On the other hand, the last occurrence of *P. delicata* at the Rupelian/Chattian (SB 22A/22B) boundary was previously reported in the Prebetic by FALCES-DELGADO and GIANETTI (2023), in Iran by YAZDI-MOGHADAM *et al.* (2018), in Oman and Yemen by SERRA-KIEL *et al.* (2016), and in Indonesia and south-east Asia by RENEMA (2002, 2007). Also, in Malta, the last occurrence of *Praerhapydionina* precedes the FO of *Miogypsinoides complanatus* (FELIX, 1973), and in Jamaica the genus is restricted to the lower Oligocene (ROBINSON & WRIGHT, 1993). The alleged early Oligocene age of the foraminiferal association containing *P. delicata* from Bahamas (FISCHER *et al.*, 2015) is debatable and is here reinterpreted as Rupelian. Therefore, in the absence of miogypsinids, the most reliable criterion for identifying the Rupelian/Chattian boundary appears to be the last occurrence of *Praerhapydionina delicata.*

Our biometric analysis of *Neorotalia burdigalensis* (Fig. 20) provides an additional criterion for recognizing this boundary. Upper Rupelian specimens show *P* values < 90 µm, whereas lower Chattian specimens yield values > 100 µm. This threshold in proloculus diameter, situated around 95 µm, should be verified in other sections, but it may offer a straightforward means of identifying the Rupelian/Chattian boundary.

The FO in the Ibi section of *Planolinderina* in SB 22B aligns with the observations of FREUDENTHAL (1969) and AKBAR-BASKALAYEH *et al.* (2020) from the Oligocene of Crete and the Qom Formation in, Iran respectively. In our samples, *Planolinderina* occurs in the uppermost part of SB 22B and in the lower half of SB 23. In eastern Turkey (Kelereşdere Section), ÖZCAN *et al.* (2010a) reported *P. escornebovensis* in the late Chattian (SB 23).

Similarly, the FO of *Heterostegina assilinoides* in SB 22B is consistent with the findings of BENEDETTI *et al.* (2018) and ÖZCAN *et al.* (2010a). ÖZCAN *et al.* (2009a) reported a population (*Heterostegina* aff. 1 *assilinoides*) exhibiting ancestral characteristics compared to typical *H. assilinoides* from the basal Chattian (lower part of SB 22B) in south-west Turkey. The basal SB 22B would also be characterised by the exclusive presence of *Nummulites bormidiensis* and transitional populations between *E. formosoides* and *E. dilatata* (HADI *et al.*, 2023; ÖZCAN *et al.*, 2009a, 2010a), although the transition between these two *Eulepidina* species was likely diachronous, occurring earlier in the Central Tethys (AKBAR-BASKALAYEH *et al.*, 2020; YAZDI-MOGHADAM *et al.*, 2025). In the Prebetic (Ibi section), we did not observe any reticulate *Nummulites* or ancestral forms of *Heterostegina* in the lower part of SB 22B; typical *H. assilinoides* firsts appears in the middle-lower part of SB 22 (Fig. 5).

In the Central Tethys (Oman, Iran) and the Indo-Pacific, the range of both *N. vascus* and *N. fichteli* is limited to the Rupelian (SB 21-22A; EHRENBERG *et al.*, 2007; RENEMA, 2007; LAURSEN *et al.*, 2009; BUCHEM *et al.*, 2010; YAZDI-MOGHADAM, 2011; AMIRSHAHKARAMI, 2013; MAGHFOURI MOGHADAM *et al.*, 2014; SERRA-KIEL *et al.*, 2016; MATSUMARU, 2017; YAZDI-MOGHADAM *et al.*, 2018, 2023a; AKBAR-BASKALAYEH *et al.*, 2020; MOHAMMADI, 2023, 2024), as confirmed by age calibration using Sr-isotope stratigraphy (EHRENBERG *et al.*, 2007; LAURSEN *et al.*, 2009; BUCHEM *et al.*, 2010). On the other hand, the biostratigraphic range of these two species in Turkey and the Mediterranean region is mainly interpreted as Rupelian-lower Chattian (SB 21-22B; DROOGER & LAAGLAND, 1986; LESS, 1991; CAHUZAC & POIGNANT, 1997, 1998; BÁLDI *et al.*, 1999; SIREL, 2003, 2015, 2020a; BASSI *et al.*, 2007; GEDIK, 2008, 2014, 2015; BRAGA & BASSI, 2011; SIREL *et al.*, 2013; ZOERAM *et al.*, 2013, 2015; GEDIK & KARADENIZLI, 2021). The last occurrence of *N. fichteli* has been reported in the late Rupelian (SB 22A) of Greece (WIELANDT-SCHUSTER, 2004) and offshore southern Iran (YAZDI-MOGHADAM *et al.*, 2025), or in the lowermost Chattian in Anatolia (GEDIK & KARADENIZLI, 2021) and the Aquitaine Basin (SZTRÁKOS & STEURBAUT, 2017). According to HADI *et al.* (2023), LESS *et al.* (2018), and ÖZCAN *et al.* (2009a, 2010a), the last representatives of the *N. fichteli* lineage in the SB 22B of Iran, western India, and Turkey correspond to *N. bormidiensis*. *Nummulites vascus* has also been reported from SB 23 in Turkey (IŞIK, 2010; IŞIK & HAKYEMEZ, 2011; SIREL & IŞIK, 2011). In the Prebetic, the last occurrence of *N. fichteli* is at the base of SB 22A (Ibi section), whereas *N. vascus* occurs from SB 21 to late SB 23.

Idalina pignattii was known only from the Rupelian (SB 21-22A) of Oman and Socotra (SERRA-KIEL *et al.*, 2016), the one reported from the Rupelian of NE Iraq (KARIM & HAMA, 2019, Fig. 15c) is actually a *Schlumbergerina*. In the Prebetic, the range of *Idalina pignattii* extends from the early Rupelian SB 21 to the early Chattian, SB 22B.

Sorites has traditionally been considered to range from the Miocene to the Recent (*e.g.*, COLE, 1965, 1969; ADAMS, 1967; LOEBLICH & TAPPAN, 1987b; RENEMA, 2002, 2007). However, several studies document its presence in Oligocene rocks from Australia (CHAPRONIERE, 1981), Japan (Ogasawara Islands; MATSUMARU, 1996), north-eastern Iraq (as "*Archaias kirkukensis*" in AL-QAYIM *et al.*, 2016, Fig. 11a, d, f; as "*Archaias asmaricus*" in KARIM *et al.*, 2012, Fig. 12i; as *Sorites* sp. 1, Pl. 3, fig. 9, and *S. orbiculus*? in HENSON, 1950), Syria (HENSON, 1950, Pl. 3, fig. 8), Malta (as "*Archaias kirkukensis*" in BRANDANO *et al.*, 2009, Fig. 4A), southern Italy (POMAR *et al.*, 2014, Fig. 2c; as "*Orbitolites*" in ZUFFARDI-COMERCI, 1930, Pl. 5, fig. 6), France (BOUDAGHER-FADEL, 2008, Pl. 6.10, fig. 6), and south-eastern Spain (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017; GRANERO *et al.*, 2020, 2022). Other reports of Oligocene *Sorites* are doubtful, such as those from the Rupelian-Chattian of Iran, which likely represent peneroplids (see Fig. 6e in SHABAFROOZ *et al.*, 2015), or from the Chattian of southern Pakistan (see Fig. 6F in

MARIANI *et al.*, 2025). Remarkably, *Sorites* is absent from the Rupelian of Oman and Yemen (SERRA-KIEL *et al.*, 2016) and has never been reported from the extensively studied Oligocene of Turkey and Iran. The earliest confirmed occurrences of *Sorites* in the Tethys are in the Rupelian of northeastern Iraq (HENSON, 1950; AL-QAYIM *et al.*, 2016). Chattian occurrences extend from the Prebetic to Iraq and Japan in the late Chattian (MATSUMARU, 1996). In France, the Oligocene occurrence of *Sorites* is limited to the reference by BOUDHAGER-FADEL (2008, Pl. 6.10, fig. 6; 2018, Pl. 6.12, fig. 6), who did not specify the age, locality, or associated Foraminifera. *Sorites* was not included in the definition of the Oligocene-Miocene Shallow Benthic Zones (CAHUZAC & POIGNANT, 1997, 1998) and was not reported by SZTRÁKOS and STEURBAUT (2017) in their exhaustive revision of foraminiferal biostratigraphy in the Aquitaine Basin (southern France). Its first appearance in the Oligocene across the Tethys, from the westernmost Tethys to the Pacific, makes *Sorites* a valuable biostratigraphic marker that should be incorporated into the definition of the SB biozonation. In the Mediterranean region, its FO corresponds to SB 22A.

Upper Chattian

In the Prebetic, the upper Chattian (SB 23) is marked by the FO of *Risananeiza* (*R. crassaparies*), *Amphistegina mammilla*, *Spiroclypeus margaritatus*, *Cycloclypeus mediterraneus*, *Elphidium crispum*, *Archaias* sp., and *Miogypsinella* (*M. complanata*, *M. formosensis*). Other characteristic species of this biozone include *Risananeiza pustulosa*, *Miogypsinella borodinensis*, *M. akcadagensis*, *Postmiogypsinella intermedia*, and *Planolinderina* sp. Additionally, based on data from the eastern Prebetic (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017), *Eulepidina dilatata*, *E. elephantina*, and *Victoriella conoidea* also occur in this interval. HAKYEMEZ *et al.* (2016) placed *Miogypsinella complanata*, *M. borodinensis*, and *Postmiogypsinella intermedia* in SBZ 23, which is correlated with planktic zone O6 (BERGGREN & PEARSON, 2005). This zone is characterised by the presence of "*Globigerina ciperoensis*" and "*Globigerinoides primordius*" (= *Ciperoella ciperoensis* and *Trilobatus primordius*, SPEZZAFERRI *et al.*, 2015; OLSSON *et al.*, 2018), along with the absence of *Paragloborotalia opima*. *Miogypsinella* (= *Miogypsinoides* auct.) *complanata* is the most common and indicative species for the late Chattian in the western basins of the Tethys (*e.g.*, HAKYEMEZ *et al.*, 2016), and its FO defines SB 23 (CAHUZAC & POIGNANT, 1997). According to SIREL and GEDIK (2011), the last occurrences of *M. borodinensis* and *M. akcadagensis* defines the upper boundary of SB 23.

In the Ibi section, however, the lower boundary of SB 23 is characterised by the FO of *Risananeiza pustulosa*, *Amphistegina mammilla*, and *Cycloclypeus mediterraneus* (Fig. 5). The FO of miogypsinids (*Miogypsinella complanata*, *M. formosensis*) seems to occur slightly higher, in the lowermost part of the FR section (Fig. 6). It remains to be determined whether this lag reflects palaeoenvironmental factors or represents distinct biostratigraphic ranges. If the latter is the case, the lower boundary of SB 23 could be redefined by the FO of *Risananeiza*, a genus exclusive of this zone.

The FO of *Amphistegina mammilla* and *Elphidium crispum* should be also considered for defining SB 23 in the Western Tethys. This is consistent with the inclusion of *Amphistegina* sp. and *Elphidium* sp. as characteristic taxa of SB 23 in Malatya Basin (SIREL & GEDIK, 2011) and with the FO of *E. crispum* at the base of the upper Chattian in the Aquitaine Basin (SZTRÁKOS & STEURBAUT, 2017). The occurrence of *A. mammilla* in the upper Chattian of the Prebetic, as well as in Turkey, Palestine, and Iran, was discussed by FERRÀNDEZ-CAÑADELL and BOVER-ARNAL (2017). Further evidence comes from Iran (SADR, 2017; HABIBI & BOVER-ARNAL, 2018), Egypt (KUSS & BOUKHARY, 2008, Pl. 2, fig. 6), Greece (WIELANDT-SCHUSTER, 2004), and the Aquitaine Basin in southern France (SZTRÁKOS & STEURBAUT, 2017).

Our biometric study of *Neorotalia burdigalensis* (Fig. 20, Table 3) draws a potential new criterion: specimens with *P* values > 115 µm may indicate the onset of the late Chattian. This threshold, however, is based on limited data and requires further confirmation.

Subdivision of Shallow Benthic zone 23

Based on the new data from the upper Chattian, two distinct associations can be recognised, primarily defined by miogypsinids (*Miogypsinella* and *Postmiogypsinella*) and the two species of *Risananeiza.* Accordingly, SB 23 in the Prebetic can be subdivided into two biozones, characterised as follows (Fig. 22):

Subzone SB 23A: Characterised by *Risananeiza crassaparies* (*P* ≤ 225 µm) and *Miogypsinella* species with X values (number of spiral chambers) > 14 (*M. complanata*, *M. formosensis*). Available data (ÖZCAN *et al.*, 2010a; FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017) suggest that *Eulepidina elephantina* may be exclusive to this sub-biozone. The lower boundary of SB 23 is currently defined by the FO of miogypsinids (CAHUZAC & POIGNANT, 1997). As discussed above, in the Ibi section, the FO of *Risananeiza pustulosa*, *Amphistegina mammilla*, and *Cycloclypeus mediterraneus* predates the FO of miogypsinids (*M. complanata/M. formosensis*) in the lowermost part of the FR section. Another potential indicator, which requires confirmation, is the occurrence of *Neorotalia burdigalensis* with *P* > 115 µm.

