

Larger porcelaneous foraminifera with a common ancestor: the Neogene Indo-Pacific *Flosculinella* and *Alveolinella* (Alveolinoidea)

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ABSTRACT

Only two alveolinoid genera, *Borelis* de Montfort, 1808 and *Alveolinella* H. Douvillé, 1907 thrive in present-day Indo-Pacific coral-reef settings. The former is widespread from the Western (Red Sea) to the Central Indo-Pacific and Caribbean Sea coasts, whereas the latter occurs in the Central and Eastern Indo-Pacific area. A third Indo-Pacific alveolinoid genus, *Flosculinella* Schubert *in* Richarz, 1910, is exclusively fossil. New fossil and Recent material and a type collection were

analysed to assess the taxonomic status of *Flosculinella* and *Alveolinella* species and understand alveolinoid phylogeny in the Indo-Pacific area.

The latest Oligocene–middle Miocene *Flosculinella globulosa*, the early–middle Miocene *F. reicheli*, *F. bontangensis*, *F. cucumoides*, *Alveolinella borneensis* and the middle Miocene–Recent *A. quoyi* are herein circumscribed in terms of shell length, diameter of the proloculus, whorl number of the first attic occurrence, and number of supplementary chamberlets in the attic floor per chamberlet in the main floor. The occurrence of the preseptal passage only and Y-shaped septula in *Borelis schlumbergeri*, *Flosculinella* and *Alveolinella* are characters of phylogenetic significance. Oligocene–early Miocene *Borelis philippinensis* is inferred as the common ancestor of these taxa.

The diversification of *Flosculinella* and *Alveolinella* occurred in the Coral Triangle of Southeast Asia during the early–middle Miocene. The northernmost occurrence of the Tortonian–Recent *A. quoyi*, widespread from Central to the Eastern Indo-Pacific areas, is in the Ryukyu Islands.

Keywords:

Palaeobiogeography

Systematics

Shallow-water carbonates

Indo-Pacific Ocean

Miocene

Recent

1. Introduction

Two alveolinoid genera *Borelis* de Montfort, 1808 and *Alveolinella* H. Douvillé, 1907, which first appeared in the middle Eocene and in the middle Miocene, respectively (e.g. Hottinger, 1974; Loeblich and Tappan, 1987), live in present-day tropical shallow-water marine environments in the Indo-Pacific. A third alveolinoid genus, *Flosculinella* Schubert in Richarz 1910, had a short evolutionary history limited to the latest Oligocene–middle Miocene (Hottinger, 1974; Lunt and Allan, 2004; Bassi et al., 2021a). The modern Indo-Pacific alveolinoid genera are represented by only two fusiform species, *Borelis schlumbergeri* (Reichel, 1937) and *Alveolinella quoyi* (d’Orbigny, 1826), and a single spherical species, *B. pulchra* (d’Orbigny, 1839). *Borelis schlumbergeri* is widespread from the Western (i.e. Red Sea) to the Central Indo-Pacific (CIP), whereas *A. quoyi* occurs in the CIP and Eastern Indo-Pacific (from the Maldives to the Hawaii islands; Reiss and Hottinger, 1984; Hohenegger, 2000; Langer and Hottinger, 2000). *Borelis schlumbergeri* has been found in fringing reefs (back-reef to fore-reef), in rock pools and intertidal settings on rubble, coral sand and plants at water depths shallower than 40 m (Cole, 1957; Hottinger et al., 1993; Langer and Hottinger, 2000; Debenay, 2012; Fajemila et al., 2015; Weinmann and Langer, 2017). *Alveolinella quoyi*, the largest living porcelaneous foraminifer, lives on sandy slopes, coral rubble on the reef slope and in sandy inter-reef environments of the euphotic zone (e.g. Reiss and Hottinger, 1984; Hohenegger, 2000, 2006; Langer and Lipps, 2003; Debenay, 2012; Renema, 2018; Bassi et al., 2022).

