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Porcelaneous larger foraminiferal responses to Oligocene–Miocene global changes

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A B S T R A C T

Sea surface temperatures (SST) have been identified as a main controlling factor on larger benthic foraminifera (LBF) living in tropical to sub-tropical shallow-water carbonate and mixed siliciclastic-carbonate platforms. Changes in SST, along with those in ocean acidification and nutrient content recorded in the global oceans throughout their history will not only continue but also be amplified in the future at an unprecedented rate of change possibly reaching levels found in the geological record. This study focuses on the Oligocene (mean SST 8 °C higher than present) and the Miocene (SST 5–8 °C higher than present) epochs which were characterized by a higher richness in porcelaneous LBF (pLBF) than today. A systematic re-assessment and comprehensive literature survey of stratigraphic ranges and palaeogeographic distribution in the Western Tethyan (Mediterranean) and Indo-Pacific regions are used to evaluate the impact of changes in SST, seawater pCO_2 and pH on the biodiversity of the Oligocene–Miocene pLBF *Alveolinella*, *Austrotrillina*, *Borelis*, *Bullalveolina*, *Flosculinella,* and *Praebullalveolina*. Two peaks in species richness were identified during the Aquitanian and Langhian–Serravallian. These peaks occurred when SST was ~29 °C, with pCO_2 of ~400 ppm and pH > 7.8. These values are comparable to those of today. The minima in species richness recorded in the Rupelian–early Chattian, in the Burdigalian and from the Tortonian onward can be correlated to the detrimental effects of both minimum (< 26 °C) and maximum (> 31 °C) SST thresholds. High pCO_2 (> 600 ppm) values, which are limited to the Rupelian–early Chattian, are also detrimental to species richness. Seawater pH higher than 7.7 did not negatively affect species richness. These historical trends have serious implications for the future diversity of pLBFs with the increasing likely scenario of rising SST and pCO_2 and lowering of pH values in the near future. These developments can potentially lead to diversity decrease and even extinction of pLBFs. However, the resilience of present-day pLBF species to rising SST and pCO_2 levels is underpinned by the evolutionary histories of their fossil counterparts during climate variations, albeit at much different rates of change.

1. Introduction

Warming and changes in ocean carbonate chemistry are stressors to shallow-water marine calcifying benthic organisms. Corals, bryozoans, molluscs, benthic foraminifera and coralline red algae are subjected to these stressors (e.g., Anthony et al., 2008; Albright et al., 2018; Abrego et al., 2021; Kerr et al., 2021; Peña et al., 2021; Li et al., 2022). The expected reaction of marine organisms to continuing climate change is complex and includes extirpation and extinction due to changing environmental conditions (see Penn and Deutsch, 2022), range shifts

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tracking variations in environmental parameters (e.g., Platts et al., 2019) as well as evolutionary responses favouring populations with higher tolerance levels (e.g., Bennett et al., 2019; Donelson et al., 2019; Palumbi et al., 2019).

Changes in sea surface temperature (SST), pH, expansions and retractions of oxygen minimum zones, and eustatism have been recorded in the global ocean throughout its history (Zachos et al., 2001; Orr et al., 2005; Norris et al., 2013; Ash et al., 2018; Miller et al., 2020). These oceanographic changes are projected to continue and be amplified in the future with an unprecedented rate of change possibly reaching levels recorded in geologic times (Gattuso et al., 2015). SSTs and trophic levels have been identified as the main constraints on larger benthic foraminiferal distribution (e.g., Belasky, 1996; Langer and Hottinger, 2000; Weinmann et al., 2016). The global distribution of modern larger benthic foraminifera (LBF) is restricted by minimum winter SSTs of 14–20 °C depending on tolerances of individual taxa to lower temperatures (Förderer et al., 2018).

In the Indo-Pacific, only two genera of porcelaneous larger benthic foraminifera (pLBF) of the superfamily Alveolinoidea thrive in present-day, reef-related tropical shallow-water marine environments: *Borelis* de Montfort, 1808 and *Alveolinella* H. Douvillé, 1907. These genera originated in the middle Eocene and in the Middle Miocene respectively (e.g., Hottinger, 1974; Loeblich and Tappan, 1987). *Borelis* is represented by *Borelis schlumbergeri* (Reichel, 1937), widespread from the Western (i.e., Red Sea) to the Central Indo-Pacific, by *B. pulchra* (d'Orbigny, 1839) from the Eastern Indo-Pacific to the Caribbean area (Bassi et al., 2021a), and by *B. matsudai* Bassi and Iryu, 2023 from the Ryukyu Islands (Bassi et al., 2023). *Alveolinella quoyi* (d'Orbigny, 1826), the only modern representative of the genus, has been identified in the Central and Eastern Indo-Pacific (from the Maldives to Hawaii; e.g., Langer and Hottinger, 2000).

In the geological record, these taxa have been found associated with other pLBF which are known only as fossils: *Austrotrillina* Parr, 1942 and *Flosculinella* Schubert *in* Richarz, 1910. *Austrotrillina* included four species ranging from the latest Eocene to the Middle Miocene (Bassi et al., 2021b), and *Flosculinella* comprised three species from the latest Oligocene to the Middle Miocene (Hottinger, 1974; Lunt and Allan, 2004; Bassi et al., 2022). The monospecific *Bullalveolina bulloides* (d'Orbigny) Reichel, 1936 has been identified only in the Rupelian of the Mediterranean area (Hottinger, 1974; Cahuzac and Poignant, 1997; BouDagher-Fadel and Price, 2021). *Praebullalveolina oligocenica* Sirel and Özgen-Erdem (*in* Sirel et al., 2013) has been identified in the Rupelian of Turkey and Oman (Sirel et al., 2013; Serra-Kiel et al., 2016). The single record of *Bullalveolina boninensis* Matsumaru, 1996 from the Oligocene of the Ogasawara Islands (Japan) needs further confirmation.

Although other pLBF occur in the present-day oceans, their morphological features, biostratigraphical ranges, and palaeobiogeographic patterns have not been assessed in detail. These living pLBF are *Amphisorus*, *Archaias*, *Marginopora*, *Peneroplis,* and *Sorites* which appeared at different times from the early Oligocene to the Middle Miocene in the Western Tethyan and Indo-Pacific areas (Lunt and Allan, 2004; Renema, 2007, 2008; Riera et al., 2019). Only two species of the exclusively fossil taxon, *Pseudotaberina* Eames in Davies, 1971 (emend. Banner and Highton, 1989), have been recorded both from the Burdigalian of India, south-eastern Asia (Renema, 2008) and Iraq (Henson, 1950). However, a reliable and up-to-date species-level circumscription is lacking in pLBF genera other than *Alveolinella*, *Austrotrillina*, *Borelis*, *Bullalveolina*, *Flosculinella,* and *Praebullalveolina* which are, therefore, the only pLBF which can be discussed in terms of palaeobiogeographic distributions and biostratigraphic ranges from the Oligocene (33.9–23.03 Ma) to the Middle Miocene (23.03–11.63 Ma) of the Western Tethyan and Indo-Pacific areas.

The species richness of pLBF that thrived in reef-related settings in the Oligocene and Early–Middle Miocene was higher than that of today. The Oligocene climate state was characterized by relatively warm global mean temperatures, flattened meridional temperature gradients, and the presence of Antarctic continental ice sheets (e.g., O'Brien et al., 2020). Recently, the Miocene, with a dynamic climate of sustained, polar amplified warmth, has been considered as a strong candidate to serve as a future climate analogue (Steinthorsdottir et al., 2021). In particular, the Miocene Climatic Optimum (MCO; c.16.9–14.8 Ma) stands out as an extended interval of sea level rise (Miller et al., 2020), > 7 °C warmer than the modern world (Steinthorsdottir et al., 2021). This interval has been considered as a particularly appropriate analogue for future climate scenarios for its higher temperatures and moderately higher pCO_2 compared with preindustrial values (e.g., Hönisch et al., 2012; Dove et al., 2013). Subsequent to the MCO, the time interval recording the abrupt cooling and a phase of Antarctic ice-sheet expansion is termed the Middle Miocene Climatic Transition (MMCT; 14.8–13.9 Ma; Steinthorsdottir et al., 2021).