Subzone SB 23B: Characterised by *Risananeiza pustulosa*, *Postmiogypsinella intermedia*, and *Miogypsinella* species with X values < 14 (*M. borodinensis*, *M. akcadagensis*).

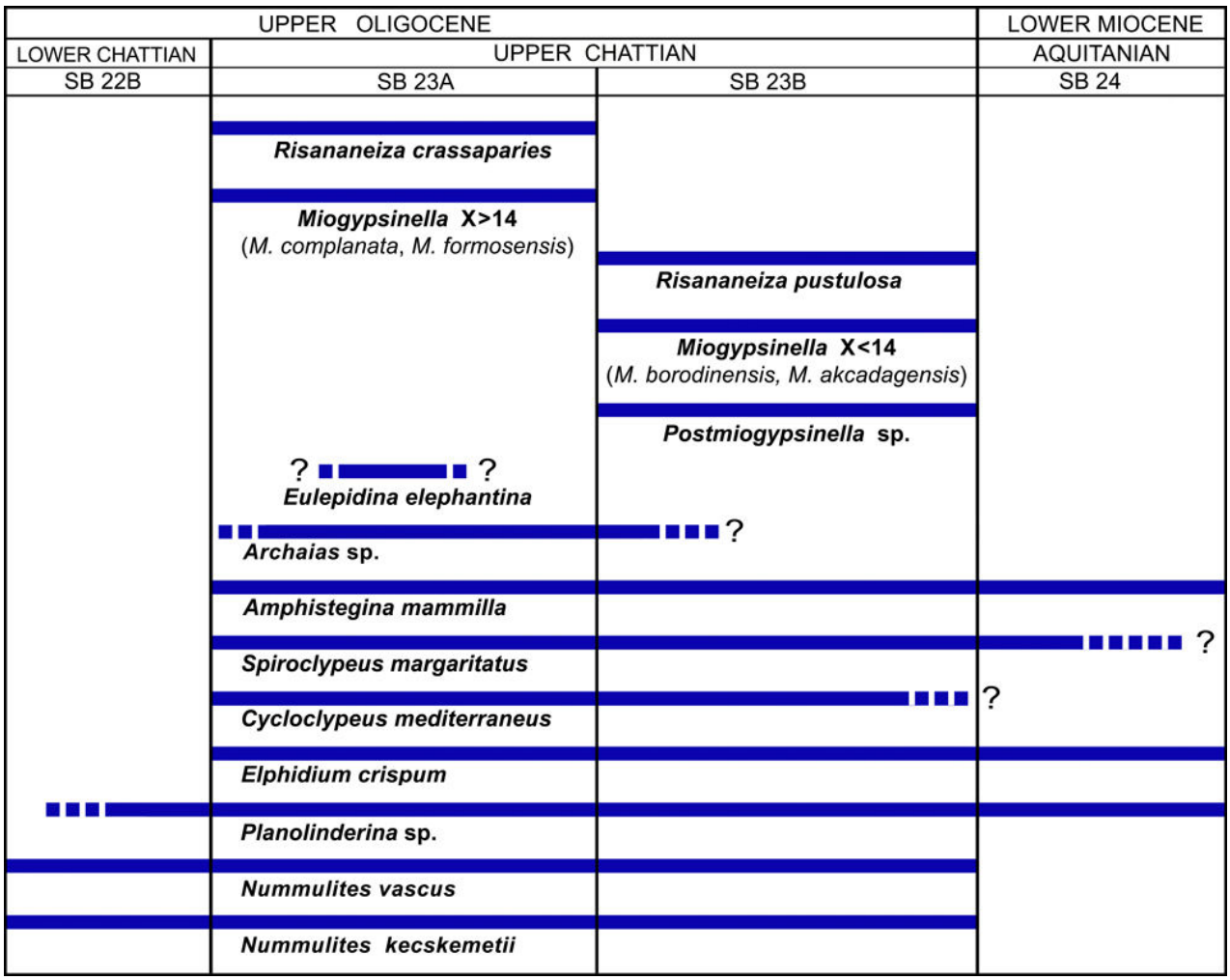


Figure 22: Biostratigraphic markers for the upper Chatian in the Prebetic Range and subdivision of Shallow Benthic biozone 23 into two sub-biozones, 23A and 23B, based on the stratigraphic distribution of *Risananeiza* and miogypsinid species.

Based on data from the Benitatxell Range (Ferràndez-Cañadell & Bover-Arnal, 2017), the late Chattian assemblage of SB 23 in the Prebetic also includes *Nummulites vascus*, *N. kecskemetii*, *Operculina complanata*, *Heterostegina assilinoides*, *Spiroclypeus margaritatus*, *Cycloclypeus mediterraneus*, *Neorotalia burdigalensis*, *Victoriella conoidea*, *Carpenteria* sp., *Biarritzina* sp., *Elphidium crispum*, *Amphistegina mammilla*, *A. bohdanowiczi*, *Asterigerina* sp., *Nephrolepidina* sp., *E. dilatata*, *E. raulini*, *Planorbulina bronnimanni*, *Planolinderina* sp., *Sphaerogypsina* sp., *Austrotrillina striata*, *Sorites* sp., *Archaias* sp., *Peneroplis thomasi*, *P. flabelliformis*, and *Schlumbergerina alveoliniformis*. Additional potential criteria, which require confirmation, include the occurrence of *Neorotalia burdigalensis* with *P* values > 130 (Fig. 20) and the FO of *Austrotrillina howchini* (with regular bifurcation of alveoli, Fig. 14D). Özcan *et al.* (2010a) suggested that in eastern Turkey, *Eulepidina dilatata* was replaced in the lower part of SB 23 by immigrant *E. anatolica* and *E. elephantina.* In the shallow facies of the Ibi and FR sections, *Eulepidina* is very rare, and the large *E. elephantina* is absent. However, in the Benitatxell Range, *E. dilatata* is found together with *E. elephantina*, while *E. anatolica* is absent (Ferràndez-Cañadell & Bover-Arnal, 2017). Based on these data, we tentatively restrict *E. elephantina* to SB 23A in the Prebetic (Fig. 22).

The subdivision of SB 23 proposed here is in agreement with the biostratigraphic data from the Aquitaine Basin reported by Sztrákos and Steurbaut (2017). They set the FO of "*Amphistegina hauerina*" (= *A. mammilla*, see Rögl and Brandstätter, 1993) at the base of the upper Chattian and distinguish two assemblages of *Miogypsinoides*, with the FO of four species (*M. bantamensis*, *M. dehaartii*, *M. lateralis*, and *M. mauretanicus*) in the middle part of the upper Chattian. Despite the differences in taxonomic interpretation, they recognised a change in the assemblage of miogypsinid species in the middle of SB 23 that likely corresponds to the subdivision proposed here.

According to the original description by Benedetti and Briguglio (2012), *Risananeiza crassaparies* is associated with "*Miogypsinoides*" *formosensis*, *Nephrolepidina morgani*, *Eulepidina dilatata*, *Operculina complanata*, *Spiroclypeus margaritatus*, *Heterostegina assilinoides*, and

Nummulites kecskemetii, which, based on the miogypsinid species, corresponds to the association characteristic of SB 23A. GEDIK (2020) reported the occurrence of *R. crassaparies* in the Rupelian-lower Chattian of Turkey. She interpreted as Rupelian-lower Chattian the association of *R. crassaparies*, *Archaias kirkukensis*, *Austrotrillina asmariensis*, *Nephrolepidina* sp., *N. praemarginata*, *Nummulites* cf. *vascus*, *H. assilinoides*, *B. pygmaea*, *Neoplanorbulinella malatyaensis*, *N. matsumarui*, and *Neorotalia burdigalensis* as "upper Chattian SBZ 23" the association of *Miogypsinella borodinensis*, *M. akcadagensis*, *M.* cf. *complanata*, *Postmiogypsinella intermedia*, and *Nephrolepidina morgani*. These two assemblages could both be of upper Chattian age and may be interpreted as SB 23A and 23B, respectively. SARFI and YAZDI-MOGHADAM (2024) reported an upper Chattian foraminiferal assemblage with *Miogypsinoides complanatus*, *M. formosensis*, *Spiroclypeus margaritatus*, *Operculina complanata*, and *Risananeiza pustulosa* from the Qom Formation in Central Iran (Dobaradar section). As stated above, measurements of their two figured megalospheric specimens (Fig. 7I-J in SARFI & YAZDI-MOGHADAM, 2024) show test and proloculus diameters within the common range for the two species. Based on both their relatively small test size and the associated miogypsinid species, these specimens are most likely *R. crassaparies*, and the assemblage corresponds to SB 23A. YAZDI-MOGHADAM *et al.* (2023c) and SARFI and YAZDI-MOGHADAM (2024) reported further *Risananeiza* occurrences from the upper Chattian of the Qom Formation in Central Iran. Based on measurements of their figured specimens, both, *R. crassaparies* and *R. pustulosa*, occur in their stratigraphic series. Furthermore, according to the sample locations, *R. crassaparies* is replaced by *R. pustulosa*, providing a sequence that records the anagenetic evolution of this monospecific genus and its potential use to distinguish the lower and upper parts of SB 23. Further occurrences of the two *Risananeiza* species in Iran are found in the sections described by RAHAGHI (1980), where *Risananeiza* (reported as "*Rotalia viennoti*") is associated either with "*Miogypsinoides complanatus*" or with *Spiroclypeus*.

Comparison with the literature shows that the FO of *Spiroclypeus margaritatus* in SB 23 agrees with ÖZCAN *et al.* (2009b), who noted that *Spiroclypeus* is unknown from Rupelian and lower Chattian deposits and extended its range to the lower Aquitanian. According to ÖZCAN *et al.* (2010a), *Heterostegina assilinoides* is replaced by *Spiroclypeus margaritatus* in SB 23. The reported "*Spiroclypeus carpathicus*" from the Rupelian of Oman (SERRA-KIEL *et al.*, 2016) is probably an *Heterostegina*, as no lateral compartments are visible (see Fig. 48.1-5 in SERRA-KIEL *et al.*, 2016). ALLAHKARAMPOUR *et al.* (2020) reported the first occurrence of *Spiroclypeus* as simultaneous with that of *Miogypsinoides* in the basal Chattian of the Asmari Formation (Zagros Basin, Iran), calibrated using Sr-isotope stratigraphy.

The reference sections for SB 23A and SB 23B sub-biozones are the Ibi and La Font Roja sections described here, which report, for the first time, the occurrence of the two species of *Risananeiza* in the same locality, as discrete stages of the same anagenetic species. The stratigraphical replacement of *R. crassaparies* by *R. pustulosa* is accompanied by a replacement in miogypsinid species.

Other sections in the Prebetic Domain: The sections of the Benitatxell Range and Rebaldí, in the Prebetic of the eastern part of Alacant province (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017). Our observations in other sections under study show that this subdivision of SB 23 would be of use for the Prebetic. To date, there are no sections in the Oligocene of the External Prebetic with data on nannofossils or magnetostratigraphy, nor with correlatable studies on planktic Foraminifera.

In other areas, a revision of the systematics of *Risananeiza* (often reported under other genera, *Neorotalia*, *Pararotalia* etc.) and miogypsinids (often reported as *Miogypsinoides*) should be performed to check if these sub-biozones are recognized. Possible sections in which the sub-biozones might be identified are:

- Aquitaine basin (southern France): A similar replacement of miogypsinids at the middle part of the upper Chattian was observed by SZTRÁKOS and STEURBAUT (2017) in sections of the western Aquitaine basin, although they did not include detailed associations for each of the sections studied.
- Turkey: The Edilme section, complemented by the Karamağara section, both in the Malatya Basin reported by GEDIK (2020) record a similar faunal distribution, with *R. crassaparies* in the lower part and *P. intermedia*, *M. borodinensis*, and *M. akcadagensis* in the upper part. Although interpreted as lower and upper Chattian, respectively by GEDIK (2020) they could correspond to SB 23A and 23B.
- Central Iran: Based on measurements of the figured specimens in SARFI and YAZDI-MOGHADAM (2024), both, *R. crassaparies* and *R. pustulosa*, occur in the upper Chattian of the Dobaradar section (Qom Fm., Central Iran). A biometrical revision of *Risananeiza* specimens in this section could compare the correlation of the replacement of *Risananeiza* species with that of miogypsinids and hence would be useful to check the use of these new sub-biozones in Central Iran and the possible correlation with the Prebetic. Further occurrences of the two *Risananeiza* species (reported as "*Rotalia viennoti*") in Iran are found in the sections described by RAHAGHI (1980) as "Aquitanian" of the same Qom Formation:

Section No. 1 S. of Daghan and Section No. 3 W, Kahak, in Qom-Kashan area.

