Biostratigraphical and palaeobiogeographical patterns of the larger porcelaneous foraminifer *Austrotrillina* Parr, 1942

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ABSTRACT

Among the Tethyan larger porcelaneous foraminifera widespread from the middle–late Eocene to the middle Miocene, *Austrotrillina* Parr, 1942 is the only genus showing a non-homogeneous shell structure. This consists of a parakeriotheca, coated by a thin, dense tectum. Four *Austrotrillina* species (*A. brunni*, *A. eocaenica*, *A. howchini*, *A. striata*) have been often used as biostratigraphical markers in the Mediterranean and Indo-Pacific areas. New materials from southeastern Spain and Central Indo-Pacific (Indonesia, Kita-daito-jima, Kikai Seamount) were studied to assess their taxonomic status, species circumscription and palaeobiogeographic patterns. Based on re-assessed shell structures *A. asmariensis* Adams is considered a junior synonym of *A. brunni* Marie.

Austrotrillina eocaenica first appears in the middle–late Eocene of Iran. Two Rupelian descendants, *A. brunni* and *A. striata*, migrated from the Western Tethys into the Indo-Pacific. *A. striata* reached Indonesia and Western Australia in the Chattian, then disappeared in the Langhian of Kita-daito-jima. *A. brunni* first occurred in the Burdigalian of Indonesia and Western Australia and disappeared in the early Serravallian of Western and South Australia. *A. brunni* and *A. striata* disappeared in the Serravallian westernmost Mediterranean (southeastern Spain). From the Burdigalian the exclusive occurrence of *A. howchini* in the Indo-Pacific areas is a possible result of the closing Tethyan Seaway, which differentiated the Mediterranean and Indo-Pacific bioprovinces. This species disappears in the latemost Langhian–early Serravallian of South Australia and in the Kikai Seamount. The palaeobiogeographic distribution of these species suggests an early Miocene active connection of Eastern Africa with the Central Indo–West Pacific.

Keywords:
Oligocene–Miocene
Shallow-water carbontes
Miliolids
Systematics
Biostratigraphy
Tethys
Mediterranean
Indo-Pacific

1. Introduction

Austrotrillinids are fossil porcelaneous larger benthic foraminifera (LBF) widespread in the Western Tethys and in the Indo-Pacific from the middle–late Eocene to the middle Miocene (e.g., Adams et al., 1983; Cahuzac and Poignant, 1997; Renema, 2007). This group, with a miliolid, trilocular growth, differs from other porcelaneous LBF in having an alveolar exoskeleton formed by numerous secondary partitions (subepidermal mesh in Loeblich and Tappan, 1986, p. 345). The porcelaneous foraminiferal shell texture consists of calcite needle, rod, lath or plate-shaped crystals (Loeblich and Tappan, 1987; Parker, 2017). The crystal arrangement can change in the shell wall from the outer shell part, through exoskeletal to endoskeletal structures (Hottinger, 2006; Parker, 2017).

Exoskeletal structures have been described from microagglutinated larger lituolids (Hottinger, 1967), orbitolinids (e.g., Hofker, 1963), soritins (Hottinger, 2001; see *Reticulotaberina jahrumiana* Nafarieh, Consorti and Caus, 2019), and the austrotrillinids (Loeblich and Tappan, 1986). The austrotrillinid alveolar structure consists of branched or unbranched parapores with a blind ending, with exoskeletal elements, such as beams perpendicular to the septum (Hottinger, 2006). This alveolar structure makes up the layered austrotrillinid shell along with a thin, outermost dense coating epiderm.

Among the porcelaneous LBF, *Austrotrillina* Parr, 1942 is the only genus showing a non-homogeneous shell texture and structure (i.e., exoskeleton). Seven *Austrotrillina* species have been described: *Austrotrillina asmariensis* Adams, 1968, *A. brunni* Marie *in* Brunn et al., 1955, *Austrotrillina eocaenica* Hottinger, 2007, *A. howchini* (Schlumberger, 1893), *A. laberynthica* Escandell and Colom, 1962*, A. paucialveolata* Grimsdale, 1952, and *A. striata* Todd and Post, 1954. As their peculiar shell structure is easily identifiable in random thin section analysis, *Austrotrillina* species have been used as biostratigraphical markers in the East Indian Letter Stages (Van Der Vlerk and Umbgrove, 1927; van Bemmelen, 1949; Marks, 1957; Cole, 1969; Todd and Post, 1970; Adams, 1984; BouDagher-Fadel and Banner, 1999; Renema, 2007). The shallow-water carbonate deposits with *Austrotrillina* species have been often related to settings above the fair-weather wave base (Buxton and Pedley, 1989; Hottinger, 1997; Beavington-Penney and Racey, 2004; Haig et al., 2020; Simmons, 2020).

Although frequently recorded in the Mediterranean region (e.g., Poignant and Lorenz, 1985), this genus has never been considered in the Western Tethyan shallow benthic zonation, which is based on Oppel zones defined by temporal ranges of nummulitids, lepidocyclinids and miogypsinids (Cahuzac and Poignant, 1997). The single exception was *Austrotrillina paucialveolata* that would mark the Mediterranean Chattian (Wielandt, 1996).

After Adams's (1968) revision of *Austrotrillina*, no re-assessment of morphological features, biostratigraphical ranges, and palaeobiogeographic patterns of species included in the genus has been performed. The purpose of this paper is to re-assess the *Austrotrillina* shell structure and, on the base of new data on species occurrences with improved age constraints, to understand the Tethyan evolutionary history and palaeobiogeography of its species. New records from southeastern Spain, Indonesia and northern Philippine Sea indicate that the genus appeared in the middle–late Eocene, diversified in the early Oligocene and the descendants disappeared in the Mediterranean and Indo-Pacific areas in the Langhian and Serravallian.

2. Materials and methods

Specimens in thin sections from hard-cemented limestone were examined, both from Hanzawa's (1940) collection from Kita-daito-jima housed at the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Sendai (IGPS; Japan), and from newly collected samples from Spain, Indonesia and the Kikai Seamount (Northern Philippine Sea). The thin sections from Indonesia and southeastern Spain are housed at the Departamento de Estratigrafía y Paleontología, University of Granada (Spain), while the collection from the Kikai seamount is stored at the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University (IGPS). The isolated specimens from Wailawi, East Kalimantan (Indonesia), are housed at the Naturalis Biodiversity Center, Leiden (the Netherland).

Structural and morphological terms are those used by Hottinger (2006). The suprageneric classification follows Loeblich and Tappan (1986, 1987). The descriptions of the analysed *Austrotrillina* species are ordered according to their stratigraphical appearance. References to published species and their records include only those in which structural diagnostic features were described and illustrated. Synonymy lists can be found in the Supplementary data.