Research into the effects of ocean acidification (increase pCO_2, lowering pH) has so far been performed on only a few species of LBFs in laboratory experiments, likely underestimating the impact of ocean acidification on their diversity at larger geographic and time scale. Here, we attempt to provide a better understanding of tropical and subtropical Western Tethyan and Indo-Pacific dynamics during warmer near-equilibrium climate states by investigating the pLBF species richness during past warm periods. We focus on the Oligocene (SST > 8 °C warmer than present; e.g., O'Brien et al., 2020) and the Miocene (SST ~10–15 °C warmer than present, 30°N–30°S; e.g., Burls et al., 2021; Steinthorsdottir et al., 2021). The data for this study is drawn from a comprehensive literature survey and systematic reviews of Oligocene–Miocene pLBF species to evaluate the impact of changes in eustatic sea-level fluctuations, SST, seawater pCO_2, and pH on the pLBF biodiversity. We analyse the biodiversity dynamics of this widespread reef-related foraminiferal group in the Western Tethys and Indo-Pacific basins during changing ocean conditions.

2. Methods

The biostratigraphical assessments of the species of *Alveolinella*, *Austrotrillina*, *Borelis*, *Bullalveolina,* and *Flosculinella* from the early Oligocene to the Late Miocene in the Mediterranean and Indo-Pacific regions were based on 341 published reports ranging from monographs on LBF to sedimentological articles (Appendix A, Supplementary data; Bassi et al., 2021a, 2021b, 2022). The first and last occurrences of the studied species are located on palaeomaps proposed by Rögl (1998), Meulenkamp and Sissingh (2003), and Kocsis and Scotese (2021).

Three types of data set were compiled (Table 1). The Stage-Level data

Table 1
Number of species of *Alveolinella*, *Austrotrillina*, *Borelis*, *Bullalveolina*, *Flosculinella,* and *Praebullalveolina* at the series (SL) and stage (StL) levels reported from the Western Tethys (WT) and Indo-Pacific (IP) basins from the Oligocene to the Miocene. Maximum number of species occurring in a single basin in each stage (intra-basin species richness, ibs). SL/Ma are species richness values normalized by series interval length in million years (/Ma; Cohen et al., 2013, updated).

	SL	StL	ibsWT	ibsIP	SL/Ma
Mess		4	1	3	
Tort		7	3	4	
L Mioc	7				1.11
Serr		10	5	5	
Lang		11	5	8	
M Mioc	11				2.53
Burd		13	5	11	
Aqui		10	4	8	
E Mioc	13				1.84
Chat		9	4	6	
Rup		9	6	4	
Oligoc	10				0.92

Oligoc, Oligocene; E Miocene, Early Miocene; M Mioc, Middle Miocene; L Mioc, Late Miocene; Rup, Rupelian; Chat, Chattian; Aqui, Aquitanian; Burd, Burdigalian; Lang, Langhian; Serr, Serravallian; Mess, Messinian; Tort, Tortonian.

regard the recorded numbers of species (species richness) to stage level. The Series-Level data include the data on species for which the stratigraphic distribution is only known at the series level. The chronostratigraphic intervals (series) are Oligocene, Early, Middle and Late Miocene. The Intra-Basin Species Richness (ibs) is the number of species recorded in the Mediterranean and Indo-Pacific. All datasets were normalized by series and stage lengths (time scale after Cohen et al., 2013, updated). The correlations between the European stages and the Letter Stages follow Lunt and Allan (2004) and Renema (2007).

Species-richness data are plotted both on a chronostratigraphic scale and on a scale of absolute age following the values for stage boundaries provided by the International Stratigraphic Chart (Cohen et al., 2013, updated). Diagnostic characters for genera and species are discussed in Bassi et al. (2021a, 2021b, 2022). When provided, the illustrations of the species in the analyzed publications helped to evaluate the taxonomic identity and the morphological diversity independently of the reported names.

The pH data cited here are based on boron isotopes of marine biogenic carbonates. It has been pointed out that boron isotope composition of the biogenic carbonates indicates the pH of their calcification sites rather than the seawater pH (see Zeebe, 2012). However, since this discussion is not the main topic of this paper, we assume that boron isotope-based pH represents seawater pH.

3. Porcelaneous larger foraminiferal records in the Western Tethys

3.1. Oligocene

Six species have been reported from the Mediterranean Oligocene (Fig. 1, Table 1). *Borelis pygmaea* has been identified in southern Italy, Turkey, Oman and Yemen (De Castro, 1987; Cahuzac and Poignant, 1997; Gedik, 2017; Serra-Kiel et al., 2016). The first appearance datum (FAD) of *Borelis inflata* is in the Rupelian of the Mediterranean and Indo-Pacific areas. This species is common in the Mediterranean, with a long-lasting occurrence up to the Tortonian (Sirel, 2003; Di Carlo et al., 2010; Benedetti, 2010). *Bullalveolina bulloides* and *Praebullalveolina oligocenica* are exclusive eastern Mediterranean and Oman species restricted to the Rupelian (Cahuzac and Poignant, 1997; Sirel et al., 2013; Serra-Kiel et al., 2016; Fig. 1). The Rupelian FAD of *Austrotrillina brunni* is in the eastern Mediterranean (Greece, Turkey; Wielandt-Schuster et al., 2004; Sirel et al., 2013; Gedik, 2017) and in the Indo-Pacific corridor (Socotra