Oligocene species in the Miocene of the External Betics

A recent paper by BOLIVAR-FERICHE *et al.* (2025) claims that in the Sierra de Marmolance (External Zones of the Betic Cordillera, Granada province), several species currently considered as Oligocene, such as *Eulepidina dilatata*, *E. formosoides*, *Nephrolepidina praemarginata*, *Nummulites fichteli*, *N. vascus*, *N. kecskemetii*, *Neorotalia* "*viennoti*" (= *N. burdigalensis*), and *Risananeiza crassaparies*, extend to the Middle Miocene, up to the Serravallian. The age assignment is based on planktic Foraminifera contained in the marls that underlie and laterally grade into the limestones hosting the larger Foraminifera. BOLIVAR-FERICHE *et al.* (2025) interpreted the larger foraminiferal assemblages as autochthonous-parautochthonous, arguing that they lack sedimentary structures "characteristic of coarse-grained sediment gravity flows", and noting both the preservation state of foraminiferal tests and the absence of mixing up of species from different facies.

Their interpretation strongly contradicts the biostratigraphic ranges documented for these species elsewhere in the Tethys. All the taxa mentioned above are widespread in other parts of the Tethys, and in all cases they are restricted to the Oligocene. As discussed previously, although in the Prebetic *Nummulites vascus* and *N. kecskemetii* occur up to the upper Chattian, their highest occurrences in the wider Tethys are in the upper Rupelian or the lower Chattian, and that of *N. fichteli* is even earlier, in the upper Rupelian. *Neorotalia burdigalensis* is considered to become extinct at the end of the Oligocene or in the basal Aquitanian (*e.g.*, CAHUZAC & POIGNANT, 1993). In the Western and Central Tethys, *Heterostegina assilinoides* is limited to the lower Chattian and is replaced in the upper Chattian by *Spiroclypeus margaritatus* (ÖZCAN *et al.*, 2010a). The latter species occurs in the upper Chattian and only locally into the lower Aquitanian (central Turkey; ÖZCAN *et al.*, 2009b). *Risananeiza* is likewise known only from the upper Chattian in the Western and Central Tethys. The proloculus diameters reported for *Risananeiza* from the Sierra de Marmolance (70 to 95 µm; BOLIVAR-FERICHE *et al.*, 2025) correspond to *R. crassaparies* and fall at the very base of the variability of the genus. They are comparable to the values observed in the lowermost upper Chattian of the Prebetic, whereas in higher stratigraphic beds the diameters increase progressively (Fig. 21). In addition to larger Foraminifera, the coralline alga *Subterraniphyllum thomasii* provides further evidence, as it is also limited to the Oligocene (BASSI & NEBELSICK, 2000; BASSI *et al.*, 2000; BASSO *et al.*, 2019).

The assemblages reported by BOLIVAR-FERICHE *et al.* (2025) consist mainly of Oligocene larger Foraminifera, with only one species, *Nephrolepidina tournoueri*, being attributable to the Miocene (Aquitanian-Burdigalian). Notably, the Marmolance assemblages lack species that are characteristic of the Lower and Middle Miocene, such as *Miogypsina* spp. or *Borelis melo*. The Miocene record of the Prebetic is rich in *Heterostegina* and *Amphistegina*, with the latter represented by large species such as *A. mammilla* and *A. lessonii*. However, in BOLIVAR-FERICHE *et al.* (2025) *Amphistegina* is neither determined at species level nor illustrated. The specimen of *Heterostegina* figured by BOLIVAR-FERICHE *et al.* (2025, Fig. 10h) shows a small megalospheric embryo, a characteristic feature of Miocene species. In contrast, the Oligocene species *H. assilinoides* possesses a megalosheric proloculus that is three to four times larger.

The assemblages from the Sierra de Marmolance reported by BOLIVAR-FERICHE *et al.* (2025) include species with different biostratigraphical ranges: Rupelian-lower Chattian (*N. fichteli*, *N. praemarginata*), upper Chattian-lower Aquitanian (*Risananeiza*, *Spiroclypeus*), and Aquitanian-Burdigalian (*N. tournoueri*). However, species of different ages are found in the same layers (*e.g.*, *N. fichteli* with *E. formosoides* and *N. tournoueri*), strongly suggesting reworking. The geological context in the External Betics during the Middle Miocene was synorogenic (*e.g.*, VERA, 2000), with olistostromes and debrites documented in the nearby Castril area during the Langhian and Serravallian. In the Sierra Marmolance, calcareous breccias with erosive bases and debris-flow deposits, dated to the Serravallian-Tortonian, were formed by the deposition of eroded material from nearby uplifts onto a shallow carbonate platform (LUPIANI MORENO *et al.*, 2006). This suggest a context in which reworking of Oligocene materials would not be unexpected. The apparent absence of mixing between species from different facies could result from the slow, steady erosion of successive layers.

Although explaining such discrete reworking may be challenging, we favor this interpretation because it is more parsimonious than the unlikely scenario of local survival during the Serravallian of numerous species that went extinct at the end of the Oligocene elsewhere in the Tethys, particularly given the absence of typical Miocene species.

Chronostratigraphy and sedimentary evolution

The two sedimentary successions studied developed within the same carbonate platform system (Fig. 1B), consistent with GEEL (2000), although they differ in age (Figs. 3, 5-6). Previous studies in the Ibi section dated the uppermost part of the succession underlying the Miocene deposits as Burdigalian (GEEL, 1995), early Chattian (GEEL, 2000) or Rupelian (HÖNTZSCH *et al.*, 2013). Our biostratigraphic data indicate that the uppermost part of the Ibi section, directly below the unconformity, is of upper Chattian age. The preserved upper Chattian record in Ibi is 12 m thick, whereas the upper Chattian record in the FR is at

least 250 m thick (Fig. 3). In Ibi, the upper Chattian platform carbonates capped by an erosional surface (Figs. 3A, 4E-F), are overlain by Miocene siliciclastic-influenced deposits. This erosional surface is characterised by widespread bioerosional features (Fig. 4F), indicating that it acted as a hard substrate during a transgressive event, most likely following a phase of subaerial exposure and erosion. Accordingly, this irregular surface is interpreted as a subaerial unconformity that, during a Miocene transgression, developed into a rockground (*sensu* FÜRSICH, 1979). This suggests that the FR represents a more distal depositional environment, whereas the Ibi section reflects a more proximal platform setting, which was subjected to significant erosion under subaerial exposure conditions. This interpretation is supported by palaeontological evidence: the Rupelian to Chattian strata in Ibi contain abundant porcellaneous Foraminifera and corals (Fig. 3A), indicative of a proximal, shallow-marine environment (*e.g.*, HOTTINGER, 1997; BUCHEM *et al.*, 2010), also indicated by the presence of hook-shaped rhodophytes that suggests the development of seagrass meadows (see *e.g.*, SOLA *et al.*, 2013). In contrast, the FR section is dominated by hyaline Foraminifera, typical of more distal and slightly deeper marine settings (*e.g.*, HOTTINGER, 1997). Consistent with this interpretation, sixteen beds bearing *Microcodium* have been identified in the Ibi section (Figs. 3A, 4D; see also GEEL, 1995). *Microcodium* is a microproblematica typically associated with continental and pedogenic environments, and its occurrence in a carbonate platform succession is commonly interpreted as an indicator of subaerial exposure (*e.g.*, KABANOV *et al.*, 2008). According to GEEL (2000), in Ibi *Microcodium* would occur on top of fans forming islands in the back-reef zone. In contrast, only two reworked *Microcodium* fragments were identified in two beds at the FR (Figs. 3B, 5E), most likely transported from proximal areas into this more distal depositional environment. Furthermore, the FR succession exhibits a higher siliciclastic input (Fig. 3B), reflecting greater detrital influence, whereas the Ibi succession is more carbonate-dominated (Fig. 3A), suggesting deposition in a relatively protected setting with limited coarse siliciclastic influx. Nevertheless, the lower part of the upper Chattian succession at the FR also recorded a major regression, which led to subaerial exposure, meteoric dissolution, and the formation of a brecciated horizon (Figs. 3B, 5A-B). However, it remains uncertain whether this breccia horizon is genetically related to the subaerial unconformity capping lower-upper Chattian platform carbonates at Ibi (Figs. 3A, 4E-F).

Despite the differences in sedimentary facies, both successions display an overall aggradational stacking pattern, indicating comparable long-term trends in accommodation and carbonate production during the Rupelian and Chattian stages. Given that the more proximal sectors of the carbonate platform system, particularly at Ibi, culminated in subaerial exposure and erosion, the aggradational architecture observed in both successions is most consistent with deposition during a highstand stage of relative sea level. The inner parts of a highstand platform are typically stacked in an aggrading pattern and are prone to subaerial exposure even during minor, lower-order relative sea-level falls, whereas the platform margin tends to prograde outward (*e.g.*, EBERLI & GINSBURG, 1989; EBERLI *et al.*, 2004).

This scenario within the External Prebetic Unit of the Betic Cordillera is consistent with observations from the Rebaldí-Benitatxell Range area (see BOVER-ARNAL *et al.*, 2017), located approximately 60 km east of Ibi and La Font Roja, within the Internal Prebetic Zone. There, Chattian proximal platform carbonates overlying a Cretaceous substrate were subaerially exposed and eroded at the Rebaldí locality. The top of these preserved Chattian carbonates also contain *Microcodium* and evolve basinward into a more distal, slightly deeper, and more continuous Rupelian-Chattian succession, giving rise to the Benitatxell Range. The platform carbonates from both Rebaldí and the Benitatxell Range mainly developed during a highstand normal regression. The occurrence of Chattian platform carbonates directly overlying Cretaceous palaeotopographic highs in parts of the Prebetic Zone also suggests deposition during a highstand stage of relative sea level.

According to the eustatic transgressive-regressive megacycles proposed by SPEIJER *et al.* in GRADSTEIN *et al.* (2020), the Priabonian was characterised by a major cycle (Pr1), which ended with a major regression near the Priabonian/Rupelian boundary. The Rupelian was also marked by a transgressive-regressive cycle (Ru1), which ended in the upper part of the stage. The late Rupelian experienced a pronounced transgressive event, followed by a long-term, progressive regression that extended through most of the Chattian Stage, culminating in a maximum regression near the Chattian/Aquitanian boundary (Ch1 cycle; see GRADSTEIN *et al.*, 2020). In the study area, the sedimentary expression of these major transgressive-regressive cycles is not evident, because the succession is characterised by an overall aggrading stacking pattern. This masking of the eustatic signal may be attributed to active tectonic subsidence in the area, related to the opening of the València Trough (*e.g.*, ROCA & DESEGAULX, 1992; GEEL, 1995; GEEL *et al.*, 1999), and a high carbonate production rate, which filled the available accommodation during the Priabonian-Chattian interval. Nevertheless, MARTÍN-MARTÍN *et al.* (2020), based on data from other sections from the Internal Prebetic Zone, mainly interpreted the development of the Oligocene-Aquitanian succession as being controlled by eustasy.

The Cenozoic succession from the Internal Prebetic Domain (the studied successions are located in the External Prebetic Unit) is interpreted as a syn-contractional tectonostratigraphic sequence

and includes two regional unconformities, mainly corresponding to upper Priabonian-lower Rupelian and Aquitanian-Burdigalian gaps (*e.g.*, MARTÍN-MARTÍN *et al.*, 2018, 2020). A notable example is the major unconformity identified in El Carxe and La Pila ranges, south-west of the study area (Murcia province), which is associated with an erosional gap spanning part of the Bartonian, Priabonian, and Rupelian. This gap has been linked to an intraplate contractional episode affecting the Iberian Peninsula (MARTÍN-MARTÍN *et al.*, 2018, 2020). MICLĂUŞ *et al.* (2025) and MARTÍN-MARTÍN *et al.* (2025) interpreted the uppermost Eocene layers of the Ibi section as Lutetian (SB 13-14) in age. Here we show that the upper part of the Eocene in the Ibi section is of Priabonian age, thus reducing their major stratigraphic gap spanning the early Lutetian to Rupelian to just the upper part of the Priabonian.

The studied area is of particular significance, as it preserves a rather continuous stratigraphic record extending from the lower Eocene to Priabonian and from the lowermost Rupelian to the upper Chattian within the External Prebetic Zone of Alacant, an interval that appears to be less continuous in the internal areas of the Prebetic Zone (*e.g.*, MARTÍN-MARTÍN *et al.*, 2018, 2020). The subaerial unconformity overlain by Miocene deposits observed at Ibi (Figs. 3A, 4E-F) could also correspond to the regional Lower Miocene unconformity documented in the Internal Prebetic Unit. This unconformity has been associated with the contractional deformation event that gave rise to the External Betics fold-and-thrust belt (*e.g.*, GEEL, 1995; MARTÍN-MARTÍN *et al.*, 2020).

Therefore, the new biostratigraphic results have implications for the tectonostratigraphic evolution of the Prebetic, because they help delineate the age and geographic extent of the tectonic phases that shaped the Prebetic shallow marine stratigraphic record. A review of regional tectonostratigraphic events is beyond the scope of this article.

Larger Foraminifera evolution and palaeobiogeography

The new data from the studied sections, together with a systematic review and critical assessment of data in the literature, allow a re-evaluation of the evolution, phylogeny, and palaeobiogeography of certain taxa during the late Eocene and the Oligocene.