Adams' (1968) species descriptions and illustrations (including types and topotypes) cover the main variability of parapores (i.e., alveoles), although he did not distinguish shell texture, shell structure and branching parapores.

In total 10 specimens from samples RGMS.603540 and RGMS.574854 (Wailawi, East Kalimantan) were micro-CT scanned using a Zeiss X-Radia versa 520 at Naturalis Biodiversity Center (by W.R.), Leiden, the Netherlands. Specimens were scanned at 80 kV and a voxel size of 0.9–1.4 µm. 3D-volumes were reconstructed and segmented using Avizo 2020.2 software

(ThermoFisher Scientific, Watham MA, United States).

2.1. Southeastern Spain

The studied specimens were collected from two localities: Ibi and Sierra de Marmolance (Fig. 1).

Ibi is a town located in the Alicante province in southeastern Spain. The study samples were collected from Rupelian-lower Chattian limestones belonging to the Prebetic Domain of the External Zones of the Betic Cordillera (Geel, 2000). During the Rupelian–early Chattian the Prebetic Domain was the proximal part of the Southern Iberian Margin (Geel, 1995; Höntzsch et al., 2013). The sampled Oligocene carbonates near Ibi formed in a back-reef setting (Geel, 1995). The study samples are from uppermost Rupelian deposits, characterized by ‘a series of overlapping washover fans with intercalations of *Austrotrillina–Praerhapydionina* grainstone and coral rubble beds’ (Geel, 2000). Upper Chattian deposits are missing in the area due to uplift and erosion.

The Serravallian specimens occur in middle Miocene limestones from the Sierra de Marmolance near Huéscar in the Granada province. This limestone succession belongs to the Subbetic Domain of the External Zones of the Betic Cordillera. The Subbetic was the distal domain of the Southern Iberian Margin, which in middle Miocene times was already deformed and partially emergent. Marls with Burdigalian–Serravallian planktonic foraminifera occur at the base and interfinger with limestones, constraining their age. The Serravallian *Austrotrillina* occurs in shallow-water bioclastic limestones rich in LBF and coralline red algae.

2.2. East Kalimantan, Indonesia

The studied specimens were collected from Mangkalihat and Wailawi (Fig. 1). The samples were collected along the banks of the Taballar River east of the Taballar village in the Mangkalihat peninsula in East Kalimantan (Borneo; Fig. 1). The Taballar limestone section cropping out in the sampled river stretch is late Aquitanian–early Burdigalian in age (Novak, 2014). The Taballar limestone is a shallow-water carbonate deposit formed in a low-energy inner platform (van der Vlerk, 1929; Wilson et al., 1999; Wilson, 2008; Novak, 2014).

Samples from the Wailawi 1 core are stored in the Naturalis Biodiversity Center collections. This core was drilled in the 1930s just south of Balikpapan Bay in East Kalimantan. The collections include well-preserved isolated LBF specimens at intervals between 320–350 m and 420–510 m depth. In both intervals *Austrotrillina* is observed in several samples. In the 510 m sample the planktonic foraminifera *Orbulina* (FO 15.1 Ma; Wade et al., 2011) and *Trilobus trilobota* have been found indicating a Langhian or younger age (Wade et al., 2011). In this interval *Planostegina* sp. is also abundant. In southeast Asia *Planostegina* occurs in the plankton zones M6–M9, roughly the middle to late Langhian, restricting the studied samples to the Langhian. Since *Planostegina* was not observed in the 320–350 m interval, an early Serravallian age for this interval is inferred from the combined occurrence of *Trybliolepidina martini* and *Nephrolepidina ferreroi*.

2.3. Northern Philippine Sea, southwestern Japan

The studied specimens were collected from Kita-daito-jima and the Kikai Seamount (Fig. 1).

Kita-daito-jima is a carbonate island located in the northwestern region of the Philippine Sea (25°55.6′–57.6′N, 131°16.9′–19.8′E). A deep borehole into atoll deposits was obtained from 431.7 m below the ground surface (mbgs) in 1934 and 1936 (Suzuki et al., 2006; Iryu et al., 2010). The material recovered from the Kita-daito-jima borehole consists exclusively of shallow-water carbonates distinguished in four lithologic units (C1, C2, C3, C4). The upper 100 m (Units C1 and C2) are pervasively dolomitized. The Oligocene to lower Miocene Unit C4 (209.3–431.7 mbgs), extending to the base of the borehole, consists of limestone probably originated from bioclastic packstone. The middle Miocene Unit C3, 105.9 m thick (103.4–209.3 mbgs), is composed of locally dolomitized rudstone along with grainstone and packstone. Studied samples were collected from Unit C4 (thin section labelled as 325.42–331.53 m; 21.7–22.1 Ma, Aquitanian) and Unit C3 (thin section 835, 15.8–16.4 Ma, Burdigalian–Langhian boundary; thin sections 753, 773–779, 14.8–15.2 Ma, Langhian). Numerical ages were determined by comparing the measured ^{87}Sr/^{86}Sr values (Ohde and Elderfield, 1992) with the global Sr calibration curve from McArthur et al. (2012), using the geologic time scale from Gradstein et al. (2012).

The Kikai Seamount (28°31'N, 131°05'E), near the axis of the Ryukyu Trench, the border between the Philippine Sea and Eurasia plates, constitutes an isolated flat-topped salient on the inner slope of the trench. The basement of the seamount continues to that of the Amami Plateau (Tokuyama et al. 1986), representing one of the Daito Ridge Group (Oki-Daito and Daito Ridges, and Amami Plateau) in the northern Philippine Sea (Hickey-Vargas, 2005). Carbonate rock cores drilled on the seamount comprise Miocene coral rudstone unconformably overlain by Early Pleistocene coral rudstone. The study specimens occur in thin sections from uppermost Langhian–lower Serravallian carbonates (Takayanagi et al., 2012).

3. Systematic palaeontology

Superfamily Miliolacea Ehrenberg, 1839

Family Austrotrillinidae Loeblich and Tappan, 1986

Genus *Austrotrillina* Parr, 1942

Type species: *Trillina howchini* Schlumberger, 1893.

Remarks: The miliolid *Austrotrillina* shell is made up of randomly-oriented microcrystals of calcite giving rise to a porcelaneous texture (Loeblich and Tappan, 1987). The chamber wall consists of an exoskeleton made up of a tectum (i.e., organic lining in Hottinger, 2000) and an exoskeletal alveolar structure, the parakeriotheca (one-layered keriotheca). Tectum and parakeriotheca generally do not occur in the nepionic chambers, except in the first three in *A. striata* (Fig. 2). These two structural characters of the shell are diagnostic for distinguishing *Austrotrillina* (Adams, 1968, p. 82; Loeblich and Tappan, 1987, p. 355).