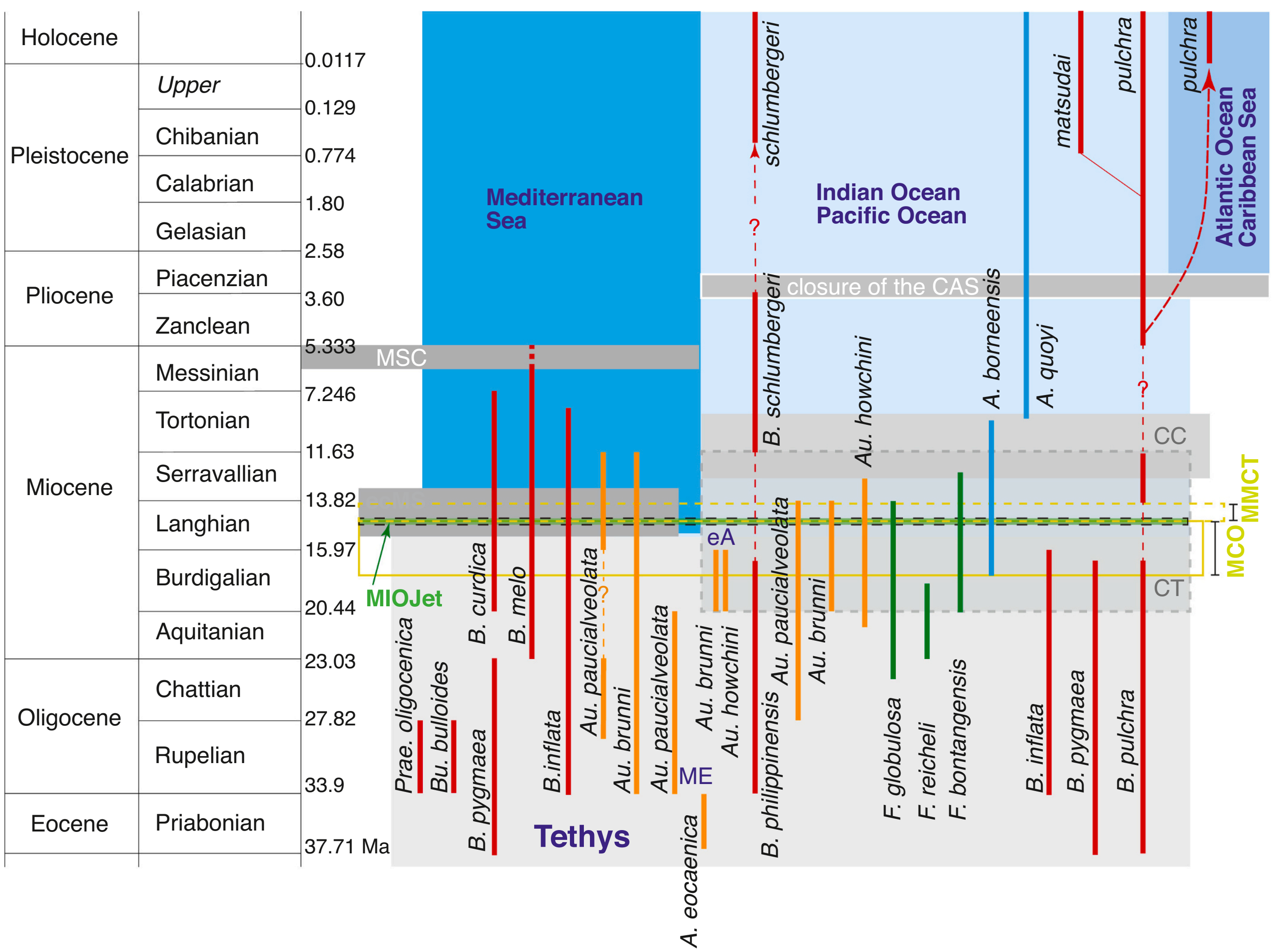

Fig. 1. Biostratigraphic patterns of the Oligocene and Miocene *Alveolinella* (*A.*), *Austrotrillina* (*Au.*), *Borelis* (*B.*), *Bullalveolina* (*Bu.*), *Flosculinella* (*F.*) and *Praebullalveolina* (*Prae.*) species. *Borelis melo*, *Borelis curdica*, *Bullalveolina bulloides* and *Praebullalveolina oligocenica* are exclusive species of the Western Tethys (Mediterranean area), whereas *Austrotrillina howchini*, *Borelis pulchra*, *Borelis schlumbergeri*, *Alveolinella* and *Flosculinella* species were identified only in the Indo-Pacific areas.
CAS, Central America Seaway; CC, Indo-Pacific carbonate crash (c. 13.2–c. 8.7 Ma); CT, Miocene Coral Triangle; eA, eastern Africa; ecMS, eastern closure of the Mediterranean Sea; MIOJet, Miocene Indian Ocean Equatorial Jet; MCO, Miocene Climatic Optimum (c.16.9–14.8 Ma); MMCT, Middle Miocene Transition (c.14.8–13.9 Ma); MSC, Messinian Salinity Crysis.

Island, western Kutch, Kuh e Pataq; Adams, 1968; Serra-Kiel et al., 2016; Susanta, 1990; Fig. 2). The first occurrence datum (FOD) of *Austrotrillina paucialveolata* (= *Austrotrillina striata*) is late Rupelian in the Mediterranean area (southern Spain; Bassi et al., 2021b), although its FAD is early Rupelian in Iraq, Oman, Iran, Socotra Island, and western Kutch (Grimsdale, 1952; Susanta, 1990; Boukhary et al., 2010; Serra-Kiel et al., 2016; Karevan et al., 2014; Fig. 2).

3.2. Early Miocene

An overall number of five species has been identified in the Early Miocene: four in the Aquitanian and five in the Burdigalian (Fig. 1, Table 1). *Borelis melo* and *B. curdica* are exclusively found in the Mediterranean area (Fig. 2). The Aquitanian FAD of *Borelis melo* is in the central-eastern Mediterranean and in the Middle East (e.g., Ctyroky et al., 1975; Karim, 1978). *Borelis curdica* has been identified mainly in the Mediterranean area with a Burdigalian FAD in south-western France (Cahuzac and Poignant, 1997) and in Iran (Hottinger, 1974; Seyrafian et al., 2011; Saleh, 2014). Eastward, the Burdigalian FODs of *Austrotrillina brunni* are from eastern Africa (Kenya; Eames et al., 1962) and western India (Dasgupta, 1977).

3.3. Middle–Late Miocene

A total of five species have been reported: *Austrotrillina brunni*, *A. paucialveolata*, *Borelis inflata*, *B. melo,* and *B. curdica* (Fig. 1, Table 1). There are many Langhian records of *Borelis melo* and *B. curdica* in the Mediterranean, the Paratethys, and the Middle East. In the Serravallian, *B. melo* occurs only in SE Spain (*B. melo*; Hottinger, 1974; Bassi et al., 2021a; Fig. 3) and Lebanon (BouDagher-Fadel and Clark, 2006), whereas *B. curdica* was reported in Israel (Buchbinder et al., 1993). The single records of *Austrotrillina brunni* and *A. paucialveolata* are from the Serravallian of SE Spain (Bassi et al., 2021b). Three species have been reported from Upper Miocene sedimentary successions. The last occurrence datum (LAD) of *Borelis curdica* is in the Tortonian of north-western Italy and Israel (Reiss and Gvirtzmann, 1966; Bassi et al., 2021a; Fig. 2). The LAD of *Borelis inflata* is in the Tortonian of north-western Italy (Bassi et al., 2021a). *Borelis melo* has been identified in the Tortonian of the Central Apennines and south-eastern Spain (Betzler and Schmitz, 1997; Brandano et al., 2016; Bassi et al., 2021a), with its LAD in the single Messinian record from south-eastern Spain (Betzler and Schmitz, 1997; Bassi et al., 2021a).

4. Porcelaneous larger foraminiferal records in the Indo-Pacific

4.1. Oligocene

Four species have been found in Oligocene rocks of the Indo-Pacific area (*Borelis inflata*, *B. philippinensis*, *B. pulchra*, *B. pygmaea*) of which *B. inflata* and *B. pygmaea* also occur in the Mediterranean. *Borelis pulchra* and *B. pygmaea*, originated in the late Eocene, whereas *B. inflata* (FAD) has been recorded throughout the Oligocene from Christmas Island (Adams and Belford, 1974) to the Philippines and Borneo (Adams, 1965; Matsumaru, 2011; Fig. 1). The types of *Borelis inflata* are from the Oligocene–Early Miocene of Sarawak (Borneo; Adams, 1964, 1965; Matsumaru, 1974). The FAD of *Borelis philippinensis* is recorded in the Rupelian Sarawak limestone (Tutoh River, Borneo; Adams, 1965; Fig. 2). An overall number of six species has been mentioned from the Chattian, including the above mentioned four *Borelis* species. *Austrotrillina paucialveolata* is a newcomer from the Western Tethys, whereas *Flosculinella globulosa* first appears (FAD) in the Chattian of the Philippines (Matsumaru, 2011, 2017) and Bikini (Cole, 1954a, 1969).

4.2. Early Miocene

A total of eleven species have been reported, with eight species in the Aquitanian and eleven in the Burdigalian (Fig. 1, Table 1). Six out of the eight Aquitanian species originated in the Oligocene. *Flosculinella reicheli* first appears in the Aquitanian of Borneo (Mohler, 1949; Adams, 1965; Hottinger, 1974). In the latest Aquitanian the FAD of *Austrotrillina howchini* took place in Kenya, Tanzania, and Indonesia (Eames et al., 1962; Adams, 1968; Bassi et al., 2021b; Figs. 2–3). The maximum species richness is recorded in the Burdigalian with eleven species. *Austrotrillina howchini* reaches the Burdigalian in southern India (Rögl and Briguglio, 2018), Borneo (Bassi et al., 2021b), the Philippines (Schlumberger, 1893), and Western Australia (BouDagher-Fadel, 2018). The Mediterranean eastward migrant *Austrotrillina brunni* occurs in the Burdigalian of Sumbawa (Indonesia, Barberi et al., 1987). The FAD of *Flosculinella bontangensis* is in Pemba Island (Tanzania; Davies, 1927; Eames et al., 1962), Borneo and Indonesia (Leupold and Vlerk, 1931; Barberi et al., 1987; Bassi et al., 2022), and the Philippines (Matsumaru, 2017). *Alveolinella borneensis* first appears (FAD) in the Burdigalian of the Moluccas (Hottinger, 1974; Fig. 2). The LADs of *Borelis inflata* and *B. pygmaea* are in Borneo (Adams, 1964, 1965; Matsumaru, 1974), and in the Philippines and Borneo (BouDagher-Fadel and Banner, 1999; Adams, 1965) respectively. The lower Burdigalian LAD of *Flosculinella reicheli* is in Borneo (Mohler, 1949; Adams, 1965; Hottinger, 1974). *Borelis inflata* and *B pygmaea* disappear (LAD) in the latest Burdigalian (Adams, 1965; BouDagher-Fadel and Banner, 1999; Matsumaru, 2017).