Neorhipidionina

The genus *Neorhipidionina* is known from the Bartonian-Priabonian of the Central Tethys: Iraq (HENSON, 1948), Iran (HOTTINGER, 2007; NAFARIEH *et al.*, 2019; CHANGAEI *et al.*, 2022), Oman and Socotra (ROBINET *et al.*, 2013; SERRA-KIEL *et al.*, 2016), and the western offshore of India (COTTON *et al.*, 2019). According to HOTTINGER (2007), it is also present in the material from Somalia in AZZAROLI (1950) and from the offshore Tunisia in BONNEFOUS and BISMUTH (1982). Its occurrence in the Priabonian of the Prebetic (Ibi section, Figs. 5, 12E1-E2) extends the palaeobiogeographical range of the genus to the westernmost Tethys.

Pfendericonus

The available data suggest that *Pfendericonus* originated in the Thanetian with small, simple forms (*P. mindanaoensis*; MATSUMARU, 2017), which evolved into larger, more complex forms in the early-middle Eocene (*P. makarskae*; SOEST, 1942; HOTTINGER & DROBNE, 1980; VECCHIO & HOTTINGER, 2007; KAYĞILI, 2016) and the earliest Priabonian (*P.* aff. *makarskae* in SERRA-KIEL *et al.*, 2016, with *P* = 215-360 µm) and then experienced a reduction in size and complexity in the late Priabonian and Rupelian (*P. globulus*; SIREL & DEVECILER in SIREL *et al.*, 2020a). This trend is similar to that observed in *Austrotrillina* across the Eocene/Oligocene boundary (see below). Although the definition of *P. globulus* includes both Priabonian and Rupelian specimens, it is mainly based on the former, and both the holotype and the type locality are of Priabonian age. A comparative study of Eocene and Oligocene specimens may reveal sufficient differences to distinguish two species. In the Ibi section, the proloculus diameter of Rupelian *Pfendericonus* appears smaller than those reported in the species diagnosis of *P. globulus* (SIREL & DEVECILER, 2020). The scarcity of data, derived from random thin sections, prevents a consistent differentiation between Priabonian and Oligocene specimens.

Pfendericonus globulus has previously been reported from the Priabonian and Rupelian of eastern Turkey (SIREL, 1997; SIREL *et al.*, 2020a). Its occurrence in the lower Rupelian of the Ibi section extends its palaeobiogeographical range by *c.* 2,500 km to the westernmost Neothethys. The reported occurrence in the lower Chattian of southeastern Iran (as "valvulinid sp." in HABIBI, 2016a) needs confirmation.

Idalina pignattii

Idalina pignattii was previously known only from the Rupelian (SB 21-22A) of Oman and Socotra Island (SERRA-KIEL *et al.*, 2016). Its occurrence in the Prebetic extends both its stratigraphic range to early Chattian (SB 22B) and its palaeobiogeographic distribution from the Central Tethys to the westernmost Tethys, nearly 6,000 km westwards. The Rupelian "*Idalina laminata*" reported by ESCANDELL and COLOM (1962) likely corresponds to *I. pignattii*. A possible additional occurrence, which requires confirmation, is from the late Chattian-Aquitanian of Cephalonia, Greece (see Fig. 4L15 in ACCORDI *et al.*, 2014). The *I. pignatti* reported from the Rupelian of north-east Iraq (Fig. 15c in KARIM & HAMA, 2019) is likely a *Schlumbergerina*.

Austrotrillina

Austrotrillina paucialveolata is easily distinguished from other Oligocene-Miocene species by its irregular and rudimentary exoskeleton, restricted to the peripheral chambers. In the Pre-

betic (Ibi section), *A. paucialveolata* occurs in the lower Rupelian (SB 21) and is replaced in the late Rupelian by *A. striata*, which has a regular exoskeleton (asmariensis or striata morphotypes) that develops earlier in ontogeny. Therefore, *A. paucialveolata and A. striata* are distinguished both by their morphostructure and by their different biostratigraphic ranges, and the former should not be considered a synonym of the latter as stated by BASSI *et al.* (2021a). *Austrotrillina paucialveolata* is very similar to *A. eocaenica*, from which it differs by a smaller test, smaller megalospheric proloculus, and a thinner basal layer (HOTTINGER, 2007; SERRA-KIEL *et al.*, 2016). According to HOTTINGER (2007), followed by BOUDAGHER-FADEL (2018), the larger test and proloculus, together with the "more differentiated exoskeleton" in *A. eocaenica*, rule out a direct ancestral phylogenetic relationship with *A. paucialveolata*. However, following the environmental crisis at the Eocene/Oligocene boundary that led to the extinction of several major groups of larger Foraminifera, a general reduction in test and proloculus size in surviving miliolid species would not be unexpected. Such a reduction is observed in other larger Foraminifera that survived extinction events (*e.g.*, in *Orbitolites* above the Bartonian/Priabonian boundary; see HOTTINGER *et al.*, 1964). A second example is found in *Pfendericonus*, as discussed above. Further support for a phylogenetic relationship between *A. paucialveolata* and *A. eocaenica* comes from the size of their microspheric forms. According to SERRA-KIEL *et al.* (2016), the microspheric form of *A. eocaenica* is large, reaching up to 2.8 mm, while no microspheric forms of Oligocene *A. paucialveolata* were observed. In our study, we identified microspheric specimens of *A. paucialveolata* in samples from the Ibi section. Two specimens from sample Ibi-121 (at 55 m) are particularly large, reaching 2.2 and 3 mm in length (Fig. 13A-B). Although the megalospheric forms of *A. paucialveolata* are smaller than those of *A. eocaenica*, the unusually large microspheric forms suggest that this trait could be a retained feature from the ancestral species, *A. eocaenica*.

The earliest occurrences of *A. paucialveolata* are reported from the lower Rupelian of Iraq (GRIMSDALE, 1952), Iran (ADAMS, 1968; HABIBI, 2016b), Oman and Socotra (GALLARDO *et al.*, 2001; SERRA-KIEL *et al.*, 2016), eastern Turkey (SIREL, 2015), Somalia (SILVESTRI, 1937), Malta and Gozo (FELIX, 1973), and the Prebetic (this study). It has also been reported, although not shown in a figure, from the lower Rupelian of Priabonia, in northern Italy (BARBIN *et al.*, 1997), and from the Rupelian (SB21-22A) of Zakynthos Island in Greece (DI CARLO *et al.*, 2010). ADAMS (1968) documented the co-occurrence of *A. paucialveolata* and *A. asmariensis* in Iraq. In the Ibi section, *A. asmariensis* replaces *A. paucialveolata*, without transitional forms, at the SB 21/22 boundary, suggesting immigration rather than in-situ evolution. This pattern indicates that *A. paucialveolata* likely originated in the Central Tethys, somewhere between eastern Turkey, Oman, and Iran. Transitional forms between *A. paucialveolata* and *A. asmariensis* appear much later, during the Burdigalian, in south-western Australia (HAIG *et al.*, 2020). The derivation of *A. paucialveolata* from *A. eocaenica* in the Central Tethys is consistent with the biogeographic distribution of the latter, which includes Iran (HOTTINGER, 2007; NAFARIEH *et al.*, 2019; RAHAGHI, 1980, reported as *A. paucialveolata*), Oman and Socotra (GALLARDO *et al.*, 2001; SERRA-KIEL *et al.*, 2016), eastern Turkey (AVŞAR, 1991; BOOTH *et al.*, 2013; SIREL, 2015, p. 39), offshore Tunisia (BONNEFOUS & BISMUTH, 1982), and possibly western Pakistan (BUKHARI *et al.*, 2016).

Austrotrillina paucialveolata gave rise to *A. striata* in the late Rupelian in the Central-Western Tethys, and subsequently spread across the Tethys, reaching Japan by the latest Rupelian-earliest Chattian (MATSUMARU, 1996, updated biostratigraphy according to WADE *et al.*, 2018).

As pointed out by ADAMS (1968, p. 93): "There can be no doubt that *A. howchini* evolved from *A. striata*". Transitional forms between *A. striata* (*asmariensis*/*striata*/*brunni* morphotypes) and *A. howchini* have been reported from the Rupelian-lower Chattian (SB 21-22) of Turkey as "*A. asmariensis*" (GEDIK, 2014, Pl. 4, fig. 1; 2015), or as "*Austrotrillina* sp." (in KAYĞILI, 2016, Pl. 19, fig. 8); from the upper Chattian or the uppermost Chattian-lower Aquitanian of Iran, as "*A. howchini*" (AMIRSHAHKARAMI, 2013, Pl. 6, fig. 9; TAHERI *et al.*, 2017, Fig. 12.8); from the Lower Miocene (upper T*e*) of India, Indonesia, and Papua New Guinea (ADAMS, 1968; ADAMS & BELFORD, 1973; BINNEKAMP, 1973; BELFORD, 1984; LUNT & ALLAN, 2004; HAIG *et al.*, 2020); and from the Middle Miocene (upper T*f*) of Christmas Island (as "*A. howchini*" in ADAMS & BELFORD, 1974, Pl. 3, fig. 7) and western Australia (CHAPRONIERE, 1984; RIERA, 2019). ADAMS (1968) considered that transitional forms between *A. striata* and *A. howchini* occur in the upper T*e*, with true *A. howchini* mainly in the lower T*f*. Considering the different correlations and chronostratigraphic interpretations of the Letter stages (*e.g.*, CHAPRONIERE, 1981; BOUDHAGER-FADEL & BANNER, 1999; LUNT & ALLAN, 2004; RENEMA, 2007; MATSUMARU, 2011), the transition from *A. striata* to *A. howchini* in the Indo-Pacific can be roughly placed in the Middle Miocene. However, this transition seems to be diachronic in this area, becoming younger toward the east. ADAMS (1968, p. 88) dated the Indonesian transitional specimens to the "Zone N8 of BANNER & BLOW (1965)", which corresponds to the upper Burdigalian-lower Langhian (HOSHI *et al.*, 2019; GRADSTEIN *et al.*, 2020). Transitional specimens from western Australia were dated to the Langhian (CHAPRONIERE, 1984) and the Langhian-early Serravallian (RIERA *et al.*, 2019). On the other hand, *A. howchini* does not replace *A. striata*. Both species occur together, although the former becomes progres-

sively more abundant, to the point that its relative abundance (*A. striata/A. howchini abundance ratio*) has been proposed as a biostratigraphic indicator for the Aquitanian-Burdigalian of Indonesia (NOVAK, 2014).

This draws a diachronic origin of transitional forms between *A. striata* and *A. howchini*, beginning in the Rupelian-early Chattian in Turkey, followed by occurrences westwards (Prebetic) and eastwards (Iran) during the late Chattian, and extending into the Indo-Pacific in the Early Miocene, with the younger forms in the Middle Miocene of western Australia, where "real *A. howchini* were not recorded" (RIERA, 2019, p. 330). This westward migratory trend was already observed by CRESPIN (1952) in the Miocene of Australia. CRESPIN (1952) noted differences in the biostratigraphic range of *A. howchini* between Indonesia (Java, Borneo) and Australia, as well as a general trend toward younger occurrences and lower abundance, also documented in other genera (*Nephrolepidina*, *Cycloclypeus*, *Miogypsina*, *Flosculinella*) from the north-west (Carnavon Basin) through south-central Australia (Adelaide Basin) to the south-west (Victoria). According to CRESPIN (1952), this south-western occurrence marks the most easterly extension of typical Indo-Pacific assemblages.

According to BASSI *et al.* (2021a), *Austrotrillina howchini* originated in the Burdigalian in western India and has not been recorded in the Mediterranean and Middle East regions. However, *Austrotrillina* with simple bifurcated alveoli occurs in the Rupelian-lower Chattian of eastern Turkey (GEDIK, 2014, 2015; KAYĞILI, 2016), in the upper Chattian of the Prebetic (this paper) and the Asmari Formation of the Zagros Basin, eastern Iran (AMIRSHAHKARAMI, 2013). Occurrences of *A. howchini* elsewhere are of Lower or Middle Miocene age (Kenya, Tanzania, India, Indonesia, Philippines), with the easternmost records in the Middle-Upper Miocene of south-eastern Australia (BOUDAGHER-FADEL, 2018). The occurrence of morphotypes of *A. howchini* with additional levels of alveolar bifurcation is poorly documented, but their origin also seems diachronic. *Austrotrillina howchini* with alveoli exhibiting two to three bifurcation levels was illustrated by BOUDHAGER-FADEL (2018, Pl. 7.1, fig. 1) from the Pata Limestone of Australia, of Middle-Late Miocene age (GALLAGHER & GOURLEY, 2007). Specimens showing alveoli with three successive bifurcations in BASSI *et al.* (2021a, Fig. 7) are from Kalimantan (Indonesia), of middle-late Langhian and Serravallian age, the latter (and younger) showing a more regular and densely packed alveolar pattern.

Summing up the above data, we conclude that *A. paucialveolata* originated from *A. eocaenica* in the Central Tethys (Turkey, Oman, Iran) during the earliest Rupelian, from where it migrated westwards, reaching the westernmost Tethys (Prebetic), and possibly also eastwards to Pakistan (KHAN, 1967). *Austrotrillina paucialveolata* evolved diachronically into *A. striata* and then into *A. howchini.* The different geographical and biostratigraphic ranges of the morphotypes (*asmariensis* / *striata* / *brunni*) can be explained by the combination of migration evens and diachronic parallel evolution.