The tectum is a thin, dense outer layer about 8–15 μm in thickness. No tiny, pore-like gaps can be recognized. This tectum would correspond to the extrados described in the miliolids, which is an outer calcite lining bounded by an outer organic lining (Parker 2017). However, since the *Austrotrillina* tectum does not subdivide chamber lumina (Hottinger 2006), it cannot be considered a test structure as the extrados defined by Parker (2017). In modern miliolids the crystal elements that form the extrados exhibit different shapes, sizes and arrangements in different taxa (Parker 2017). No comparison of tectum and extrados has been performed so far.

The tectum lines the parakeriotheca coating the lateral chamber wall. The alveole recesses are of varying depth and end blind beneath the tectum. Consequently, they are parapores *sensu* Hottinger (2006). The parakeriotheca is characterized by parapores. These parapores show different sizes and shapes, characterizing three different alveolar arrangements.

Beams are exoskeletal partitions occurring in the proximal part of the chamber lumen near the previous chamber (Hottinger, 2006). The beams, perpendicular to the chamber septum and to the lateral chamber wall, produce subsutural alcoves with blind endings.

Among the seven *Austrotrillina* species known in literature (*A. asmariensis*, *A. brunni*, *A. eocaenica*, *A. howchini*, *A. laberynthica*, *A. paucialveolata*, *A. striata*), the parakeriotheca, the diameter of the proloculus and the occurrence of beams and subsutural alcoves are reliable characters at species level distinguishing *A. eocaenica*, *A. brunni*, *A. striata* and *A. howchini* (Table 1). In Tables 2–4, the stratigraphical and palaeogeographical distributions of *Austrotrillina* species are listed.

Austrotrillina eocaenica Hottinger, 2007

(see Supplementary data for the synonymy list)

Type reference and figures: *Austrotrillina eocaenica* Hottinger, 2007, p. 5, pl. 1, fig. 2 (bottom); pl. 2, figs 2–9 (fig. 4, holotype); pl. 12, fig. 8 (left).

Diagnosis: Shallow and coarse parapores (i.e., alveoles in Hottinger 2007, p. 5) arranged in parallel rows. Proloculus 24–32 μm in diameter with a narrow and low flexostyle (Hottinger 2007, pl. 2, fig. 9). Nepionic apparatus (6–8 chambers) lacks parakeriotheca (Table 1). Beams between parapores and subsutural alcoves.

Stratigraphical distribution: *Austrotrillina eocaenica* has been found in the early?–middle Lutetian–Priabonian of western Dhofar (Oman) and Socotra Island (Serra-Kiel et al., 2016), Bartonian and Priabonian of Iran (Shiraz; Rahaghi, 1980, p. 31, fig. 14; Hottinger, 2007), and the Priabonian of Tunisia (Bonnefous and Bismuth, 1982) and southern Oman (Gallardo et al., 2001). The coarse parakeriotheca and the thick basal layer distinguish this species from *A. striata* (as *A. paucialveolata* in Rahaghi, 1980; Hottinger, 2007). Although assessing the shell structure is difficult in the low-quality photo of the single illustrated specimen from Tunisia (Bonnefous and Bismuth, 1982, pl. 4, fig. 1), the possible occurrence of shallow parapores ascribes the specimen to *A. eocaenica*. The only illustrated Priabonian specimen from southern Oman shows a coarse parakeriotheca comparable to that of *A. eocaenica* (Gallardo et al., 2001, pl. 1, fig. 12). The illustrated Eocene specimens from western Pakistan (Boukhari et al., 2016, figs 5–7) are miliolids since they lack parakeriotheca.

Austrotrillina brunni Marie, 1955

Fig. 3.

(see Supplementary data for the synonymy list)

Type reference and figures: *Austrotrillina brunni* Marie *in* Brunn et al., 1955, p. 203, pl. 9, figs 4–8 (fig. 5, holotype).

Diagnosis: Parallel fine parapores, almost with constant diameter. Proloculus ranging from 100 to 250 μm in diameter with narrow flexostyle. Parakeriotheca not present in the wall of the nepionic apparatus (Table 1). No beams, no subsutural alcoves.

Studied material: The analysed specimens are from the Burdigalian–Langhian boundary in Miocene limestones of Kita-daito-jima (Japan) and from Serravallian limestones of Sierra de Marmolance (southeastern Spain).

The parapores (*c.* 100 μm long and *c.* 20 μm in diameter), making up a fine alveolar parakeriotheca, are straight and sub-perpendicular to the overcoating tectum. The lateral chamber wall is tiny porous (i.e., thin parakeriotheca; Figs 2A–3). The proloculus (*c.* 250 μm in diameter) has a narrow and low flexostyle. The very thin wall of the nepionic apparatus, with flexostyle, has no parakeriotheca.

Remark: Marie (*in* Brunn et al., 1955) introduced a new *Austrotrillina* species (*A. brunni* Marie, pl. 9, figs 4–8) from the Chattian–Aquitanian of Greece. The illustrated specimens do not clearly show the characters of the parakeriotheca. However, Marie's (1955) specimens of *A. brunni* were re-illustrated by Adams (1968, pl. 6, figs 6–8) showing a fine parakeriotheca with no branching parapores (Table 1). In re-assessing the stratigraphy and palaeoecology of Oligocene–lower Miocene sedimentary sequences of the Mesohellenic Basin, Wielandt-Schuster et al. (2004) illustrated a Rupelian *Austrotrillina* specimen from the Mesolouri stratigraphical section cropping out near Pentalofon (north-western Greece), the type locality of *A. brunni*. The specimen (as *A. asmariensis* in pl. 4, fig. 21 in Wielandt-Schuster et al., 2004) shows fine parapores. The occurrence of fine parapores which are not branching ascribe the specimen to *A. brunni*.

Adams (1968) introduced *A. asmariensis* because his specimens differed from *A. striata* in having an alveolar shell from the third chamber of the nepionic apparatus and thinner parapores. The nepionic apparatus of the Adams's specimens, showing a very thin wall with low and narrow flexostyle (see Adams, 1968, pl. 1, fig. 9 and pl. 5, fig. 8), has no parakeriotheca. The Adams's types differ from *A. howchini* in having non-branching parapores (Adams, 1968, p. 84). The occurrence of fine parapores from the third chamber and the absence of beams and subsutural alcoves are, therefore, distinctive characters of both *A. brunni* and *A. asmariensis* (Marie *in* Brunn et al., 1955, p. 203; Adams, 1968, pp. 82–83; Table 1).