4.3. Middle–Late Miocene

Among the eight Langhian species, three of them disappear (LAD; *A. brunni*, *A paucialveolata*, *F. globulosa*; Fig. 3) in Western Australia, Kita-daito-jima and Java (BouDagher-Fadel and Lokier, 2005; O'Connell et al., 2012; Riera et al., 2019; Bassi et al., 2021b). In the Serravallian, only *Alveolinella borneensis* and *B. pulchra* last over the stage, whereas *Austrotrillina howchini* and *Flosculinella bontangensis* disappear (LAD; Fig. 2). The last records of *A. howchini* are from Indonesia and the Kikai Seamount (Barberi et al., 1987; Bassi et al., 2021b), and those of *F. bontangensis* are from northern and western Australia (Chaproniere, 1984; Riera et al., 2019). No records have so far been reported for *Borelis philippinensis/B. schlumbergeri* in the Middle Miocene and for *B. pulchra* in the Langhian (Bassi et al., 2021a). The Middle Miocene records the highest number of LAD with those of *Austrotrillina brunni*, *A. howchini*, *A. paucialveolata*, and all the *Flosculinella* species (Figs. 1–2). Four species have been reported for the Tortonian and three for the Messinian (Fig. 1, Table 1). There are two FADs in the Tortonian: the one of *Borelis schlumbergeri* in Guam and the Philippines (Cole, 1954b; Matsumaru, 1974) and that of *Alveolinella quoyi* in Indonesia. The LAD of *Alveolinella borneensis* also took place in Indonesia (Cole, 1957; Renema et al., 2015; Bassi et al., 2022; Fig. 2). The Messinian species (*Alveolinella quoyi*, *Borelis pulchra*, *B. schlumbergeri*) are still thriving in the present-day Indo-Pacific (Langer and Hottinger, 2000; Bassi et al., 2021a, 2022).

4.4. The Aquitanian and Langhian peaks of richness

The number of *Alveolinella*, *Austrotrillina*, *Borelis*, *Bullalveolina*, *Flosculinella,* and *Praebullalveolina* species recorded worldwide shows a strong increase from the Oligocene to the Miocene. Considering the total species names reported in the literature in each chronostratigraphic unit, at the series level species richness increases from the Oligocene (10 species) to the Early–Middle Miocene (13 and 11 species, respectively) and then dropped in the Late Miocene (7 species; Table 1, Fig. 4). At stage level, the maximum richness (13 species) is recorded in the Burdigalian and the minimum (4 species) in the Messinian (Table 1, Fig. 4).

If only the number of species identified separately in the Western

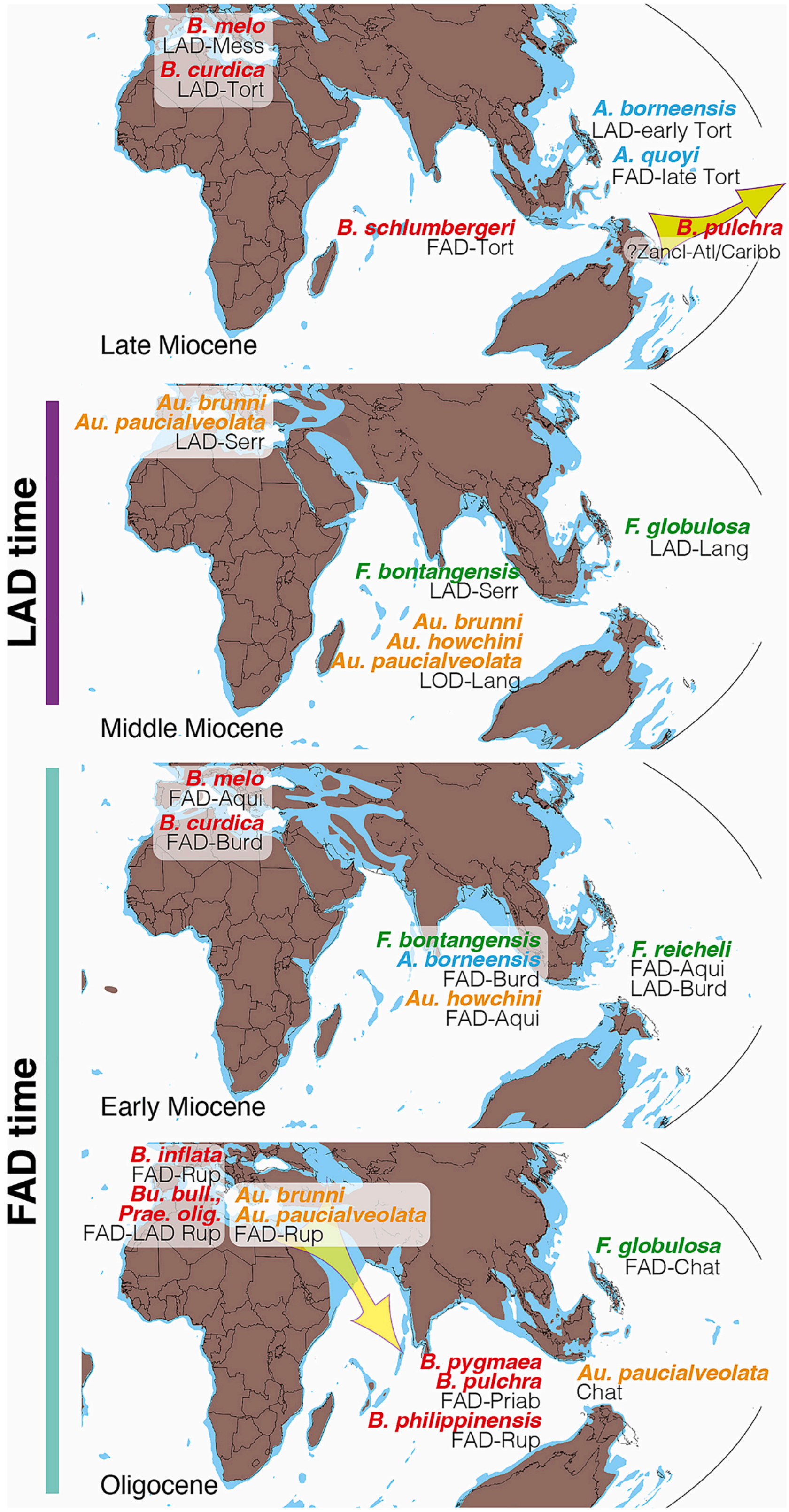

Fig. 2. First appearance data (FAD) and last appearance data (LAD) of *Alveolinella*, *Austrotrillina*, *Borelis*, *Bullalveolina*, *Flosculinella*, *Praebullalveolina* species in the Western Tethys and in the Indo-Pacific. The early Chattian is characterized by the highest number of FAD. The Langhian species contributing to the second peak in richness disappeared at the Langhian–Serravallian boundary, followed by a decrease in richness. Compare with Figs. 4–5.
Palaeogeographic maps modified from Rögl (1998), Meulenkamp and Sissingh (2003) and Kocsis and Scotese (2021).
Au., *Austrotrillina*; *A.*, *Alveolinella*; Aqui, Aquitanian; *B.*, *Borelis*; *Bu. bull.*, *Bullalveolina bulloides*; *Prae. olig.*, *Praebullalveolina oligocenica*; Burd, Burdigalian; Chat, Chattian; *F.*, *Flosculinella*; Lang, Langhian; LOD; Last Occurrence Datum; Rup, Rupelian; Serr, Serravallian; Tort, Tortonian; Zancl-Atl/Caribb, Zanclean-Atlantic/Caribbean.