In larger benthic foraminifera, the apertural face and shell morphology reflect functional adaptations related to their locomotion, feeding, and photosymbiosis (Hottinger, 2000, 2005; Hohenegger, 2018). Both *Alveolinella* and *Borelis* possess diatom symbionts (Hottinger, 1983). Photosymbiosis may be inferred from shell morphology and shell architecture to capture light (Leutenegger, 1984; Brasier, 1993; Hottinger, 2000; Hohenegger, 2011, 2018). The large fusiform tests of *Borelis schlumbergeri* and *Alveolinella quoyi* expand their surface through lengthening the skeleton in an axial direction which is occupied by the protoplasm with symbionts below the outer shell surface (Severin and Lipps, 1989; Hohenegger, 2009). Living individuals of *A. quoyi* can only fill an average of 39 % of their chamber space with protoplasm (Severin and Lipps, 1989). The increase in their shell size during ontogeny is positively related to an increase in the number of apertures. These are likely to strengthen the fixation on substrate by multiplying the attachment through a bundle of pseudopods (Hottinger, 2006a; Hohenegger, 2018).

The purposes of this study are (1) to assess the taxonomic status of *Flosculinella* and *Alveolinella* species to understand their phylogeny in the Indo-Pacific area, (2) to describe newly

discovered Y-shaped septula in *A. quoyi* already known in *B. schlumbergeri*, and (3) to assess the phylogenetic history of these taxa. The discovery of Y-shaped septula was possible due to analysis of modern and fossil material of *A. quoyi* from the Ryukyu Islands and Indonesia. Interestingly, the putative Indo-Pacific ancestor of *Flosculinella* appeared in the Oligocene while that of *Alveolinella* first occurs in the early Miocene. These taxa show shell traits in common with middle Eocene *Borelis* (aligned septula, only preseptal passage present and lack of postseptal passage).

2. Material and methods

This study was carried out on collected larger benthic foraminiferal specimens from fossil and modern coral-reef related settings. Fossil *Flosculinella globulosa*, *F. reicheli* and *F. bontangensis*, from Indonesia and the Maldives, and *Alveolinella quoyi* from Okinawa-jima (Ryukyu Islands), were examined in rock thin sections. The types of *F. cucumoides* are preserved as thin sections in the collections of the Museum Victoria, Melbourne, Australia, and were re-photographed for this study.

In the Taballar Limestone (Wilson et al., 2007; Novak, 2014; Renema et al., 2015), *F. globulosa* and *F. reicheli* were identified from the lower Burdigalian interval (Mankalihat, East Kalimantan, Indonesia). *F. bontangensis* is found in the Kutei Basin (East Kalimantan) from the upper Burdigalian to Serravallian interval (Bontang area, East Kalimantan, Indonesia; type area; Novak et al., 2013; Renema et al., 2015) and in Wailawi (south of Balikpapan Bay, East Kalimantan) from the Langhian or younger age (Bassi et al., 2021b). Additional material of *Flosculinella bontangensis* was studied also from the Serravallian platform carbonates in the Maldives (Reolid et al., 2020).

Specimens of *Alveolinella borneensis* were collected from close to the Langhian–Serravallian boundary of the Stadion stratigraphic section near Samarinda (East Kalimantan, Indonesia), from sediments inside a large strombid shell from the Serravallian of Pacitan (East Java, Indonesia; 12.2 Ma), and from several localities in the Tortonian of the Kutai basin (Sangatta, East Kalimantan, Indonesia) ranging from 11.6 Ma to 9.4 Ma in age (Renema et al., 2015). The Stadion specimens occur associated to *Nephrolepidina ferreroi* and *Cycloclypeus annulatus* suggesting an age older than the Langhian–Serravallian boundary (Marshall et al., 2015; Santodomingo et al., 2015).