The types of *A. asmariensis* (Adams, 1968, pl. 1, figs 1–12) cannot be morphologically separated from the ones of *A. brunni* and, therefore, the former is considered a subjective junior synonym of the latter species (ICZN, 1999, Arts. 23.9.3 and 81.2.3). The affinities between *A. brunni* and *A. asmariensis* were highlighted by Adams (1968, p. 85) stating that *brunni* resembled the *A. striata*/*asmariensis* group. He considered *A. brunni* as a possible transitional form between *A. striata* and *A. howchini* (p. 89).

Stratigraphical distribution: In the Mediterranean area, *A. brunni* ranges from the Rupelian to the Serravallian, disappearing after the eastern closure of the Mediterranean Sea (Bassi et al., 2007, text-fig. 9; Fig. 10). Nonetheless, BouDagher-Fadel and Lokier (2005, fig. 3) considered *A. striata* and *A. brunni* restricted to the early Miocene. *Austrotrillina brunni* shows a wide geographical distribution from the Western Tethys (e.g., Gallardo et al., 2001; Bassi et al., 2007; Serra-Kiel et al., 2016; Ferràndez-Cañadell and Bover-Arnal, 2017) to Western Australia (Riera et al., 2019; Table 2).

In the Mediterranean area, the Serravallian records are represented by the studied specimens from the Sierra de Marmolance, while no Serravallian specimens have been found in the Middle East. Early Serravallian *A. brunni* is present in Western Australia, representing the youngest occurrence of *Austrotrillina* in the Pacific area (Riera et al., 2019). Upper Langhian–lower Serravallian specimens from the Trealla Limestones (Western Australia) have been considered to be '*Austrotrillina asmariensis* or transitional forms between *A. asmariensis* and *A. howchini*' (Riera et al., 2019, p. 331, figs 14(5–13)). In the illustrated specimens the occurrence of the flexostyle (figs 14 (5–6, 8a–9a)) and the absence of the parakeriotheca in the wall of the nepionic apparatus confirm the ascription to *A. brunni*. The coeval specimen from the lower–middle Miocene Nullabor Limestone (South Australia) is also ascribed to *A. brunni* because of the closed-spaced alveoli and absence of alcoves (O'Connell et al., 2012, fig. 5F; Table 2).

Austrotrillina striata Todd and Post, 1954

Figs. 4–6.

(see Supplementary data for the synonymy list)

Type reference and figure: *Austrotrillina striata* Todd and Post, 1954, p. 555, pl. 198, fig. 9 (holotype).

Diagnosis: Coarse parapores. Proloculus 50–130 µm in diameter with narrow flexostyle. Parakeriotheca not present in the wall neither of the nepionic apparatus nor of the first three chambers (Table 1). No beams, no subsutural alcoves.

Studied material: The analysed specimens are from the latemost Rupelian of the Ibi area (southeastern Spain; Fig. 4), from the Aquitanian and Langhian limestones of Kita-daito-jima (Japan; Fig. 5), and from the Serravallian deposits of Sierra de Marmolance (southeastern Spain; Fig. 6).

The parapores (*c*. 90 µm long and *c*. 50 µm in diameter; Figs 1B, 4B, 5F), rounded in transversal section, are large, straight, tubular in shape, perpendicular to the tectum. In the parakeriotheca, this alveolar arrangement makes the lateral chamber wall highly porous (i.e., coarse parakeriotheca; Figs 1B, 4–6). The nepionic apparatus (proloculus *c*. 130 µm in diameter) has a flexostyle and the first three chambers do not show parakeriotheca.

Remarks: No textural and structural differences were found between *A. striata* and *A. paucialveolata*. Their nepionic apparatus with flexostyle (Adams, 1968, pl. 3 and pl. 4, figs 10, 13) is followed by three first chambers with no parakeriotheca (Table 1). In addition, their overlapping stratigraphical and palaeogeographical distributions question the separation of these species (e.g., Adams, 1968; BouDagher-Fadel, 2018; Yazdi-Moghadam et al., 2018; Table 1).

Austrotrillina paucialveolata Grimsdale 1952 has been described from Oligocene deposits of Kirkuk (Iraq). According to Grimsdale (1952, p. 229) the four illustrated types show throughout the shell large parapores 'coarser and less regular than in *Austrotrillina howchini*'. Adams (1968) stated that *A. asmariensis* and *A. paucialveolata* might be synonymous (p. 91) but the occurrence of large-sized parapores in *A. paucialveolata* disputes this interpretation. The single report of *Austrotrillina howchini* from the Chattian of southeastern Spain (Hottinger, 1963) corresponds in fact to *A. striata* (see also Adams, 1968, pl. 3, figs 5–6 as *A. paucialveolata*).

Stratigraphical distribution: *Austrotrillina striata* appears from the Rupelian in the Western Tethys (Middle East; Serra-Kiel et al., 2016) and from the Chattian in the Indo-Pacific area (Indonesia; Table 3). In the Middle East, this species disappears in the early Burdigalian (e.g., Roozpeykar and Moghaddam, 2016; Daneshian and Dana, 2019). In the Western Tethys, the two records from the Rupelian and Chattian of southeastern Spain (Hottinger, 1963; see also Adams, 1968; Ibi, this study) are followed by a Serravallian occurrence in the southeastern Spain (this study).

In the Pacific area, *Austrotrillina striata* ranges from the Rupelian (Eniwetok, Todd and Low, 1960; Midway Atoll, Cole, 1969; Todd and Post, 1970) to the middle Miocene (Western Australia; Adams, 1984; Chaproniere, 1984; Lunt and Allan, 2004; Langhian in Kita-daito-jima, this study). This latter occurrence represents the northernmost record in the western Pacific marking the limit of shallow-water carbonate depositional systems. In Indonesia, it has been recorded from Tf1, roughly equivalent to the Burdigalian (Novak, 2014). The Serravallian record from southeastern Spain represents the last occurrence of this species in the Mediterranean area (Table 3, Fig. 10).

Austrotrillina howchini (Schlumberger) Parr, 1942

Figs. 7–9.

(see Supplementary data for the synonymy list)

Type reference and figures: *Austrotrillina howchini* (Schlumberger) Parr, 1942, p. 361, fig. 1; holotype illustrated by Schlumberger (1893), pl. 3, fig. 6.

Diagnosis: Parakeriotheca with branching parapores in four bifurcating orders. Proloculus 70–150 μm. Beams occur approximately along the chamber suture, where they contact the basal layer at the chamber bottom forming a row of subsutural alcoves (Table 1).