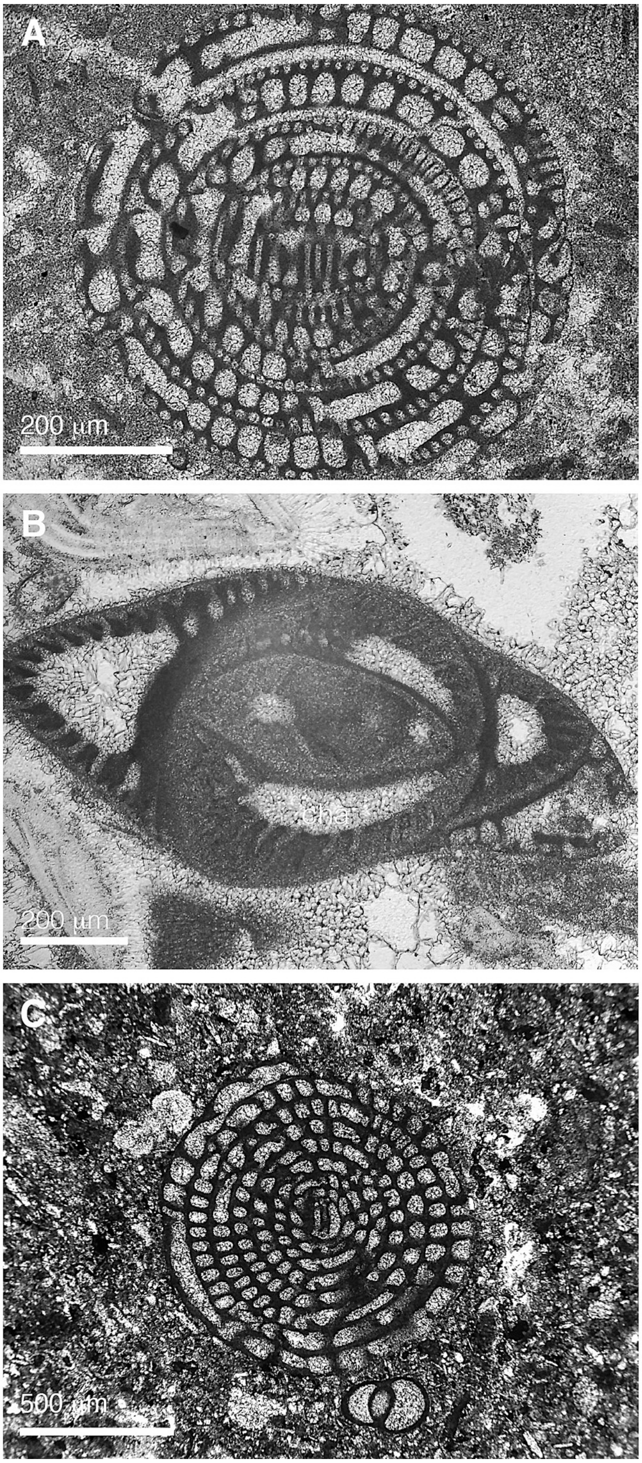

Fig. 3. Some studied species which occur exclusively in the Mediterranean (*B. melo*) or in the Indo-Pacific (*F. globulosa*, *A. howchini*, *A. borneensis*). Compare with Fig. 1.
Flosculinella globulosa (Rutten, 1917) (A) first occurs in the Chattian of Indo-Pacific and disappears in the Langhian (specimen from the early Burdigalian, Tallabar Limestone, Mankalihat Peninsula, East Kalimantan, Indonesia).
Austrotrillina howchini (Schlumberger, 1893) (B) appeared in the Aquitanian (eastern Africa, western India, Indonesia and Western Australia) and disappeared in the latest Langhian–early Serravallian (specimen from the early Burdigalian, Tallabar limestone, East Kalimantan, Indonesia).
Borelis melo (Fichtel and Moll, 1798) (C) appeared in the Aquitanian of the Western Tethys, and is the single species reaching the Messinian (specimen from Cabo de Gata, south-eastern Spain).

Tethys (Mediterranean area) and in the Indo-Pacific is considered (ibsWT, ibsIP; Fig. 4), there was a similar value in the Western Tethys (from 6 to 5) and a more evident rise in the Indo-Pacific (from 4 to 11) from the Rupelian to the Burdigalian–Langhian. Later, in the Messinian the ibsWT dropped to a single species (*Borelis melo*) and the ibsIP to three species (*Borelis pulchra*, *B. schlumbergeri*, *Alveolinella quoyi*). *Borelis melo* disappeared in the Mediterranean Messinian, whereas the three Indo-Pacific species are still living.

Regarding the species richness normalized to the interval length (Fig. 5, Table 1), at series level there is an increase from the Oligocene (0.92) to the Middle Miocene (2.53), followed by a Late Miocene drop (1.11). At the stage level, the three curves (i.e., StL/Ma, ibsWT/Ma, ibsIP/Ma) follow a fluctuating trend. The number of species increased abruptly from the Chattian to the Aquitanian, dropped in the Burdigalian, increased again in the Langhian–Serravallian, and then finally dropped in the Messinian. The Mediterranean and Indo-Pacific trends are similar.

The highest richness recorded in the Langhian in the Indo-Pacific (3.72) is comparable to the value in the Aquitanian peak (3.09). The lowest richness (0.52) occurs in the Mediterranean Messinian where only one species has been identified.

5. Discussion

5.1. Factors controlling the development and distribution of pLBF

The main local factors constraining the environmental distribution of larger foraminifera are irradiance, water energy, nutrients and substrate (Reiss and Hottinger, 1984; Hottinger, 1997; Hohenegger, 1999; Girard et al., 2022). However, water temperature is the main factor influencing their geographical distribution at a global scale (Hohenegger, 1999; Langer and Hottinger, 2000; Förderer et al., 2018).

Reduced shell growth, photosynthetic efficiency and changes in reproductive outputs are all effects of prolonged SST above thresholds of $\geq$31 °C (Schmidt et al., 2016; Doo et al., 2014; Fujita et al., 2014; Stuhr et al., 2017; Prazeres et al., 2017a; Hohenegger et al., 2019; Pinko et al., 2020) and below <25 °C (Fujita et al., 2014; Kinoshita et al., 2021; Reymond et al., 2022). Algal symbiosis can enhance calcification of photosymbiont-bearing hosts (i.e., LBF). However, because diverse groups of modern LBF host a wide variety of endosymbiotic algal types which differ among the hyaline perforated and pLBF, different calcification processes occur in hyaline and porcelaneous LBFs (e.g., Leutenegger, 1984; Reymond et al., 2013; Prazeres et al., 2017a). Reliable knowledge on endosymbiotic algae-temperature relationship affecting the growth is lacking in pLBF genera other than *Amphisorus*, *Marginopora,* and *Sorites* (Fujita et al., 2014; Kinoshita et al., 2021; Reymond et al., 2022).

Combined prolonged high temperature and light stress inactivate the photosystem, induce bleaching and reduce energy storage (Kawahata et al., 2019). This brings about increased susceptibility to bacterial/algal infection, diseases, changes in symbiont genotypes, and eventual death of the larger host foraminifer (van Dam et al., 2012; Prazeres et al., 2016, 2017b; Kawahata et al., 2019). Only two species of hyaline larger foraminifera (*Amphistegina lobifera*, *Pararotalia calcariformata*) are extremely high-temperature tolerant and able to photosynthesize and calcify at temperatures of up to 36 °C (Doo et al., 2014). Among the studied pLBF, *Alveolinella* is known to be affected by water temperature > 32 °C (Doo et al., 2014). The limits of other studied taxa are unknown.