Peneroplis

Peneroplis evolutus, *P. thomasi*, and *P. flabelliformis* have been considered species of the Central Tethys region, occurring in Iran, Iraq, and Turkey (*e.g.*, HENSON, 1950; ADAMS & BOURGEOIS, 1967; RADOIČIĆ, 1981; YAZDI-MOGHADAM, 2011; AMIRSHAHKARAMI, 2013; ZOERAM *et al.*, 2015; HOSEINZADEH *et al.*, 2015; HABIBI, 2016a, 2016b; YAZDI-MOGHADAM *et al.*, 2021, 2023a). According to SERRA-KIEL *et al.* (2016), *Peneroplis thomasi* is absent in Oman (Dhofar and Socotra), where the genus is instead represented by *P. flabelliformis*, *P.* cf. *evolutus*, and other smaller species. The westernmost occurrences of *P. thomasi* and *P. evolutus* reported in the literature are unfigured records from the Oligocene of Malta (FELIX, 1973), northern Italy (BARBIN & BIGNOT, 1986; BARBIN *et al.*, 1997), and southern Italy (SARTORIO & VENTURINI, 1988, p. 167). Subsequent studies of the Attard Formation in Malta (BRANDANO *et al.*, 2009; GATT, 2022; and references therein) did not recognise these larger *Peneroplis* species. The presence of *P. flabelliformis*, *P. evolutus*, and *P. thomasi* in the Prebetic extends their palaeobiogeographical distribution to the westernmost Tethys. The presence of two additional Peneroplidae, *Peneroplis peramplus* and *Spirolinella emmae*, is particularly noteworthy, as it suggests that the Prebetic functioned as a sub-bioprovince, hosting both immigrant and endemic species.

Sorites

The systematics of *Sorites* (Soritidae) remain difficult to resolve. No consensus has been reached regarding the definition of either fossil or recent species (see COLE, 1965; CRAPON de CAPRONA d'ERSU & BENIER, 1985; LOEBLICH & TAPPAN, 1987a; GUDMUNDSSON, 1994; HOTTINGER, 2001). Molecular studies of different species and their symbiotic algae (HOLZMANN *et al.*, 2001; POCHON *et al.*, 2001; GARCIA-CUETOS *et al.*, 2005; MERKADO *et al.*, 2013) have revealed substantial genetic divergence both between geographic regions and among habitats. MERKADO *et al.* (2013) concluded that *Sorites* is polyphyletic, and POCHON and PAWLOWSKI (2006) argued that the considerable cryptic diversity in recent *Sorites* prevents reliable species identification based solely on morphological features, which are largely shaped by ecological conditions. In this context, characterizing the species from the Prebetic Oligocene is unlikely to provide significant insight into the systematics of the genus, other than extending the issue to the Oligocene.

There is multiple evidence for the presence of *Sorites* in rocks of Oligocene age (Table 5). However, the palaeobiogeographical distribution of *Sorites* in the Oligocene Tethys is discontinuous.

While *Sorites* is abundant in upper Rupelian and Chattian beds in the Prebetic, its occurrence in the Oligocene of France is limited to a reference by BOUDAGHER-FADEL (2008), who did not specify the age, locality, or faunal association. *Sorites* was not included in the definition of the Oligocene-Miocene Shallow Benthic zones by CAHUZAC and POIGNANT (1997, 1998), nor was it reported by SZTRÁKOS and STEURBAUT (2017) in their exhaustive revision of the foraminiferal biostratigraphy of the Aquitaine Basin (southern France). In the Central Tethys, evidence of Oligocene *Sorites* from Syria and northern Iraq (HENSON, 1950; AL-QAYIM *et al.*, 2016), but it is absent in the Rupelian of Oman and Yemen (SERRA-KIEL *et al.*, 2016) and has never been reported from the extensively studied Oligocene of Turkey and Iran. Beyond the Tethys, *Sorites* occurs in the upper Oligocene of the Indo-Pacific, including south-eastern Japan, eastern Australia and western Papua. This discontinuous distribution is puzzling and suggests a polyphyletic origin, consistent with the conclusions of MERKADO *et al.* (2013) based on molecular phylogenetic analyses of soritids and their algal symbionts.

The abundance of *Sorites* in the Oligocene of the Prebetic, compared with its minor occurrences in Italy, France and Malta suggests a possible origin in the westernmost Tethys. The few records of Oligocene *Sorites* in the Mediterranean, already noted by ADAMS (1978, p. 62), are likely related to the rarity of shallow platform facies. However, Oligocene shallow-water carbonate facies are well-developed in Turkey, Oman, and Iran, where *Sorites* has never been reported. This distribution (Table 5) suggests that two lineages of *Sorites* originated during the Oligocene: one in the Prebetic, which migrated eastward as far as Iraq, and a second in the Indo-Pacific (Japan, Australia, Papua). The Miocene-Recent *Sorites*, with its cosmopolitan distribution including the Caribbean, may therefore include descendants of these two lineages.

Table 5: Oligocene occurrences of *Sorites*. References: **1)** FERRÀNDEZ-CAÑADELL & BOVER-ARNAL (2018), this study; **2)** BOUDAGHER-FADEL (2008); **3)** ZUFFARDI-COMERCI (1930); **4** DE CASTRO (1987); **5)** POMAR *et al.* (2014); **6)** BRANDANO *et al.* (2009); **7)** HENSON (1950); **8)** KARIM *et al.* (2012); **9)** AL-QAYIM *et al.* (2016); **10)** MATSUMARU (1996); **11)** CHAPRONIERE (1984); **12)** LUNT (in HESEMANN, 2017).

Locality	Referred to as	Reported age	Reference and figured specimens
SE Iberia	*Sorites* sp.	Late Rupelian–Chattian	(1) Figs. 9a–c
S France	*Sorites* sp.	Oligocene	(2) Pl. 6.10, fig. 6
S Italy	*Orbitolites*	Senonian	(3) Pl. 5, fig. 6
	?*Sorites*	Oligocene	(4) Pl. 5, fig. 1
	Sorites sp. 1	lower Chattian	(5) Figs. 2c, 6B, 10A
Malta	*Archaias kirkukensis*	upper Rupelian	(6) Fig. 4b
Syria	*Sorites* sp. 1	Upper Oligocene	(7) Pl. 3, fig. 8
NW Iraq	*Archaias asmaricus*	Late Oligocene	(8) Fig. 12i
NE Iraq	*Archaias kirkukensis*	Rupelian	(9) Figs. 11a, d, f
	Sorites sp. 1	Upper Oligocene	(7) Pl. 3, fig. 9
	S. orbiculus?	Lower Oligocene–Middle Miocene	(7) only Miocene forms figured
Eastern Australia	*Sorites* sp.	Late Oligocene–Middle Miocene	(10) Pl. 14, figs. 8–10
Western Papua	*Sorites* sp.	Oligocene Td (? SB 22)	(11) FEU-1009899
Ogasawara, Japan	*Sorites orbiculus*	Late Oligocene	(12) Pl. 87, figs. 11–13
	Amphisorus hemprichii	Late Oligocene	(12) Pl. 86, figs. 6–10

Archaias

The genus *Archaias* originated in the middle Eocene of the Caribbean region (ROBINSON & WRIGHT, 1993) and ranged into the lower Chattian (SEIGLIE *et al.*, 1977; BASSI *et al.*, 2007; HOTTINGER, 2007).

In the Tethys Realm, Oligocene *Archaias* has been reported mainly from the Central Tethys: from the Bartonian-Rupelian of Oman and Socotra (GALLARDO *et al.*, 2001; SERRA-KIEL *et al.*, 2016), from the Rupelian and Chattian of central and eastern Turkey (TURNOVSKY, 1955; SIREL, 1997, 2003; SIREL *et al.*, 2013; GEDIK, 2014, 2015; HAKYEMEZ *et al.*, 2016; KAYĞILI, 2016; HABIBI, 2016a, 2018; KAYĞILI & AKSOY, 2019), from Iran and Iraq (SMOUT & EAMES, 1958; HENSON, 1950; HABIBI 2016a; HABIBI & BOVER-ARNAL, 2018; NAFARIEH *et al.*, 2019; HABIBI *et al.*, 2024), and from the Rupelian of Pakistan (KHAN, 1967). In the Mediterranean region, *Archaias* has been documented from the Chattian of north-eastern Italy (BASSI, 2007). Other reports from this region are debatable, such as those from the upper Rupelian of Mallorca (COLOM, 1935) or from the Chattian of Malta by FELIX (1973, not shown in a figure) and BRANDANO *et al.* (2009, Fig. 4A, most likely a *Sorites*). The reference to *Archaias* from the upper Oligocene of Apulia in southern Italy by CAHUZAC and POIGNANT (1992), based on SARTORIO and VENTURINI (1988), is incorrect; the latter only figures *Austrotrillina*, *Spirolina*, and peneroplids (*Peneroplis thomasi*, see p. 167 in SARTORIO & VENTURINI, 1988). The presence of *Archaias* in the

FR section extends the palaeobiogeographical distribution of the genus to the westernmost Tethys.

Praebullalveolina

Praebullalveolina originated in the upper Eocene (SB 19-20) with the type species *P. afyonica* (SIREL & ACAR, 1982; SERRA-KIEL *et al.*, 1998a; SIREL, 2015). It is represented in the lower Oligocene SB 21 by two species, *P. oligocenica* and *P. minuta*, in central and eastern Turkey (SIREL & ACAR, 1982; SIREL, 2015). The former was reported from the Rupelian (without distinguishing between SB 21 and 22B) of Dhofar (Oman) and Socotra (Yemen) by SERRA-KIEL *et al.* (2016). The *Praebullalveolina* specimens reported from the uppermost Eocene to earliest Oligocene of Priabona (Italy) by BARBIN *et al.* (1997, Pl. figs. 1-6) likely belong to the Eocene *P. afyonica*. These specimens are associated with *Praerhapydionina delicata* and *A. paucialveolata*; the latter (not illustrated in BARBIN *et al.*, 1997) may correspond to *A. eocaenica*. The occurrence of both *P. oligocenica* and *P. minuta* in the lower Rupelian of the Prebetic (FERRÀNDEZ-CAÑADELL, 2024; this study) extends their known palaeobiogeographical range to the westernmost Tethys.

Praebullalveolina differs from the Rupelian genus *Bullalveolina* (REICHEL, 1937) in the number of rows of alveoli and apertures, one or two in the former, and two or three in the latter (HOTTINGER, 1974; SIREL & ACAR, 1982). However, *Bullalveolina* has been rarely reported since REICHEL (1937) erected the genus. Documented occurrences are restricted to southern France, southern Spain, central Italy, Sicily, and Crete (*e.g.*, REICHEL, 1936; HOTTINGER, 1974, 2006; POIGNANT, 1998). Two reports need confirmation: *Bullalveolina* sp. from north-western Iran (YAZDI-MAGHADAM, 2011) and *B. boninensis* from the Oligocene of Ogasawara Islands, Japan (MATSUMARU, 1996). The latter was insufficiently illustrated, and no diagnostic characters of *Bullalveolina* are visible in the published photographs.

Another species, *Praebullalveolina curdica*, traditionally considered a *Borelis* species, was recently transferred to the genus *Praebullalveolina* by SIREL *et al.* (2020b) based on the presence, in topotypes, of several characters, such as the alternate pattern of Y-shaped septula and supplementary chamberlets with secondary apertures, shared with *P. afyonica*, *P. oligocenica*, and *P. minuta*. Recent studies have followed this generic adscription to *Praebullalveolina* (*e.g.*, SHARIFI *et al.*, 2023; YAZDI-MOGHADAM *et al.*, 2023b). This species appears in the late Early Miocene, however, there are no records of *Praebullalveolina* (nor *Bullalveolina*) from the Chattian and the Aquitanian. The occurrence of *P.* aff. *oligocenica* in SB 23 of the eastern Prebetic (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017) was based on a single specimen and requires confirmation.

Praebullalveolina-Bullalveolina and *Borelis* represent two parallel lineages that originated in the Eocene and persisted into the Oligocene. The alleged origin of the *Praebullalveolina-Bullalveolina* lineage from Eocene *Borelis* (BOUDAGHER-FADEL & PRICE, 2021) is debatable, as the lineages exhibit different characters (*e.g.*, aligned vs. alternate septula). HOTTINGER (1974) noted that *B. bulloides* does not usually occur together with *Borelis*, suggesting that they had a different ecological distribution, the former being adapted to deeper environments. Whereas the *Borelis* lineage has a continuous record from the Middle Eocene to extant species (*e.g.*, BASSI *et al.*, 2021b), the *Praebullalveolina-Bullalveolina* lineage is discontinuous, with species documented from the Priabonian (*P. afyonica*), Rupelian (*P. minuta* and *P. oligocenica*, *B. bulloides*), and Burdigalian-Tortonian (*P. curdica*). Additional data are required to clarify the phylogeny, as well as the biostratigraphic and palaeobiogeographical distribution, of this lineage.