Studied material: The analysed specimens are from lower Burdigalian deposits of East Kalimantan (Indonesia; early Tf1 in Novak, 2014), from the late Langhian–early Serravallian of Wailawi (East Kalimantan) and from the Langhian–early Serravallian of the Kikai Seamount. The parapores, decreasing in diameter outwardly, are branching in the parakeriotheca (Figs 1C, 7, 8C). From the chamber lumen the first order of parapores bifurcates in the second order, which gives rise to the third and then to the fourth order. The parapores are rounded in transversal section (Figs 7, 8C, 8H, 9A, 9C, 9G). The diameter of the parapores decreases from the first (*c*. 40–55 μm in diameter) to the fourth order (*c*. 25 μm; Fig. 7). The first-order parapores are longer (*c*. 75 μm long) than those in the subsequent orders (*c*. 35 μm long). Within specimens there is an ontogenetic increase in complexity of the parapores, with more orders of parapores in later chambers. The late Aquitanian–lower Burdigalian specimens show thinner walls than the Serravallian ones and the parapores are usually of first to third orders. In the youngest thicker-shelled specimens the parapores are not perpendicular to the chamber, making the parakeriotheca pattern more complex. The walls of the nepionic apparatus (proloculus *c*. 150 μm in diameter) and of the first three chambers are lined by a parakeriotheca. No flexostyle has been recognized. Beams and subsutural alcoves present (Figs 8B, 8F, 9A, 9E).

Remarks: Most of the *Austrotrillina howchini* reports are inadequately illustrated since they do not show the branching parapores in the parakeriotheca and subsutural alcoves (Table 1). The occurrence of branching parapores in the parakeriotheca is a distinctive character for this species which, together with *A. eocaenica*, bears subsutural alcoves (Table 1). The diameters of first-order parapores are larger than those of *A. brunni* (Marie *in* Brunn et al., 1955; Adams, 1968; Bassi et al., 2007; Ferràndez-Cañadell and Bover-Arnal, 2017) and comparable to those of *A. striata* (Todd and Post, 1954; Adams, 1968). This is the only *Austrotrillina* with no flexostyle (Table 1).

Stratigraphical distribution: Records of *Austrotrillina howchini* are from the early Miocene of Kenya and Tanzania (Williams, 1962, p. 18, Fundi Isa Limestones; Nyagah, 1995, Baratumu Formation; Banner and Highton, 1989; Table 4) and late Te5–early Tf1 from Indonesia (Novak, 2014; this study). Confirmed lower Miocene records are from Tanzania (Pemba Island; Adams, 1968, pl. 6, fig. 1; BouDagher-Fadel, 2018), western India (Adams, 1968; Banner and Highton, 1989), Philippines (Schlumberger, 1893) and Western Australia (BouDagher-Fadel, 2018; Table 4). The Burdigalian record in southern India is represented by isolated specimens whose shell shapes and decorticated shells do not show clearly the parakeriotheca of *A. howchini* (Rögl and Briguglio, 2018). The *A. howchini* reported from the Australian Burdigalian (Chaproniere, 1976, 1977, 1984) corresponds to *A. brunni* (as *A. asmariensis* in Riera et al., 2019, p. 330; Table 2). Crespin's (1954, 1955) specimens from Southern Australia are inadequately illustrated since they do not show the alveoli. The Haig et al.'s (2020, figs 8F–H) specimens from the Burdigalian Trealla Limestone, Western Australia, are characterized by the absence of alcoves and the occurrence of parakeriotheca in the first three chambers supporting placement in *A. brunni* (Tables 1–2). The studied late Aquitanian–lower Burdigalian *A. howchini* specimens along with the late Langhian–early Serravallian ones (Barberi et al., 1987) are the only illustrated records of this species in Indonesia (Fig. 9).

In the Langhian, *Austrotrillina howchini* is reported only from South Australia (Pata Formation in Lukasik and James, 1998; Adams, 1968, pl. 2, figs 3–7; BouDagher-Fadel, 2018, pl.

7.1, figs 1–3; Gallagher and Gourley, 2007, no illustration). The studied uppermost Langhian–lower Serravallian and Serravallian *A. howchini* from Kalimantan and from the Kikai Seamount respectively is the last occurrence of this taxon in the Indo-Pacific.

4. *Austrotrillina* shell structure

Symbiosis in LBF is performed by harbouring different microalgal (diatoms, dinoflagellates, chlorophytes, red algae) and bacterial communities in localized shell compartments (Hohenegger, 2009; Prazeres and Renema, 2019). The alveolar exoskeletal structures have been considered egg-holders hosting symbionts (e.g., Hottinger, 2000, 2006) and the different keriotheca types of fusulinids have been explained by relationships with symbiotic algae or cyanobacteria (Vachard et al., 2004). The wide parapores occurring in the coarse parakeriotheca of *A. eocaenica* and *A. striata* likely hosted symbiotic microalgae which, in the narrow parapores in *A. brunni* and in the branching parapores in *A. howchini*, adjusted their optimal position according to irradiation intensity by displacement from exposed to the unexposed side of their host (e.g., Hottinger, 2006; Prazeres and Renema, 2019).

In all four species, the chamber floor is characterized by a basal layer, consisting of a thickening of the tectum of the previous whorl (Figs 3–9; Adams, 1968, fig. 3A; Hottinger, 2007, p. 5; BouDagher-Fadel, 2018, p. 226). The basal layer, occurring in many imperforate LBF (fusulinids, alveolinoids; Loeblich and Tappan, 1987; Fleury and Fourcade, 1990; Hottinger, 2006), in miliolid *Austrotrillina* species becomes much thicker than the external chamber wall.

Among the miliolids, only *Pseudomassilina* Lacroix, 1938 shows a porcelaneous wall perforated by dense, anastomosing canaliculae (very thin parapores), which appear to only puncture the porcelain (Parker, 2017, p. 141). The canaliculae are similar in diameter and their density increases in later chambers. This rather complicated shell texture resembles those of *Austrotrillina brunni* and *A. howchini* but differs from them in having very tiny canaliculae opened to the exterior (parapores have a blind ending) and in the absence of the basal layer (which seems to be restricted to fossil taxa; Parker 2017, p. 139). The Burdigalian *Pseudomassilina macilenta* and *P. quilonensis* occur in southern India (Kerala; Rögl and Briguglio, 2018). Present-day *Pseudomassilina australis*, *P. macilenta* and *P. robusta* (Chen and Lin, 2017; Parker, 2017) are the only larger porcelaneous foraminifera with a canaliculate shell wall in the Indo-Pacific area. A possible evolutionary link between *Austrotrillina* and *Pseudomassilina* requires further study.