Reduced surface ocean pH and $CaCO_3$ saturation state (i.e., ocean acidification) is detrimental to most marine organisms and ecosystems (e.g., Waldbusser et al., 2015). Present-day surface-pH values in the oceanic areas where pLBF occur are higher than ~8 (Jiang et al., 2019). In *Amphisorus* and *Marginopora*, growth and calcification tend to be reduced at elevated $p\mathrm{CO_2}$ levels of ~600 ppm and pH of < ~7.7 (Kuroyanagi et al., 2009; Fujita et al., 2011; Doo et al., 2014; Oron et al., 2020). Martinez et al. (2018) found a 50% decrease in growth rate of

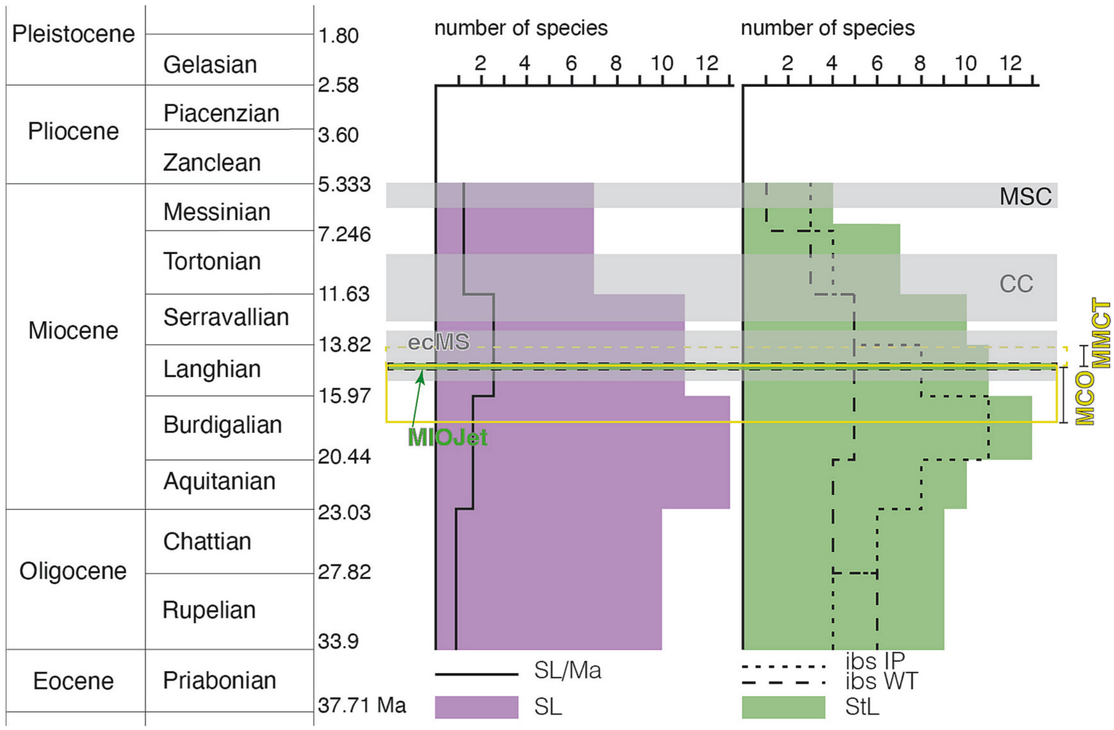

Fig. 4. Species number plots of *Alveolinella*, *Austrotrillina*, *Borelis*, *Bullalveolina*, *Flosculinella,* and *Praebullalveolina* from the Oligocene to the Miocene of the Western Tethys (WT) and Indo-Pacific (IP) areas at series (SL) and stage (StL) levels. The series level data normalized by series length (SL/Ma) and the intra-basin species richness (ibs) are also shown. At the series level, species richness shows the peak in the Early Miocene then decreases in the Late Miocene. At the stage level, the peak is in the Burdigalian with a drop in the Messinian. The ibsIP is always higher than the ibsWT. For abbreviations see Fig. 1.

Archaias angulatus after 28 days at pH 7.6. *Peneroplis* spp. showed some recovery abilities to short exposure (e.g., 3 days at pH 6.9 to 1 month at pH 7.4) to acidified conditions (Charrieau et al., 2022). These data suggest that pLBF are more vulnerable (i.e., lower calcification/dissolution) with elevated *p*CO2 (> ~ 600 ppm) and low pH (< 7.7) seawater than the hyaline foraminifera. Kawahata et al. (2019) concluded that, since the hyaline LBF are more resilient to these constraining pCO_2/pH levels, they will dominate over porcelaneous foraminifera in reef communities in the future.

5.2. Porcelaneous larger foraminiferal richness and global changes

The laboratory data (i.e., SST, pCO_2, pH values) as presented in previous paragraphs, coupled with the sea-level changes, are compared to and discussed in terms of estimated Oligocene–Miocene values for the studied pLBF species richness. As global SST, pCO_2, pH values are plotted against absolute ages, they are compared here to species richness data normalized by interval length. Among the pLBF that survived the Eocene–Oligocene biotic crisis (i.e., *Archaias*, *Austrotrillina*, *Borelis*, *Lacazinella*, *Peneroplis*, *Praearchaias*, *Praebullalveolina*; Hottinger, 1974; Loeblich and Tappan, 1987; Cahuzac and Poignant, 1997; Serra-Kiel et al., 1998; Sirel, 2015; BouDagher-Fadel and Price, 2021) only species of *Austrotrillina* and *Borelis* show robust taxonomic, biostratigraphic and palaeobiogeographic records (Bassi et al., 2021b, 2022). The other taxa have so far rarely been quoted in literature and identified only locally with scattered stratigraphical data available. The studied pLBF thrived in proximal shallow-water carbonate settings mostly above the fair-weather wave base (e.g., Buxton and Pedley, 1989; Betzler and Chaproniere, 1993; Hottinger, 1997; Beavington-Penney and Racey, 2004; Simmons, 2020), affected by sea-level and SST changes (Renema et al., 2008).

The data normalized by interval length show that the Oligocene increasing trend in richness of the studied pLBF species is positively correlated to sea-level rise and SST increase (Chattian; Miller et al., 2020; Westerhold et al., 2020; Fig. 5). These two factors brought about a wider proximal shallow-water carbonate habitat availability at the beginning of the pLBF diversification. The Aquitanian maximum species richness occurs after an eustatic drop (Miller et al., 2020), corresponding to the expansion of the Antarctic ice sheet (Zachos et al., 2001; Fig. 5), and the upper Chattian collision of the Southeast Asia with the Australia (Hall, 2002). These events likely favoured the evolution of the pLBF in widening shallow-water carbonate settings in the Western Tethys and Indo-Pacific (e.g., Renema et al., 2008; Maurizot et al., 2016; Cornacchia et al., 2021). The Aquitanian maximum species richness does not support the proposed Mediterranean biocalcification crisis (Brandano et al., 2017). The Aquitanian peak in richness corresponds, in fact, to a relatively long time span of constant SST of ~28–30 °C in the tropical areas (Steinthorsdottir et al., 2021). This temperature range, positively related to LBF growth (e.g., Narayan et al., 2022), likely favoured the increase in pLBF richness. The subsequent decrease in species richness during the Burdigalian parallels the global warming of the oceans (Steinthorsdottir et al., 2021) that resulted in tropical temperatures higher than the above-mentioned threshold of ≥31 °C.

The Aquitanian peak of species richness corresponds to pCO_2 at ~400 ppm (Table 2), a value which remains nearly stable during the Miocene after the drop at the Rupelian–Chattian boundary. Low pCO_2 values of < ~400 ppm have been recorded from the Chattian to the Serravallian (Zhang et al., 2013; Sosdian et al., 2018). Present-day *Amphisorus hemprichii*, *A. kudakajimensis*, *Marginopora rossi,* and *M. vertebralis* decrease in calcification rates at elevated pCO_2 (>790 ppm; Kuroyanagi et al., 2009; Fujita et al., 2011; Schmidt et al., 2014; Reymond et al., 2022), which are comparable to those estimated for the Rupelian when the pLBF richness is at its minimum (Fig. 5).