Borelis

Oligocene *Borelis* includes two widely recognised species, *B. inflata* and *B. pygmaea*. Although *B. inflata* was originally defined from Borneo (ADAMS, 1965), it occurs mainly in the Western Tethys, including Sicily, southern Italy, Greece, and eastern Turkey (BASSI *et al.*, 2021b). *Borelis pygmaea* occurs in the Central Tethys and the Indo-Pacific and is the only species reported from the Oligocene of Oman and Socotra (SERRA-KIEL *et al.*, 2016) and Iran (SEYRAFIAN *et al.*, 2011; MOHAMMADI *et al.*, 2015; MOHAMMADI, 2023). Two additional Oligocene species have more restricted distribution: *B. merici*, known only from Turkey (SIREL & GÜNDÜZ, 1981; GEDIK, 2017), and *Borelis* sp. 1 from the Prebetic.

A main characteristic of the Prebetic *Borelis* is the absence of *B. pygmaea*. This species has been reported from southern Italy (DE CASTRO, 1987; BASSI *et al.*, 2021b) and south-eastern Spain (BRAGA & BASSI, 2007). However, the latter record is highly dubious and can be discarded, as it is based on a single section with an oval test and no evident axial thickening. Specimens from southern Italy show some notable particularities: some lack the characteristic axial thickening of *B. pygmaea* and are probably *B. inflata* (*B. philippinensis* according to BASSI *et al.*, 2021b), whereas others display Y-shaped septula (see Pl. 4, figs. 1, 4-5 in DE CASTRO, 1987), a feature characteristically absent in this species. In our samples, *B. inflata* occurs alongside a second species, *Borelis* sp. 1, which differs from *B. inflata* in having a higher elongation index and from *B. pygmaea* in having a smaller *EI* and poorly developed axial thickening (Fig. 17). A possible explanation is that only *B. inflata* reached this westernmost part of the Tethys, subsequently diverging into other morphotypes or species: those from south-eastern Italy reported by DE CASTRO (1987) and *Borelis* sp. 1 from the Prebetic. The latter is similar, although more elongated, to specimens assigned to *B. merici* from Turkey, which occur together with *B. inflata* and *B. pygmaea*. *Borelis pygmaea* occurs in the Central Tethys and the

Indo-Pacific, and is the only species recorded in the Oligocene of Oman and Socotra (SERRA-KIEL *et al.*, 2016) as well as in Iran (SEYRAFIAN *et al.*, 2011; MOHAMMADI *et al.*, 2015; MOHAMMADI, 2023).

We conclude that only *B. inflata* reached the westernmost part of the Tethys, where it diverged into distinct morphotypes or species: those from south-eastern Italy described by DE CASTRO (1987), and *Borelis* sp. 1 from the Prebetic. A similar endemic divergence may have originated *B. merici* in Turkey.

The systematics of *Borelis* remain unresolved. Studies of Oligocene *Borelis* are based on random thin sections, and the species diagnoses rely on very limited data. The recent revision by BASSI *et al.* (2021b) represents a valuable attempt to clarify the systematics, phylogeny, and palaeobiogeography of the genus, but it is hampered by this scarcity of data. Moreover, the different species of *Borelis* have been defined based on different diagnostic characters. For example, HOTTINGER (1974) used the number of chambers per whorl at test diameter of 1 mm to define *B. inflata*, and the number of chamberlets per 1 mm chamber length to define *B. pygmaea*. These two characters are visible in different sections (equatorial and axial, respectively), are not mutually exclusive, and cannot be applied to the small species *B. pulchra*, which never attains 1 mm in test diameter. Both HOTTINGER (1974) and BASSI *et al.* (2021b) considered the presence of Y-shaped septula as a diagnostic character. The latter author used this character to distinguish two groups: one derived from the Eocene *B. vonderschmitti*, in which Y-shaped septula are absent (including *B. inflata*, *B. pulchra*, and *B. pygmaea*), and a second group characterised by the presence of Y-shaped septula (including *B. philippinensis*, *B. melo*, *B. curdica*, and *B. schlumbergeri*). The presence of Y-shaped septula in *B. philippinensis* is ambiguous: they appear only sporadically, restricted to the outer whorls, and may be entirely absent in random sections of adult specimens (*e.g.*, see Fig. 6A-B in BASSI *et al.*, 2021b). Furthermore, *B. curdica* has recently been transferred to *Praebullalveolina* by SIREL *et al.* (2020b), based on the revision of topotypes, and recent publications follow this generic assignment (*e.g.*, SHARIFI *et al.*, 2023; YAZDI-MOGHADAM *et al.*, 2023b). The specimens illustrated in SIREL *et al.* (2020b) show alternate septula, consistent with those figured in the original description of "*Neoalveolina melo curdica*" (see REICHEL, 1937, Pl. 10, fig. 7). Most reports of *Borelis curdica* in the literature rely on the variable presence of Y-shaped septula and do not provide sufficiently clear sections to distinguish whether the septula are alternate or aligned. Consequently, the assignment of these specimens to either *Borelis or Praebullalveolina* remains uncertain. Some specimens attributed to *Borelis curdica* (*e.g.*, BASSI *et al.*, 2021b, Figs. 9-11) exhibit aligned septula, characteristic of *Borelis* rather than *Praebullalveolina*, and only a few Y-shaped septula. These Y-shaped forms represent irregular septula that locally converge or diverge with adjacent ones, rather than true bifurcations forming intercalated alveoli as in *Praebullalveolina* or *Bullalveolina*. GAGIĆ (1984) reported the co-occurrence of *Borelis melo* and *B. curdica* throughout the Badenian (= uppermost Burdigalian-middle Serravallian; HOHENEGGER *et al.*, 2015) of Serbia. Some of the specimens he figured as *B. curdica* show aligned septula together with Y-shaped septula, indicating that they are true *Borelis* (see Pl. 2, fig. 2, in GAGIĆ, 1984). Therefore, the presence of Y-shaped septula may represent a sporadic feature in populations of *B. melo*, and three similar morphotypes (*Borelis* with and without Y-shaped septa, and *Praevullalveolina* with Y-shaped septa) likely coexisted during the Miocene.

Another character used in the systematics of *Borelis*, the axial (columellar) thickening, appears to be variable and possibly related to test elongation. Although it is generally regarded as a characteristic trait of Oligocene species, especially *B. pygmaea*, axial thickenings are already present in the new Priabonian species *B. dizerae* and *B. sozerii*, recently described by ACAR and BOZKURT (2025) from the upper Priabonian of eastern Turkey, despite their small, subspherical to ovoid tests.

Considering all the above, the classification and phylogeny of *Borelis* proposed by BASSI *et al.* (2021b) remain open to debate. The taxonomic difficulties associated with *Borelis* are further complicated by similar issues in *Praebullalveolina* and *Bullalveolina*, because the Miocene '*curdica*' species may include both *Borelis* and *Praebullalveolina* species, and because the Chattian-Aquitanian record of these alveolinids in the Central and Western Tethys is incomplete. The *Borelis* specimens reported here do not provide a solution; instead, they suggest plastic (ecophenotypic?) variability in test morphology, particularly in elongation index and axial thickening. A more robust species definition based on additional characters, especially those related to the initial chambers, is needed, and this will depend on a substantial expansion of the available quantitative data.

The Oligocene species of *Borelis* probably originated from Priabonian ones. According to BASSI *et al.* (2021b), *Borelis inflata*, *B. pulchra*, and *B. pygmaea* show morphological affinities with *B. vonderschmitti*, mainly based on the absence of Y-shaped septula. The reported occurrence of *B. pygmaea* in the Priabonian (BASSI *et al.*, 2021b, p. 17, Fig. 2), based on MATSUMARU (2011, not shown in a figure), requires confirmation. On the other hand, BASSI *et al.* (2021b) placed the origin of *B. pygmaea* either in the Priabonian (BASSI *et al.*, 2021b, p. 17, Fig. 2) or in the Rupelian (BASSI *et al.*, 2021b, Table 1), and did not consider the other two species (*B. globosa* and *B. parvula*) reported as Priabonian by MATSUMARU (2011), whom

they regarded, instead, as Miocene species originating in the Aquitanian.

Although the two late Priabonian species recently described by ACAR and BOZKURT (2025) are practically identical, it is particularly noteworthy that this *Borelis* population exhibits axial thickenings, a feature previously considered exclusive to Oligocene species (characteristic of *B. pygmaea*). A second character highlighted by ACAR and BOZKURT (2025), the presence of Y-shaped septula in *B. laxispira*, *B. dizerae*, and *B. sozerii*, is debatable. Nevertheless, the characters displayed by these new species challenge the phylogenetic scheme proposed by BASSI *et al.* (2021b), which relies on the presence of Y-shaped septula, and, instead, suggest the existence of a second late Priabonian lineage of *Borelis* that may be related to the Rupelian *B. pygmaea*. The morphological variability observed among geographically distinct populations of *Borelis*, in terms of elongation index, axial thickening, and Y-shaped septula, points toward mosaic evolution, in which different Oligocene populations independently developed one character or another. Species with well-developed axial thickening and elongated tests (*B. pygmaea*) occur mainly in the Central Tethys and the Indo-Pacific and represent the only form in the Oligocene of Oman and Socotra (SERRA-KIEL *et al.*, 2016) as well as in Iran (SEYRAFIAN *et al.*, 2011; MOHAMMADI *et al.*, 2015; MOHAMMADI, 2023). Forms lacking axial thickening tend to have less elongated tests and are distributed throughout the Tethys (*e.g.*, *B. inflata*, *B. philippinensis*, and *B. merici*). Populations with intermediate characters, *i.e.*, poorly developed axial thickening and variable elongation indices (*B. merici*, *Borelis* sp. 1), are found in the Mediterranean region and Turkey.

Axial thickening is a character already present in Eocene species, which are likely monophyletic, and is, to some extent, allometrically linked with highly elongated tests. Therefore, it could theoretically appear in any Oligocene population colonizing a new geographical area. This may be the case for *Borelis* sp. 1, which could have arisen from an immigrant population of *B. inflata* in the westernmost Tethys. Although this hypothesis complicates the interpretation of *Borelis* phylogeny, and particularly its biostratigraphy, it likely represents a more realistic explanation of the genus's evolutionary patterns. The picture becomes even more complex when the other Eocene-Oligocene alveolinid lineage, *Praebullalveolina-Bullalveolina*, is considered. The recent reassignment of the Miocene (Burdigalian-Tortonian) *Borelis curdica* to *Praebullalveolina* (SIREL *et al.*, 2020b) clarifies the distinction between forms with and without Y-shaped septula, which would belong to different genera. However, this reassignment also introduces an additional challenge, as there are no known records of *Praebullalveolina* or *Bullalveolina* from the Chattian and Aquitanian. According to BASSI *et al.* (2021b), "*B. curdica*" originated from *B. melo*, which in turn derived from westwards migrants of *B. philippinensis*. This hypothesis is based on the alleged presence of Y-shaped septula in *B. philippinensis* and *B. melo*. However, as stated above, topotypes of "*Borelis*" *curdica* from REICHEL's locality (Derge section, south-eastern Turkey) show characters (Y-shaped septula with supplementary chamberlets, a secondary aperture with alveoli, and alternating septula) that are inconsistent with the genus *Borelis* and instead correspond to *Praebullalveolina* (SIREL *et al.*, 2020b). However, based on the available data, the sporadic presence of specimens with Y-shaped septula in populations of *B. melo*, co-occurring with *Praebullalveolina* cannot be ruled out.

Nummulites vascus and *N. fichteli*

The last occurrences of *N. vascus* (see above) suggests a diachronous extinction, beginning at the end of the Rupelian (SB 22A) in the Indo-Pacific and, to some extent, in the Central Tethys (Iran-Oman), and generally progressing westwards. The reported last occurrences of *N. vascus* are placed in the lower Chattian (SB 22B) in eastern Turkey (SIREL, 2003, 2015), the Vienna Basin (BÁLDI *et al.*, 1999), and northern Italy (BRAGA & BASSI, 2011), and in the upper Chattian (SB 23) in south-central Turkey (IŞIK, 2010; IŞIK & HAKYEMEZ, 2011; SIREL & IŞIK, 2011). The last occurrence of the reticulate *Nummulites* (*N. fichteli*/"*N. intermedius*"/*N. bormidiensis*) in the central-western Tethys has been reported in the upper Rupelian (SB 22A) of offshore southern Iran (YAZDI-MOGHADAM *et al.*, 2025) and Greece (WIELANDT-SCHUSTER, 2004), and in the lower Chattian (SB 22B) in western India (LESS *et al.*, 2018), Iran (HADI *et al.*, 2023), eastern and western Turkey (SIREL, 2003; GEDIK, 2008; ÖZCAN *et al.*, 2009a, 2010a; GEDIK & KARADENIZLI, 2021), the Vienna Basin (BÁLDI *et al.*, 1999), and the Aquitaine Basin (SZTRÁKOS & STEURBAUT, 2017). In the Prebetic, the last occurrence of *N. fichteli* was observed at the base of SB 22A in the Ibi section, whereas *N. vascus* persists into the uppermost part of SB 23.