5. Palaeobiogeography and evolutionary pattern

The four *Austrotrillina* species show different stratigraphical and biogeographical distributions in the Tethyan areas. The parakeriotheca characters, the diameter of the proloculus and the occurrence of beams and subsutural alcoves are diagnostic at species level (Table 1). The first appearance of shallow, coarse parapores in *A. eocaenica* followed by the appearance of fine and coarse parapores in *A. brunni* and *A. striata* respectively indicates that the two latter species derived from the Lutetian–Priabonian ancestor. This is supported by the increasing proloculus size over time (from the Lutetian–Priabonian to the Serravallian; Table 1), which is frequently observed in LBF lineages (de Mulder, 1975; Benedetti et al., 2010; Renema, 2015). After the biological crisis suffered by the larger foraminifera at the Eocene-Oligocene boundary, *Austrotrillina* species diversified in the Oligocene and migrated eastward. This diversification is nearly coeval with that of some nummulitids, the lepidocyclinids and the miogypsinids in the Western Tethys (de Mulder, 1975; Drooger, 1993; Cahuzac and Poignant, 1997). The successive changes in the complexity of the parakeriotheca represented by the branching parapores along with the absence of the flexostyle in *A. howchini* point to a subsequent evolutionary step from the ancestors *A. brunni–A. striata*. Increasing complexity in parakeriothecal structures has been recognised from early to advanced fusulinids (Hottinger, 2000) and in the alveolar exoskeleton and parapores of some larger agglutinated foraminifera (Hottinger, 1967, 2001; Banner et al., 1991; Kaminski, 2004).

Austrotrillina eocaenica occurs only in the Lutetian–Priabonian of the Middle East (Hottinger, 2007; Serra-Kiel et al., 2016). In the Mediterranean area, *A. brunni* ranges from the Rupelian to the Serravallian, while *A. striata* ranges from the Chattian to the Serravallian (this study; Tables 2–3, Fig. 10).

From the eastern Western Tethys (Greece, Turkey, Iran; Adams, 1968) the Rupelian eastward migrants of *Austrotrillina brunni* and *A. striata* arrived in the modern Arabian Sea (Serra-Kiel et al., 2016; Tables 2–3, Fig. 11). The two species likely followed the shallow clock-wise India to Indonesia current which flowed off the modern Andaman Sea coasts and finally mixed with western Pacific Ocean waters (Gourlan et al., 2008). This current potentially enhanced the eastward migration of *Austrotrillina* species by reducing transit times across the modern Central Indo-Pacific. After appearing in the Western Tethyan Rupelian, *A. striata* reached Southeast Asia (Adams, 1965; Renema, 2007; BouDagher-Fadel, 2018) and Western Australia (Chaproniere, 1984) in the Chattian (Table 3, Figs 10–11). Its last record in Indonesia is at the Aquitanian–Burdigalian boundary (top Te; Lunt and Allan 2004), while in Borneo, Queensland Plateau and Western Australia it has been recorded from the Burdigalian (Chaproniere, 1983; Betzler and Chaproniere, 1993; BouDagher-

Fadel et al., 2000; Haig et al., 2020). The species persisted until the Langhian of Kita-daito-jima in the northern Central Indo-Pacific (this study; Figs 10–11).

In the Central Indo-Pacific, *Austrotrillina brunni* occurs first in the Burdigalian of Kenya (Eames et al., 1962) and Indonesia (Barberi et al., 1987; BouDagher-Fadel, 2018) and of Western Australia (Riera et al. 2019; Table 2, Fig. 11). The species reached Kita-daito-jima in northern Central Indo-Pacific (this study) at the Burdigalian–Langhian boundary. In the Central Indo-Pacific, its last occurrences are from the Langhian of Java (BouDagher-Fadel and Lokier, 2005) and from the Langhian–early Serravallian of Western and South Australia (O'Connell et al., 2012; Riera et al., 2019).

During the early Burdigalian, the closing Tethyan Seaway represented a biogeographic barrier for the marine biota bringing about the differentiation into Mediterranean and Indo-Pacific bioprovinces (Reuter et al., 2009). As a possible result of such a biogeographic restriction, *Austrotrillina howchini*, which occurs in the early Miocene of Kenya and Tanzania (Williams, 1962; Adams, 1968; Kent et al., 1971; Adams et al., 1983; BouDagher-Fadel, 2018), has not been recorded in the Mediterranean and Middle East regions. *A. howchini* appears in the Burdigalian in western India (Adams, 1968), Indonesia, Philippines (Schlumberger, 1893; Adams, 1965; Novak, 2014; BouDagher-Fadel, 2018; this study; Table 4, Fig. 10). The occurrences of *Austrotrillina howchini* in Eastern Africa and in the Central Indo-West Pacific area suggest an early Miocene active biogeographic connection between these two areas (Figs 10–11). In the early Miocene, the Central Indo-Pacific area corresponds to the centre of marine biodiversity known as the Coral Triangle (e.g., Renema et al., 2008; Obura, 2016; Reuter et al., 2019). In this area, *A. howchini* often occurs together with the alveolinoid *Flosculinella* species found in the early Miocene of Maldives, Indonesia and Ryukyu Islands (Lunt and Allan, 2004; Renema, 2007; Renema et al., 2015). The last occurrence of this species is in the early Serravallian of Indonesia (this study), the latemost Langhian–early Serravallian of the Kikai Seamount (this study; Table 4), and in the Langhian of South Australia (Adams, 1968).

As for the other characteristic LBF of the Western Tethyan and Indo-Pacific area (e.g., *Heterostegina sensu lato*, *Cycloclypeus*, reticulate nummulitids, alveolinoids), no record of *Austrotrillina* has been reported from the Oligocene–Miocene of the Caribbean realm (Robinson 1995). This can be related to the fact that from the early Oligocene the Tethyan LBF migrants followed preferentially the eastward dispersal route (see Benedetti et al., 2018). Oligocene–Miocene westward migrations of nummulitids and alveolinoids from the Tethys to the Caribbean realm have never been recorded (e.g., BouDagher-Fadel, 2018; Bassi et al., 2021). The only possible westward migrants are the Burdigalian lepidocyclinids and *Cycloclypeus* from southeast Asia to eastern Mediterranean (Özcan and Less, 2009; Renema, 2015).

6. Concluding remarks

Four *Austrotrillina* species (*Austrotrillina brunni*, *Austrotrillina eocaenica*, *A. howchini* and *A. striata*) are widespread in the Western Tethys and in the Indo-Pacific from the middle Eocene to the middle Miocene. New records from southeastern Spain, Indonesia and western Pacific allowed defining the species descriptions according to the shell structure, which consists of a tectum and a parakeriotheca with subsutural alcoves. The parakeriotheca can be thin (*A. brunni*), coarse (*A. eocaenica*, *A. striata*) and with branching parapores (*A. howchini*).