During the Burdigalian global warming, the species richness increases to the maximum of 11 species in the Indo-Pacific. However, the richness normalized by the interval length is lower than that in the Aquitanian (2.46 *versus* 3.09; Table 1, Fig. 5). Considering that pCO_2 levels are comparable in the two stages, the increased Burdigalian SST at

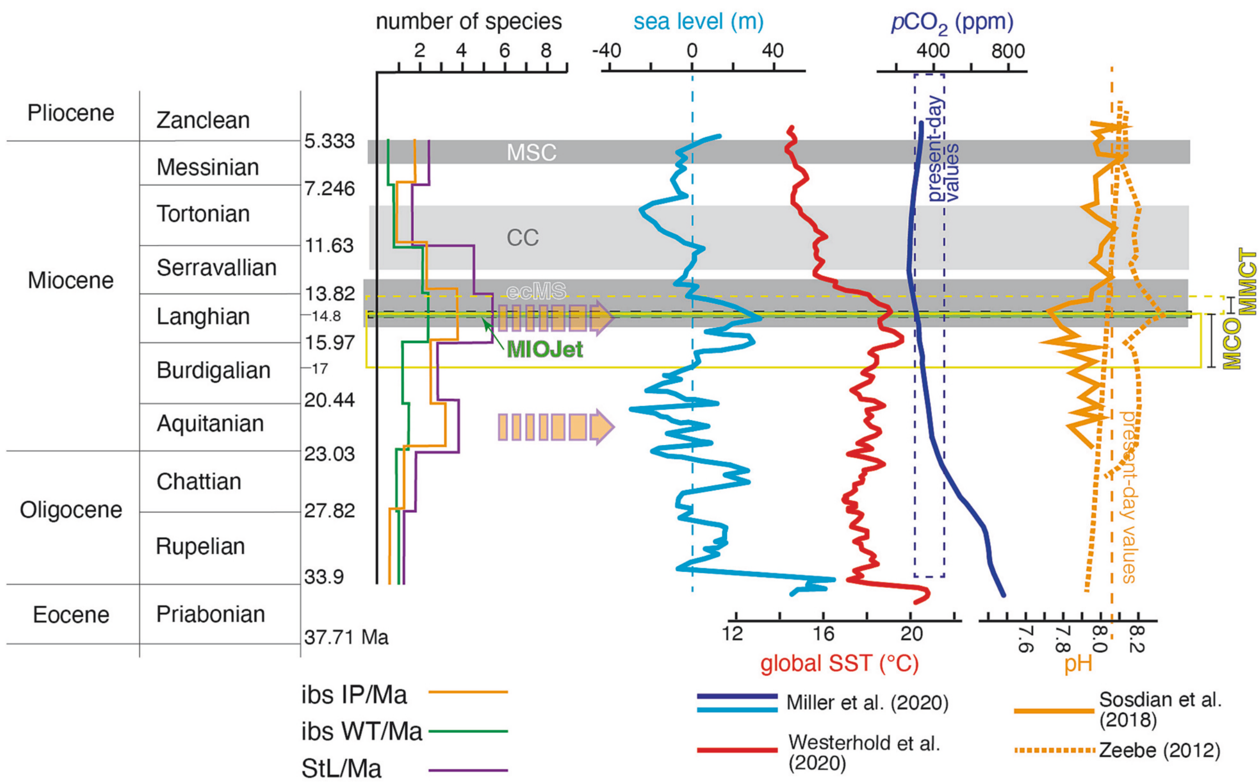

Fig. 5. Stage level (StL) and intra-basin species (ibs) richness normalized by stage length (/Ma) compared with the global eustatic curves, global SST estimates, pCO_2 and pH mean values. At the beginning of the evolution of the studied pLBF group the Oligocene species richness increases up to the Aquitanian peak (orange arrow). This increase is positively correlated to the Chattian peaks in sea-level curve (e.g., Miller et al., 2020) and global SST (e.g., Westerhold et al., 2020). The Burdigalian decrease in diversity follows a substantial sea-level fall. The Langhian peak in richness (orange arrow) corresponds to a sea-level highstand and SST peak, at the late MCO. This peak in richness is recorded in shallow-water reef-related areas, expanded latitudinally during the MCO. Sea-level rises, and the nearly coeval global SST increase, might have played a role in diversification of pLBF by widening and enhancing habitat availability. The post-Langhian decrease in diversity might be more driven by SST as it considerably affected the Mediterranean pLBF richness. Further details in the text. For abbreviations see Fig. 1.

values higher than the threshold of ≥31 °C effectively constrained the diversity of pLBF. Despite the high Burdigalian SST and the significantly flattened latitudinal temperature gradients, pCO_2 is similar to that of today, making this time slice an interesting warm-climate analogue (Steinthorsdottir et al., 2021).

The closure of the Tethyan Seaway created a barrier separating the Mediterranean and Indo-Pacific bioprovinces during the early Burdigalian (Reuter et al., 2009). This barrier prevented the migrations of marine species between the two provinces. In the Early Miocene, the Central Indo-Pacific was the centre of marine biodiversity (e.g., Renema et al., 2008; Obura, 2016; Reuter et al., 2019) which is reflected in a pLBF richness higher than that in the Mediterranean (Table 1). In the Mediterranean, the ibsWT/Ma increases from the Burdigalian (1.12) to the Langhian (2.33; Table 2) confirming that environmental conditions were favourable to the pLBF and contradicting the interpreted deterioration of trophic conditions in carbonate factories (e.g., Pomar et al., 2017).

The Langhian peak in species richness of the Miocene corresponds to sea-level and global SST peaks, occurring at the late MCO (Zachos et al., 2008; Steinthorsdottir et al., 2021; Fig. 5). The Langhian peak in pLBF richness is recorded in shallow-water reef-related areas, expanded latitudinally during the MCO (Steinthorsdottir et al., 2021), when temperature difference between the tropics and mid-latitudes was small (Westerhold et al., 2020; Burls et al., 2021) and SST records reveal an E–W gradient of ~4 °C across the Pacific (Fox et al., 2021). Some recent studies estimate peaks of pCO_2 close to, or above 800 ppm during the MCO (Sosdian et al., 2018) and suggest that cooling after the MCO was paired with a drop in pCO_2 (Super et al., 2018).

The MMCT interval, associated with a significant freshening of the tropical eastern Indian Ocean relative to the western Pacific Ocean, was characterized by the constriction of the already relatively shallow Indonesian Seaway and an eustatic fall (59 ± 6 m, John et al., 2011) which modified the surface ocean circulation and hydrography in the Indo-Pacific (Sosdian and Lear, 2020). The disconnections of small shallow-water areas and the decrease in SST to ~26.5 °C (Steinthorsdottir et al., 2021; Table 2) brought about the isolation of pLBF populations with their decrease in richness in the Serravallian (5 species; Fig. 1, Table 1).

Considering that pCO_2 did not change markedly during the Early–Middle Miocene (~400 ppm; Foster et al., 2012; Zhang et al., 2013; Sosdian et al., 2018) and the estimated pH ranged from 7.8 to 8.2 (Zeebe, 2012; Sosdian et al., 2018; Table 2), pLBF richness was not affected by these values. This confirms the laboratory data carried out on living pLBF whose shell calcification is vulnerable only over a threshold at $pCO_2 > \sim 600$ ppm and a pH lower than 7.7.

Along with the highest number of LAD of the studied taxa at the Langhian–Serravallian boundary, the subsequent Serravallian decrease in species richness mimics the SST curve and it also co-occurs with two important events detrimental for the LBF: the eastern closure of the Mediterranean Sea (ecMS) and the onset of the Miocene Indian Ocean Equatorial Jet (MIOJet; Fig. 5). The Indo-Pacific corridor closed or underwent restrictions intermittently since the Burdigalian until the ecMS at the Langhian–Serravallian boundary (e.g., Rögl, 1999; Bialik et al., 2019).