Nummulites kecskemetii

Nummulites kecskemetii has been reported from the Chattian (SB 22B-23) of Hungary (LESS, 1991, 1999; BÁLDI *et al.*, 1999), southern France (as *N. bouillei* in BUTT, 1966; DROOGER *et al.*, 1971, and CAHUZAC & POIGNANT, 1997; see BÁLDI *et al.*, 1999), northern Spain (FERRÀNDEZ-CAÑADELL *et al.*, 1999), the Prebetic (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017; this study), southern Italy (PARENTE & LESS, 2019), north-western Greece (WIELANDT-SCHUSTER *et al.*, 2004), eastern and south-western Turkey (ÖZCAN *et al.*, 2009a, 2010a), Central Iran (AKBAR-BASKALAYEH *et al.*, 2020), and western India (LESS *et al.*, 2018; SARASWATI *et al.*, 2018). According to LESS *et al.* (2018) and PARENTE and LESS (2019), this species shows no significant morphological change across its entire stratigraphic range. *Nummulites kecskemetii* has been considered an immigrant from the Caribbean (LESS, 1991; LESS *et al.*, 2018; AKBAR-

BASKALAYEH *et al.*, 2020), based on its unusually small proloculus and its similarity to the American *Nummulites panamensis*. Whereas this hypothesis is difficult to confirm, it is equally difficult to dismiss. It is consistent with the biostratigraphic range of these morphologically similar Caribbean forms and forms from the Tethys.

Heterostegina

According to LESS *et al.* (2008), no *Heterostegina* are recorded from the Rupelian of the Western Tethys, and the Oligocene *H. assilinoides* is not related to the Bartonian-Priabonian lineages of *H. reticulata* or *H. gracilis*. LESS *et al.* (2018) placed the FO of *H. assilinoides* in the SB 22A in western India, whereas ÖZCAN *et al.* (2009a) reported an ancestral population (*Heterostegina* aff. 1 *assilinoides*) from the basal part of SB 22B in south-western Turkey. In the Prebetic (Ibi section), typical *H. assilinoides* firsts appears in the lower-middle part of SB 22. Taken together, these data suggest that this Oligocene lineage of *Heterostegina* originated in the late Rupelian in the Central Tethys and migrated westward, reaching western Turkey by the earliest Chattian and, somewhat later, the westernmost Tethys in the early Chattian.

Cycloclypeus

The postulated replacement of *C. mediterraneus* by the immigrant *C. eidae* in the early or middle Chattian (LAAGLAND, 1990; CAHUZAC & POIGNANT, 1997; ÖZCAN & LESS, 2009; RENEMA, 2015) was not observed in the studied sections, where *Cycloclypeus* is scarce. All the specimens in our samples can be attributed to *C. mediterraneus* (Fig. 9F-G).

Risananeiza

A review of the literature shows that *Risananeiza* (previously reported as *Neorotalia*, *Pararotalia*, *Rotalia*, or *Bozorgniella*) is mainly restricted to Spain (DIDON *et al.*, 1961; FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017; GRANERO *et al.*, 2022; BOLIVAR-FERICHE *et al.*, 2025), Italy (RENZ, 1936; BASSI *et al.*, 2007; BRANDANO *et al.*, 2009; BENEDETTI & BRIGUGLIO, 2012; MARINO *et al.*, 2022), and Egypt (BOUKHARY *et al.*, 2008). Its presence in the Central Tethys is restricted to eastern Turkey (SANCAY *et al.*, 2006; IŞIK, 2010; IŞIK & HAKYEMEZ, 2011; SIREL & IŞIK, 2011; GEDIK, 2020), Iran (RAHAGHI, 1980; DANESHIAN & HOSSEINZADEH, 2010; HOLAKOUEE *et al.*, 2018; MAGHFOURI MOGHADAM *et al.*, 2014; SADR, 2017; SARFI & YAZDI-MOGHADAM, 2024), and probably north-eastern Iraq (see Pl. 2, figs. f, h in GHAFOR & AHMAD, 2021). *Risananeiza* is absent in Oman and Socotra (SERRA-KIEL *et al.*, 2016).

The two known species, *R. pustulosa* and *R. crassaparies*, had not previously been found in the same succession and have been interpreted as different ecomorphotypes, with *R. pustulos*a inhabiting the middle ramp and *R. crassaparies* the high-energy zones of the inner and middle ramp (BENEDETTI *et al.*, 2025). Here, we show that the smaller species, *R. crassaparies*, occurs in the lower part of SB 23, associated with *Miogypsinella* with X values > 14, whereas *R. pustulosa*, is found in the upper part of SB 23, associated with *Miogypsinella* with X values < 14 and *Postmiogypsinella*. The two species therefore represent different stages of an anagenetic lineage spanning the late Chattian.

Postmiogypsinella

Postmiogypsinella, represented by a single species, *P. intermedia*, has been reported from the Malatya Basin (from where it was originally described; SIREL & GEDIK, 2011) and the Sivas Basin in eastern Turkey (HAKYEMEZ *et al.*, 2016), from Central Iran (YAZDI-MOGHADAM *et al.*, 2023c), and from the Prebetic Domain in the south-eastern Iberian Peninsula (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017; this study). It is likely that some reports of "*Miogypsina*" or "*Miogypsinoides*" from this area in the literature actually correspond to *Postmiogypsinella* (*e.g.*, see Pl. 6, figs. 3-4 in SADR, 2017).

The proposed origin of *Postmiogypsinella* from *Risananeiza* (GEDIK, 2020) is debatable (*e.g.*, BENEDETTI *et al.*, 2025). This hypothesis is based mainly on the supposed occurrence of *R. crassaparies* in the Rupelian (discussed above). Furthermore, according to GEDIK (2020) *Postmiogypsinella* would be the ancestor of *Miogypsinella.* This scenario is unlikely, as it would require a complex form (with lateral chambers) to evolve into a simpler form (without lateral chambers), which is also contradicted by their biostratigraphic ranges (Fig. 22). An alternative hypothesis to explain the structural similarities among *Miogypsinella*, *Postmiogypsinella*, and *Risananeiza*, as well as the scarce occurrence of apparent intermediate forms (*e.g.*, see Fig. 12A in FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017), is that these genera descended from a common ancestor, with one lineage giving rise to *Risananeiza* and a second lineage giving rise to *Miogypsinella* and subsequently to *Postmiogypsinella*.

Eulepidina

According to AKBAR-BASKALAYEH *et al.* (2020) and YAZDI-MOGHADAM *et al.* (2025), the transition from *Eulepidina formosoides* to *E. dilatata* was likely diachronous, occurring earlier in the Western Tethys and later in the Central Tethys. ÖZCAN *et al.* (2010a) suggested that in eastern Turkey, *E. dilatata* was replaced in the lower part of SB 23 by immigrant *E. anatolica* and *E. elephantina.* According to LEMOINE and R. DOUVILLÉ (1904) and LAAGLAND (1990), microspheric forms of *E. dilatata* have sometimes been confused with *E. elephantina*, which CAHUZAC and POIGNANT (1997) considered a synonym of the former. WIELANDT-SCHUSTER (2004, p. 193), who summarised the geographic reports of *E. elephantina*, from the Aquitaine Basin to the Middle East and East Africa, also recommended treating these citations with caution because the species name has been widely applied to large lepidocyclinids, even those in random sections. In the shallow facies of the Ibi and

FR sections, *Eulepidina* is very rare, and the large *E. elephantina* is absent. However, in the Benitatxell Range (eastern Prebetic), *E. dilatata* occurs together with *E. elephantina*, while *E. anatolica* is absent (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017).

Amphistegina mammilla

The first occurrence of *Amphistegina mammilla* can be placed in the late Chattian of the Western and Central Tethys, with records from Iran (SADR, 2017; HABIBI & BOVER-ARNAL, 2018), Palestine (HENSON, 1936), northern Syria(?) (HENSON, 1937), Egypt (KUSS & BOUKHARY, 2008), Greece (WIELANDT-SCHUSTER, 2004), the Aquitaine Basin in southern France (SZTRÁKOS & STEURBAUT, 2017), and the Prebetic (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017). As noted previously (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017), this contradicts the current hypothesis that set the origin of *A. mammilla* in the Lower Miocene of the Indo-Pacific region, from where it supposedly migrated westward to the Central Paratethys (Vienna Basin) in the Middle Miocene (*e.g.*, RÖGL & BRANDSTÄTTER, 1993; HARZHAUSER & PILLER, 2007). Instead, we conclude that *A. mammilla* originated in the Western Tethys or the western part of the Central Tethys during the late Chattian.

Lilliput effect across the Eocene/Oligocene boundary?

The large Bartonian and early Priabonian *Pfendericonus* species (*P. makarskae*, *P.* aff. *makarskae* of SERRA-KIEL *et al.*, 2016) are replaced in the late Priabonian and Rupelian by the smaller and simpler *P. globulus* (SIREL, 1997; SIREL *et al.*, 2020a; this study). A similar reduction in size and complexity is observed in the replacement of the middle-upper Eocene *Austrotrillina eocaenica* by the Rupelian *A. paucialveolata*. Comparable trends have been documented in other larger Foraminifera, such as *Orbitolites* across the Lutetian-Bartonian and Bartonian-Priabonian boundaries (*e.g.*, HOTTINGER *et al.*, 1964). This reduction in size appears to correspond to the phenomenon described as the *Lilliput effect* (URBANEK, 1993), which has been observed in other foraminiferal groups as well as in invertebrates and vertebrates following extinctions event (*e.g.*, KELLER & ABRAMOVICH, 2009; SONG *et al.*, 2011, and references therein).

Diversity

In the Western Tethys, the marine Oligocene is scarcely represented, particularly in shallow-water carbonate platform facies (*e.g.*, HOTTINGER, 1963; SIREL, 1997; BASSI *et al.*, 2007). This scarcity has contributed to the general perception of low to very low diversity of porcellaneous Foraminifera in the Western Tethys during the late Paleogene. Our results offer a new perspective. During Oligocene times, carbonate shallow-water platforms developed along the southern margin of the Iberian Peninsula. These platforms host rich assemblages of porcellaneous larger Foraminifera, revealing high diversity that includes species previously known only from the Central Tethys, as well as taxa likely endemic to this region. The newly documented occurrence of Oligocene taxa in the Prebetic, together with the revision of several genera (*Austrotrillina*, *Borelis*, *Risananeiza*), provides new insights into the patterns of origin, evolution, diversity, and migration of larger Foraminifera during the late Eocene and Oligocene.

The lower Rupelian (SB 21) assemblage of porcellaneous Foraminifera was reported in a previous study (FERRÀNDEZ-CAÑADELL, 2024), and included two new species, *Spirolinella emmae* and *Peneroplis peramplus*, which are potentially endemic to the Prebetic realm. Two additional species, *Idalina pignattii* and *Pfendericonus globulus*, reported for the first time from the Western Tethys, are now added to this assemblage, along with *Schlumbergerina alveoliniformis*, previously considered to originate in the upper Chattian (SB 23; FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017). The complete lower Rupelian assemblage of larger Foraminifera, thus, comprises 15 species of porcellaneous taxa, in addition to indetermined peneroplids, indeterminate Spiroloculinidae (Fig. 11H-K), miliolids, and ophthalmidids.

A considerable change in the foraminiferal assemblage in the upper Rupelian-lower Chattian (SB 22), is marked by the disappearance of *Spirolinella emmae* and *Peneroplis peramplus* and the replacement of *Austrotrillina paucialveolata* by *A. striata*, and the FO of *Borelis*, *Sorites*, *Nephrolepidina*, *Eulepidina*, and *Amphistegina bohdanowiczi*. Despite these changes, the overall diversity of porcellaneous foraminifers in terms of species number remains constant. The Eocene/Oligocene boundary (SB 22A/22B) is not biostratigraphically evident, as it corresponds to a facies change in which the dominant forms shift from porcellaneous to hyaline species, potentially masking true first and last occurrences.

The dominance of hyaline Foraminifera continued into uppermost Chattian (SB 23), the beginning of which is indicated by the FO of several taxa, including *Risananeiza*, *Spiroclypeus*, *Cycloclypeus*, *Miogypsinella*, *Amphistegina mammilla*, *Elphidium crispum*, and *Victoriella conoidea*. Porcellaneous taxa become scarce or rare, represented by *Austrotrillina striata*, *Austrotrillina* ex. interc. *striata-howchini*, and the FO of *Archaias* sp.

The Oligocene assemblage of Foraminifera thus includes 22 porcellaneous species, some previously unreported in the Western Tethys and some endemic to this realm. Considering that certain species could not be determined (*e.g.*, lepidocyclinids, victoriellids), a rough estimate of foraminiferal diversity in the Ibi and the FR sections includes more than 20 species in the Priabonian, over 40 species in the Rupelian, and about 40 in the Chattian. The Rupelian and Chattian assemblages differ in composition (as do the associations of Shallow Benthic zones 21, 22, and 23), but they share some species, resulting in a total amount of at least 60 different species recognised throughout the Oligocene of the Prebetic.