The genus appeared in the Western Tethyan middle Eocene, diversified in the Early Oligocene and the descendants reached the Serravallian in the Mediterranean and Pacific areas. The Iranian Bartonian–Priabonian *Austrotrillina eocaenica* is the oldest austrotrillinid. The Western Tethyan Rupelian *Austrotrillina brunni* and *A. striata* migrated eastward in the Indo-Pacific region.

Austrotrillina striata reached Indonesia and Western Australia in the Chattian. The species persisted until the Langhian of Kita-daito-jima in the northern Central Indo-Pacific. *A. brunni*, first occurring in the Burdigalian of Indonesia and Western Australia, reached Kita-daito-jima in northern Central Indo-Pacific at the Burdigalian–Langhian boundary. In the Central Indo-Pacific, its last occurrences are from the Langhian of Java and Kita-daito-jima, and from the early Serravallian of Western and South Australia. *A. brunni* and *A. striata* disappeared in the westernmost Mediterranean (southeastern Spain) in the Serravallian.

Austrotrillina howchini, occurring in the early Miocene of eastern Africa, western Indian, Indonesia and Western Australia, has not been recorded in the Mediterranean region. Its lower Miocene occurrence in these areas is a possible result of the closing Tethyan Seaway which brought about the differentiation into Mediterranean and Indo-Pacific bioprovinces. This palaeobiogeographic distribution suggests an early Miocene active connection of Eastern Africa with the Central Indo–West Pacific. The last occurrence of this species is in the latemost Langhian–early Serravallian.

Author statement

D.B., J.C.B., Y.I. designed this study. Md.A., M.B.-F., J.A., W.R., H.T. contributed to sampling and analysis. Interpretation of data, discussion of the results, and writing of the manuscript were done by all authors.

Declaration of Competing Interest

None.

Acknowledgements

This study was supported by local research fund of the University of Ferrara (2016–2020) and FIR2018 (D.B.). This paper is a scientific contribution of the Project MIUR–Dipartimenti di Eccellenza 2018–2022 and of the PRIN 2017RX9XXXY (Biota resilience to global change: biomineralization of planktic and benthic calcifiers in the past, present and future). Samples from the Tallabar limestone in East Kalimantan were collected in a field campaign (June 2011) in the frame of the Throughflow Initial Training Network, funded by the Marie Curie Actions Plan, Seventh Framework Programme of the European Union [grant 237922]. J.A. and J.C.B. were funded by the research project PGC2018-099391-B-100 of the Spanish Ministerio de Ciencia, Innovación y Competitividad, and the research group RMN190 of the Junta de Andalucía. DB sincerely acknowledges the International Joint Graduate Program in Earth and Environmental Sciences (GP-EES) for the invitation to the Tohoku University. We are grateful for the collection support from Mr. Jun Nemoto, curator of the Museum of Natural History, Tohoku University. We appreciated the Editor Richard Jordan and an anonymous reviewer for their constructive comments.

Supplementary data.

Supplementary data to this article can be found online at: …xxx…

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Figure and table captions

Fig. 1. Geographic locations of the newly studied *Austrotrillina* records. 1, southeastern Spain (Ibi and Sierra de Marmolance); 2, Mangkalihat and Wailawi, East Kalimantan, Indonesia; 3–4, northern Philippine Sea, Japan (3, Kita-daito-jima; 4, Kikai Seamount).

Fig. 2. Shell structures characterising the exoskeleton in *Austrotrillina* Parr, 1942. The schemes refer to the shell boundary between two successive chambers. A, *Austrotrillina brunni* Marie *in* Brunn et al., 1955. B, *Austrotrillina striata* Todd and Post, 1954. C, *Austrotrillina howchini* (Schlumberger, 1893). Shell structure of *A. eocaenica* differs from that of *A. striata* in having subsutural alcoves (see Table 1). Abbreviations: alc, alcove; bl, basal layer; fle, flexostyle; par, parapores; par-1, parapores of first order; par-4, parapores of four order; prol, proloculus; te, tectum. Schematic drawing, not to scale. Colour online.

Fig. 3. *Austrotrillina brunni* Marie *in* Brunn et al., 1955. A, tangential sub-transversal section showing the fine parakeriotheca and the basal layer; Burdigalian–Langhian boundary, Kita-daito-jima, Hanzawa's (1940) collection, sample 835 (202.66 m); Institute of Geology and Paleontology, Graduate School of Science, Tohoku University (IGPS), Sendai, Japan. B–C, tangential sections of deformed specimens showing the fine parakeriotheca coated by the tectum; Serravallian, Sierra de Marmolance. Abbreviations: bl, basal layer; cha, chamber; par, parapores; te, tectum. Scale bars represent 0.250 mm.

Fig. 4. *Austrotrillina striata* Todd and Post, 1954; latemost Rupelian, Ibi, Alicante; southeastern Spain. A, C–D, sub-transversal sections showing the nepionic apparatus and the coarse parakeriotheca coated by the tectum. B, tangential section showing the parapores. Abbreviations: cha, chamber; fle, flexostyle; par, parapores; prol, proloculus; te, tectum. Scale bars represent 0.250 mm.

Fig. 5. *Austrotrillina striata* Todd and Post, 1954; Kita-daito-jima, northern Philippine Sea. A, Aquitanian; B–H, Langhian. A, core sample 325.42–331.53 m. B, core sample 753 (156.53 m). C, core sample 774 (166.39 m). D, core sample 775 (166.96 m). E, core sample 776 (167.52 m). F, core sample 777 (168.08 m). G, core sample 778 (168.61 m). H, core sample 779 (169.12 m). B, Hanzawa's (1940) collection; Institute of Geology and Paleontology,

Graduate School of Science, Tohoku University (IGPS), Sendai, Japan; Langhian, Kita-daito-jima; tangential sub-transversal section, specimen illustrated in Hanzawa (1940, pl. 42, fig. 1, IGPS Coll. Cat. no. 21493). Abbreviations: bl, basal layer; cha, chamber; par, parapores; te, tectum. Scale bars represent 0.250 mm.

Fig. 6. *Austrotrillina striata* Todd and Post, 1954; Serravallian, Sierra de Marmolance; southeastern Spain. A, C–E, sub-transversal sections showing the miliolid trilocular growth and the coarse parakeriotheca underlying the tectum. B, F, tangential sections of deformed specimens. Abbreviations: cha, chamber; par, parapores; prol, proloculus; te, tectum. Scale bars represent 0.250 mm.