The temperature asymmetry of ~4 °C across the Pacific Ocean throughout the Middle Miocene limited the eastward dispersion of pLBF species (Fox et al., 2021). In fact, the easternmost records of pLBF are from the Early Miocene of Bikini and the Midway Atolls (*Austrotrillina*

Table 2
Maximum number of species of *Alveolinella*, *Austrotrillina*, *Borelis*, *Bullalveolina*, *Flosculinella*, and *Praebullalveolina* occurring in a single basin in each stage (intra-basin species richness, ibs) normalized by interval (stage, St) length in million years (/Ma; Cohen et al., 2013, updated) reported from the Western Tethys (WT) and Indo-Pacific (IP) areas from the Oligocene to the Miocene. Ranges (min, minimum; max, maximum) of published SST, pCO_2 and pH estimates for the Oligocene–Miocene. For abbreviations see Table 1.

	StL/Ma	ibsWT/Ma	ibsIP/Ma	SST °C (min/max)	SST °C (mean)	pCO_2 ppm (min/max)	pCO_2 ppm (mean)	pH (min/max)
Mess	2.09	0.52	1.57	21/27.5 [a]	24 [a]	395/400 [d]	397 [d]	7.95/8.12 [e]
Tort	1.60	0.68	0.91	21/27.5 [a]	24 [a]	395/400 [d]	397 [d]	7.9/8.2 [e]
Serr	4.57	2.28	2.28	16/30 [a]	26.5 [a] (30.4 [c])	390/400 [d]	395 [d] (243 [c])	7.95/8.15 [e] (8 [c])
Lang	5.12	2.33	3.72	29/33 [a]	31 [a] (30.8 [c])	390/410 [d]	400 [d] (332 c)	7.7/8.15 [e] (7.9 [c])
Burd	2.91	1.12	2.46	31.5/35.5 [a]	33.5 [a] (30.9 [c])	400/410 [d]	405 [d] (225 c)	7.8/8.04 [e] (8.03 [c])
Aqui	3.86	1.54	3.09	27.6/30 [a]	28.8 [a]	380/420 [d]	400 [d]	8.03°[e]
Chat	1.88	0.84	1.25	28.5/30.05 [b]	29.3 [b]	410/730 [d]	570 [d]	7.95/8.05 [e]
Rup	1.32	0.99	0.66	25.5/29 [b]	27.3 [b]	670/1088 [d]	879 [d]	7.8/7.95 [e]

[a] Steinthorsdottir et al. (2021).
[b] O'Brien et al. (2020).
[c] Foster et al. (2012).
[d] Zhang et al. (2013).
[e] Zeebe (2012); Sosdian et al. (2018).

paucialveolata; Bassi et al., 2021b), whereas the successive records from these areas are Late Miocene in age (*Borelis schlumbergeri*; Bassi et al., 2021a).

From the Middle Miocene onward, a global cooling is recorded (Sosdian et al., 2018; Westerhold et al., 2020). From the Serravallian onward, the species richness underwent a dramatic drop until the Messinian following the global SSTs. This drop coincides with the abrupt cooling associated with the glaciation step at 13.9 Ma (Sosdian and Lear, 2020).

Although in the Serravallian–Tortonian the central Mediterranean was connected to the Atlantic via the Betic and Rifean Straits and was not affected by significant regional volcanism or weathering (Kocsis et al., 2008; Cornacchia et al., 2018), species richness is half of that during the Langhian, confirming the negative influence of the sea-level drop and the cooling SST (< ~26 °C in Foster et al., 2012; Fig. 5). The minimum species richness both in the Mediterranean and Indo-Pacific is recorded in the Tortonian (Fig. 5) when the SSTs were globally low with strong latitudinal gradients and intensified monsoons (e.g., Holbourn et al., 2013, 2018; Steinthorsdottir et al., 2021). The few global eustatic highstands and the cooling in the Middle–Late Miocene brought about a prolonged episode of reduced carbonate deposition which marked the Indo-Pacific carbonate crash (c.13.2–c. 8.7 Ma; Lübbers et al., 2019; Mathew et al., 2020; Fig. 5), likely reducing the shallow-water carbonate settings where the pLBF thrived.

The complex Mediterranean geodynamics in the early Messinian brought about several regional sub-basins along with the closure of the last Betic corridor (Martín et al., 2009; Manzi et al., 2013; Gennari et al., 2018). The single species identified in the Mediterranean occurs in south-eastern Spain (*Borelis melo*, Cabo de Gata; Betzler and Schmitz, 1997; Bassi et al., 2021a) and disappeared at the Messinian Salinity Crisis.

During the Late Miocene, SSTs still ranged between 10 °C and 15 °C warmer than modern in the high latitudes, and 2–4 °C warmer in the tropics (Burls et al., 2021). In the Messinian, the Indo-Pacific underwent a steep SST cooling, an episode referred as the Late Miocene Cooling (LMC; Steinthorsdottir et al., 2021). Tropical upwelling sites in parallel with the mid- and high latitudes recorded an average cooling of nearly 4C° (Holbourn et al., 2018). During the Messinian, average SSTs range from 27.8 to 28.5 °C (Warter et al., 2015), indicating slightly cooler SST conditions compared with the present day. The species richness at that time is half of that of the Langhian peak. In the Early Pliocene, before the closure of the Central America Seaway (O'Dea et al., 2016), the single *Borelis pulchra* probably migrated eastwards to Central America (Bassi et al., 2021a).

Modelled Late Miocene ocean estimated pH values (Shankle et al., 2021) are not detrimental to pLBF calcification and growth (e.g., Oron et al., 2020). The occurrence of the studied pLBF is limited to three species (*Borelis pulchra*, *B. schlumbergeri*, *Alveolinella quoyi*), still extant, at the SST lower than 28 °C (e.g., Lu et al., 2021).

6. Concluding remarks

The impact of changes in sea level, SST, seawater pCO_2, and pH on the species richness of *Alveolinella*, *Austrotrillina*, *Borelis*, *Bullalveolina*, *Flosculinella,* and *Praebullalveolina* was evaluated by means of a systematic re-assessment and a comprehensive literature survey of their Oligocene–Miocene occurrences in the Western Tethyan and Indo-Pacific regions.

The beginning of the evolution of the studied pLBF group corresponds to the Chattian sea-level highstand and high global SSTs. The peaks in richness, identified in the Aquitanian and Langhian–Serravallian sub-tropical and tropical latitudes, occurred when SST was ~29 °C.

The pLBF richness curves show the detrimental effects of high pCO_2 (> 600 ppm) in the Rupelian–early Chattian, of high tropical SST (> 31 °C) recorded during the beginning of MCO, and of low tropical SST (< 26 °C) in the Tortonian. Seawater pH higher than 7.7 did not negatively affect species richness. The post-Langhian decrease in diversity might be more driven by SST, as it considerably affected the Mediterranean pLBF richness. Sea-level highstands and the nearly coeval global SST increase might have played a role in diversification of Oligocene–Miocene pLBF by widening and enhancing habitat availability. The post-Langhian decrease in diversity might be more driven by cooling SST as it considerably affected the Mediterranean pLBF richness. Förderer et al. (2023) identified an increasing widening bimodal latitudinal pattern of modern LBF species diversity. This latitudinal pattern influences the central Indo-Pacific LBF diversity which is likely to be pushed outside of the currently realized niches of most species. This pattern is, in fact, followed by the pLBFs during the analyzed time frame of the present study.

Many aspects must be considered in discussing whether or not pLBFs will be able to keep up with the ongoing unprecedented speed of sea-level rise and global warming. This depends on numerous factors and their future entails a number of possibilities including eventual adaptation to these extreme stressors, geographic range shifts, the reaction and fate of co-occurring species within complex environments which may or may be not advantageous to the presence of pLBFs, regional extirpation and even extinction. Although ocean acidification increases pLBF habitat complexity, it is projected to adversely affect shallow-water reef-related ecosystems. Nonetheless, there are large areas where SST and pH are higher than the mean global change over the 21st century, such as the Western Pacific Warm Pool located in the region around Indonesia and Papua New Guinea where pLBF diversity and abundance are highest. Despite the expected stronger warming of the equatorial and northern subtropical oceans and the stronger acidification of the Southern Ocean (Mortenson et al., 2021), pLBF could survive in refugia/regions with small changes to SST and pH as is the case with *Marginopora* in the Coral Sea (Renema, 2018).

Declaration of Competing Interest

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

Data availability

No data was used for the research described in the article.

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Appendix A

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