Geological context

The scarcity of upper Eocene-Oligocene shallow platforms with porcellaneous Foraminifera, as well as their low diversity in the Western Tethys, represents, to some extent, a biased record. During this interval, the western Mediterranean was extensively affected by the Alpine orogeny, coupled by a major sea-level rise. In the Alpine domain (south-eastern France, Switzerland, northern Italy), the Priabonian record, limited to SB 19-20 biozones, was dominated by nummulitid and orthophragmine facies, which were overlain by deeper "*Globigerina* marls". This facies change was diachronous, beginning in the late Eocene in the eastern sector and in the Oligocene in the west (FERRÀNDEZ-CAÑADELL *et al.*, 2023b). By the early Priabonian, the south Pyrenean foreland basin became endorheic, and the marine record was replaced by continental facies. In northern Iberia (Cantabria), the Pyrenean orogeny reactivated Hercynian faults, and the remnants of the Oligocene carbonate platform is preserved within flysch deposits, including mass flows and olistoliths, where Oligocene larger Foraminifera are intermixed with Eocene and Cenomanian species (FERRÀNDEZ-CAÑADELL *et al.*, 1999). The Alpine domain extended towards the south-east with the collision of the African, Alboran, Iberian plates. Furthermore, carbonate platforms rich in Oligocene larger Foraminifera were mainly destroyed under this compressional context. Shallow platform deposits of the Internal Betics of southwestern Spain, which also were very rich in larger Foraminifera, are preserved only in Miocene-Pliocene conglomerates (FERRÀNDEZ-CAÑADELL, pers. obs.). Taken together, this evidence suggests that tectonics and eustasy were the main factors explaining the poor record of upper Eocene-Oligocene larger Foraminifera in the Western Tethys, both due to the scarcity of shallow platforms and the widespread destruction of the few that did exist. The apparently low diversity of porcellaneous forms in the Western Tethys is therefore, likely an artifact, as indicated by the rich Oligocene porcellaneous foraminiferal fauna recorded in the Prebetic.

8. Summary and conclusions

The poor fossil record of Oligocene larger Foraminifera, particularly porcellaneous species, in the Western Tethys has contributed to the prevailing view that their diversity was low compared to the Central Tethys. To some extent, this perception is an artefact resulting from the scarcity and underdevelopment of shallow-water carbonate facies in the Mediterranean region during the Oligocene, or of their subsequent destruction during the Alpine orogeny, combined with the effects of eustatic megacycles.

The Prebetic in south-eastern Iberia represents an exception. The succession cropping out in Ibi and La Font Roja, spanning from the lowermost Rupelian to the upper Chattian (SB 21-23), contains a remarkable diversity of larger Foraminifera throughout the entire Oligocene. Several genera traditionally considered restricted to the Middle East are documented here for the first time in this area, providing new insights into the palaeobiogeography of the upper Eocene and Oligocene larger Foraminifera. This study builds upon previous results from the Ibi section (FERRÀNDEZ-CAÑADELL, 2024) and from the Rebaldí-Benitatxell Range area (FERRÀNDEZ-CAÑADELL & BOVER-ARNAL, 2017).

The rich diversity of the Oligocene Internal Prebetic, which includes some potential endemic forms, challenges current hypotheses regarding the origin and early diversification of species that later spread across the Tethys. The continuity of the succession throughout almost the entire Oligocene enabled the study of the evolutionary history of several genera, providing new insights into their evolutionary trends and introducing new biometrical criteria for biostratigraphy. Comparison with biostratigraphic records of similar age reveal diachronic evolutionary patterns in different parts of the Tethys for certain genera, such as *Austrotrillina*, with implications for biostratigraphic interpretation and correlation, as well as in migration pathways.

The main results of this study are summarised below:

- Several species of larger Foraminifera are reported for the first time in the westernmost Tethys: *Neorhipidionina* in the Priabonian; *Pfendericonus globulus* in the lower Rupelian; *Idalina pignatti*, *Peneroplis evolutus*, *P. flabelliformis*, and *P. thomasi* in the Rupelian-lower Chattian; and *Austrotrillina howchini*, *Elphidium* cf. *crispum*, and *Archaias* sp. in the upper Chattian.
- *Pfendericonus globulus* is a valid species occurring in the Priabonian and Oligocene, distinct from Thanetian-middle Eocene forms. Detailed study could reveal differences between Priabonian and Rupelian forms, which could be useful in biostratigraphy.
- *Neorotalia burdigalensis* is characteristic of the Oligocene Tethys, but ranges from the Eocene to the Lower Miocene, showing a gradual increase in proloculus size. A detailed biometrical study could provide a new biostratigraphic marker for the Priabonian-Chattian interval.
- In absence of miogypsinids, the last occurrence of *Praerhapydionina delicata* appears to be the best criterion for identifying the Rupelian/Chattian boundary. The FO of *Heterostegina assilinoides* may also indicate SB 22B, but a revision of Oligocene *Heterostegina* is needed. A further proposed criterion is the occurrence of *Neorotalia burdigalensis* with $P > 90$ µm.

- Four *Austrotrillina* species are considered valid: *A. eocaenica*, *A. paucialveolata*, *A. striata*, and *A. howchini.* The Rupelian *A. paucialveolata* is most probably a descendant of the Priabonian *A. eocaenica*. The species currently considered, *A. asmariensis*, *A. striata*, and *A. brunni*, are actually morphotypes of a single *A. striata*. The high variability in growth type and protoconch diameter prevents the use of these characters in species diagnoses. *Austrotrillina howchini*, characterised by a complex exoskeleton with bifurcated alveoli and narrow chamber lumina (and not by the absence of flexostyle), originated diachronically from *A. striata*, with earliest occurrences in the Chattian of the Prebetic and the Middle East, and later occurrences in the Middle Miocene of Australia. Previously considered an Indo-Pacific Miocene species, *A. howchini* probably originated in the late Rupelian-early Chattian of Turkey.
- In the Prebetic, *Borelis* is represented by two species, *B. inflata* and *Borelis* sp. 1. The latter shows characters intermediate between *B. inflata/B. merici* and *B. pygmaea*. Small *Borelis* specimens from the Prebetic are interpreted as juvenile forms, and the current diagnoses and biostratigraphic interpretation of *B. pulchra* are questioned.
- *Praebullalveolina-Bullalveolina* and *Borelis* are two parallel lineages of alveolinids that originated in the Eocene and extend into the Oligocene. *Praebullalveolina-Bullalveolina* is known from the Priabonian and the Rupelian, whereas *Borelis* ranges from the Priabonian to the Recent. The recent re-assignment of topotypes of the Miocene species *Borelis curdica* to *Praebullalveolina* (SIREL *et al.*, 2020b) implies a gap in the fossil record of the latter genus spanning the Chattian-Aquitanian. The re-assignment also calls into question the reliability of Y-shaped septula as a diagnostic character and further complicates the interpretation of phylogenetic relationships between the two lineages.
- The genus *Sorites* seems to be polyphyletic. Its abundance in the Oligocene of the Prebetic, compared with minor occurrences in Italy, Malta and France and its absence in the Oligocene of Turkey, Oman, and Iran, suggests a possible origin in the westernmost Tethys. A second, parallel lineage seems to have originated in the Indo-Pacific (Japan, Australia, Papua). This polyphyletic origin is consistent with molecular phylogenetic data from recent species.
- In the Prebetic, the last occurrence of *N. fichteli* was observed at the base of SB 22A in the Ibi section. In contrast, *N. vascus* and *N. kecskemetii* persist up to the latest SB 23. The last occurrences of *N. vascus* suggest a diachronous extinction, beginning at the end of the Rupelian (SB 22A) in the Indo-Pacific and roughly progressing westwards.
- The Western Neothethys miogypsinids lacking lateral chamberlets, traditionally assigned to *Miogypsinoides*, actually belong to the genus *Miogypsinella*. Four species of *Miogypsinella* (= *Miogypsinoides* auct.), which differ in the number of spiral chambers, together with *Postmiogypsinella intermedia*, occur in the Chattian of the Prebetic.
- The two known species of *Risananeiza*, *R. crassaparies* and *R. pustulosa*, recently interpreted as ecophenotypic forms of the same species, actually correspond to partial intervals of a continuous, anagenetic species that spans the entire late Chattian (SB 23).
- The stratigraphic distribution of the two *Risananeiza* species, combined with that of miogypsinid species, allowed us to differentiate two sub-biozones within Shallow Benthic zone 23: The lower sub-biozone, SB 23A, is characterised by *Risananeiza crassaparies*, *Miogypsinella complanata*, *M. formosensis*, and *Eulepidina elephantina*. The upper sub-biozone, SB 23B, is characterised by *Risananeiza pustulosa*, *Miogypsinella borodinensis*, *M. akcadagensis*, and *Postmiogypsinella intermedia*.
- *Pfendericonus* and *Austrotrillina* experienced a *Lilliput effect* through the Eocene-Oligocene transition, marked by a reduction in test size, proloculus size, and overall morphological complexity.
- The evolution of larger Foraminifera species is gradual and diachronic, as evidenced by morphological changes in *Austrotrillina* and by the varying timing of transitional forms and new morphotypes across the Tethys. Diachronic evolution in foraminiferal species or lineages must be considered when establishing biostratigraphic correlations between distant regions.
- *Amphistegina bohdanowiczi* originated from *Asterigerina* during the Rupelian and evolved into *A. mammilla* in the late Chattian. The presence of *A. mammilla* in the earliest late Chattian in the Ibi section challenges the current interpretation that places its origin in the Indo-Pacific and its migration to the Western Tethys during the Miocene.
- The studied sections reveal a remarkable diversity of Foraminifera: more than 20 species in the Priabonian, over 40 species in the Rupelian, and about 40 in the Chattian, with a total of approximately 62 species recognised throughout the entire Oligocene. Furthermore, the Oligocene

Prebetic was likely a centre of origin of several taxa, such as *Austrotrillina*, *Sorites* or *Amphistegina*, which later expanded eastwards to the Central Tethys.

As previously shown for other genera, the evolution and extinction of larger Foraminifera species in different bioprovinces are diachronic, and polyphyletism occurs (*e.g.*, MERKADO *et al.*, 2013; RENEMA, 2015; FERRÀNDEZ-CAÑADELL *et al.*, 2023a, 2023b). Biostratigraphic correlations across bioprovinces must therefore account for possible diachronism in evolutionary and extinction patterns. Assigning the same species name to populations from different bioprovinces with a similar anagenetic development can be misleading and may lead to erroneous interpretations of biostratigraphy, palaeobiogeography, and migration events.

Biostratigraphic correlation and the interpretation of palaeobiogeographical distribution and migration events are strongly influenced, and often distorted, by several factors:

a) Subjective systematics, which may lead different authors to assign the same form to different species, or to changes in taxonomy as knowledge of the groups improves. Examples include the varying species assignments of *Austrotrillina* populations or the occurrences of the genus *Risananeiza* prior to its formal erection in 2008, when they were reported as other rotaliid genera.

b) Local absence or lack of depositional environments with favourable conditions for certain groups. For instance, the general scarcity of shallow facies of Priabonian and Oligocene age in the Western Tethys.

c) Erroneous biostratigraphic interpretations of faunal changes caused by abrupt environmental shifts. An example is the transition from porcellaneous-dominated to hyaline-dominated facies in several Oligocene sections, linked to eustatic transgressive-regressive megacycles.

d) Changes in chronostratigraphic interpretations based on new relative or numerical dating. For example, historical revisions of the term "Aquitanian" (*e.g.*, EAMES, 1953; DROGGER, 1964) or the redefinition of the Priabonian GSSP and the Eocene/Oligocene boundary using isotopic, planktic foraminiferal, and calcareous nannoplankton events, which affect the timing of Eocene larger foraminiferal extinctions (*e.g.*, the extinction of orthophragminids now placed in the lowermost Oligocene).

e) Diachronic parallel evolution and extinction of species, as well as polyphyletic origin of genera.

Palaeobiogeographic and diversity studies should therefore go beyond an uncritical compilation of literature citations. They must include a review of historical changes in systematics, phylogeny, biostratigraphy, chronostratigraphy, and the specific chronostratigraphic history of each locality. This study addresses some of these biases and misinterpretations and offers a new perspective on the Oligocene of the Western Tethys. Nevertheless, several questions remain unresolved, such as the origin and possible polyphyletism of *Sorites* and *Amphistegina*. In addition, several forms observed in the samples could not be identified due to the low number of specimens or the absence of loose specimens suitable for biometric analysis on centred sections, particularly in lepidocyclinids. Future research should address these limitations to refine the biostratigraphy and biodiversity of the Prebetic, thereby improving our understanding of the palaeobiogeography of Oligocene larger Foraminifera from the Tethys.

Acknowledgements

This study is a contribution to projects CGL 2015-69805-P and PID2020-113912GB-100, funded by the Spanish Ministry of Science and Innovation and the European Regional Development Fund (ERDF); the I+D+i research project IBERCAFO (PID2024-159218NB-I00), funded by MCIN/AEI/10.13039/501100011033 and the European Regional Development Fund (ERDF), and the Grup de Recerca Reconegut per la Generalitat de Catalunya 2021 SGR-Cat 00349 "Geologia Sedimentària". The authors are grateful to Alejandro GALLARDO GARCIA (Laboratory of Palaeontology, Faculty of Earth Sciences, University of Barcelona) for his fine work preparing the thin sections. We would like to thank the reviewers, Lorenzo CONSORTI and Mohsen YAZDI-MOGHADAM, as well as the editors George PLEŞ and Robert SCOTT for their constructive comments which helped to improve the manuscript.

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Appendix

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