Fig. 7. *Austrotrillina howchini* (Schlumberger, 1893); middle–late Langhian (A) and Serravallian (B), Wailawi, East Kalimantan, Indonesia. A–B, micro-computed tomographic scanning 3-D rendered model with shell removed. Departing from the chamber (cha), the branching parapores of first order (par-1) bifurcate outwardly in subsequent order (from par-2 to par-4). The first-order parapores are longer (*c.* 75 µm long) than those in the subsequent orders (*c.* 35 µm long). Scale bars represent 0.250 mm. Colour online.

Fig. 8. *Austrotrillina howchini* (Schlumberger, 1893); (Tf1) early Burdigalian, Taballar limestone, Taballar river, East Kalimantan, Indonesia. A–F, tangential sub-transversal sections showing the miliolid trilocular growth and the branching parapores of different orders (par-1, first order; par-b, second-to-fourth order) in the parakeriotheca underlying the tectum (te). G–H, tangential sections. Abbreviations: alc, alcove; b, beam; bl; basal layer; cha, chamber; prol, proloculus. Scale bars represent 0.250 mm.

Fig. 9. *Austrotrillina howchini* (Schlumberger, 1893); latemost Langhian–early Serravallian, Kikai Seamount, northern Philippine Sea. A–F, tangential sub-transversal sections. G–H, tangential sections. Abbreviations: alc, alcove; b, beam; bl; basal layer; cha, chamber; par-1, parapores of first order; par-b, parapores of second-fourth order; te, tectum. Scale bars represent 0.250 mm.

Fig. 10. Biostratigraphical patterns of the middle Eocene–Miocene *Austrotrillina* species. The middle Eocene *Austrotrillina eocaenica* is the ancestor of the Oligocene–Miocene species. *A. brunni* and *A. striata* appeared in the Rupelian of Western Tethys. Their westernmost

occurrences are in southeastern Spain (1, Ibi; 2, Sierra de Marmolance; this study). These two species migrated eastward in the Indo-Pacific area via Indonesia reaching the Central Indo-Pacific in the latemost Rupelian and its northern part in the Aquitanian (3, Kita-daito-jima, this study). In this area both species disappeared in the early Langhian (4, this study). In Western Australia *A. brunni* lasted until the early Serravallian. The rarely recorded *A. howchini* occurs in the early Miocene of Kenya, Tanzania and Indonesia (5, this study), and disappeared in the latemost Langhian–early Serravallian in the central (Kalimantan, this study) and northern Central Indo-Pacific (6, Kikai Seamount, this study). Time scale after Cohen et al. (2021, updated). Colour online.

Abbreviations: Au, Australia (w, western; ne, northeast); CIP, Central Indo-Pacific; eA, eastern Africa; ecMS, eastern closure of the Mediterranean Sea; EIP, eastern Indo-Pacific; En, Eniwetok Atoll; InB, Indonesia–Borneo; Kd, Kita-daito-jima; Ma, Midway Atoll; ME, Middle East; Md, Mediterranean area; Oi, Ogasawara Island.

Fig. 11. Palaeogeographic locations of the first appearance data of *Austrotrillina brunni* (1, green) and *A. striata* (2, purple) in the eastern Western Tethys, and the first occurrence data of *Austrotrillina brunni* (8–9) and *A. striata* (3–7) in the Indo-Pacific (A). *A. brunni* and *A. striata* migrated from the eastern Western Tethys (Middle East areas) into the modern Arabian Sea during the early Rupelian (yellow shaded area). *A. striata* reached Indonesia and Western Australia in the Chattian (3–4), whilst *A. brunni* first occurs in these areas in the Burdigalian (8–10; B). *A. brunni* (9, 13, 17) and *A. striata* (4, 14) disappeared in the Pacific Langhian and in the Mediterranean Serravallian (18; C). The lower Miocene *A. howchini* appeared in eastern Africa, western Indian, Indonesia and Western Australia (10–12; B) and disappeared in the latemost Langhian–early Serravallian (16–18; C). Occurrences refer to citations in Tables 2–4 in which detailed information on each record can be found. Compare with Fig. 9. Colour online. Palaeogeographic maps modified from Harzhauser and Piller (2007) and Kocsis and Scotese (2021).

Numbers refer to localities: 1, Wielandt-Schuster et al. (2004, Greece), Sirel et al. (2013, central Turkey), Serra-Kiel et al. (2016, Dhofar, Socotra Island), this study (Ibi); 2, Grimsdale (1952, Kirkuk, Iraq), Boukhary et al. (2010, UAE, Oman), Serra-Kiel et al. (2016, Dhofar, Socotra Island); 3, Adams (1965), BouDagher-Fadel (2018, Indonesia); 4, Chaproniere (1983, Western Australia); 5, Todd and Low (1960, Eniwetok atoll); 6, Cole (1969, Midway Atoll); 7, Matsumaru (1996, Ogasawara Island); 8, Barberi et al. (1987, Indonesia); 9, Riera et al. (2019, Western Australia), Haig et al. (2020, Western Australia); 10, Eames et al. (1962, Kenya, Sabaki River), Adams (1968, Pemba Island, Malabar); 11, Novak (2014), this study (Indonesia); 12, BouDagher-Fadel (2018, Western Australia); 13–14, this study (Kita-daito-jima); 15, O'Connell et al. (2012, South Australia); 16, Adams (1968, South Australia); 17, this study (Kalimantan); 18, this study (Kikai Seamount); 19, this study (southeastern Spain).

Table 1. Comparison of diagnostic shell characteristics of *Austrotrillina* species and related stratigraphical setting. Species are listed according to their first appearance reported in literature. Based on data from: 1, Hottinger (2007), Serra-Kiel et al. (2016); 2, Marie (*in* Brunn et al., 1955), Adams (1968), Bassi et al. (2007), Sirel et al. (2013), Ferràndez-Cañadell and Bover-Arnal (2017), Riera et al. (2019), this study; 3, Todd and Post (1954), Adams (1968), this study; 4, Parr (1942), Carter (1964), Adams (1968), this study.
Abbreviations: subsut, subsutural; *, parakeriotheca not present in the wall of the nepionic apparatus; **, parakeriotheca not present in the first three chambers.

Table 2
Stratigraphical and palaeogeographical distribution of *Austrotrillina eocaenica* and *Austrotrillina brunni*. tran, transitional forms.

Table 3
Stratigraphical and palaeogeographical distribution of *Austrotrillina striata*.

Table 4
Stratigraphical and palaeogeographical distribution of *Austrotrillina howchini*. *T*, *Trillina*.