Studied fossil *Alveolinella quoyi* occurs in the Calabrian–Chibanian (Pleistocene) Kourijima Formation of the Ryukyu Group outcropping in the Motobu Peninsula (samples M62_5 from Ohama, Motobu town; 167 Tobaru Core 12B-4–13.0 m and 16 Tobaru Core 13B-7–5.98 m from

Tobaru, Motobu town; N1-2-5 and N1-3-5 from Nakasone, Nakijin village; Yamamoto et al., 2006; Iryu et al., 2006) and in the Calabrian–Chibanian Sobe Formation in the Yomitan–Onna area (sample 362 from Maeda, Onna village; Muraoka et al., 2005), Okinawa-jima, Ryukyu Islands. Fossil *A. quoyi* was also studied from the Tortonian of Sangatta (Kalimantan; 8.9–9.3 Ma; Renema et al., 2015) and Messinian of Bengalon (Kalimantan; Renema et al., 2015), from the Pliocene of Malaysia (Togopi; Whittaker and Hodgkinson, 1979) and Waigeo (West Papua, Indonesia) and from the earliest Pleistocene of Cebu (Philippines).

The present-day *Alveolinella quoyi* was collected from Vanuatu and the Ryukyu Islands. The Vanuatu specimens were collected from the fore-reef of Esperitu Santo (Vanuatu) in 25–30 m water depth (15°33'11"S, 167°13'11"E). The Ryukyu specimens occurred in coral rubble on a fore-reef slope (15 m water depth) at Kushibaru, Aka-jima (26°12'46.7"N, 127°16'28.8"E), and in coral rubble on a fore-reef slope (35 m water depth) at northwest of Irabu-jima (24°51'53.5"N, 125°09'11.8"E).

The studied samples are stored in the Dipartimento di Fisica e Scienze della Terra of the University of Ferrara, in the Departamento de Estratigrafía y Paleontología of the Universidad de Granada, Naturalis Biodiversity Center (Leiden, the Netherlands), and in the Institute of Geology and Paleontology of the Tohoku University. The studied isolated specimens were micro-computed tomographic scanned in the Dipartimento di Fisica e Scienze della Terra of the University of Ferrara. The fossil specimens were, for the largest part, well without infillings of the chambers, allowing their volume segmentation, highlighting the complex shell structure. The internal cement was sparry calcite, not affecting the LBF microcrystalline texture (porcelaneous). The micro-computed tomographic scanning 3D-models were rendered with shell removed, in order to highlight the volumes occupied by protoplasm within the shell and the arrangement and communications among chambers and chamberlets. Detailed micro-computed tomographic method performed on LBF have been described by Kellner et al. (2019) and Macher et al. (2021). The micro-computed tomographic system consists of a Hamamatsu L9421-02 tungsten X-ray microfocus tube with an anode voltage of 70 kVp. The used current was 100-110 μ A. Rotation step ranges between 0.5° to 1°, with an exposure time of 1 second. The reconstructed voxel size was 5x5x5 μ m³ with the reconstruction algorithm FDK on GPU. The X-ray detector collects hundreds of angular shadow images while the object rotates, thereafter, a computer program (Di Domenico, 2014), developed on CUDA framework and including alignment optimization, uses a modified Feldkamp algorithm allowing the reconstruction of data throughout the full 3D volume. Scanning Electron Microscopy analyses were performed at the University of Ferrara. Additional studied specimens were micro-computed tomographic scanned in the Zeiss XRadia Vera 520 at Naturalis Biodiversity Center.

Architectural and morphological terms are those used by Smout and Eames (1958), Hottinger (1960, 2006b) and Hottinger et al. (1993). The suprageneric classification follows Loeblich and Tappan (1987) and Fleury and Fourcade (1990). The analysed *Flosculinella* and *Alveolinella* species are listed in the systematic palaeontology chapter according to their stratigraphical appearance. Synonymy lists can be found in the Supplementary data.

3. Systematic palaeontology

Superfamily Alveolinoidea Ehrenberg, 1839.

Family Borelidae Schmarda, 1871.

Subfamily Borelinae Schmarda, 1871.

Remarks: In describing the foraminiferal shell structures Hottinger (2006b) redefined the terms floor and attic for endoskeletal elements. These terms still appear to be the only ones that can unambiguously be applied to these shell elements. Within the larger porcelaneous foraminifera of the superfamily Alveolinoidea in a chamber the floors ('planchers' in Reichel, 1937; Hottinger, 1960; Fleury and Fourcade, 1990) separate superposed regular layers of chamberlets. The foramina corresponding to the basal layer of chamberlets are named f1, those of the second layer f2, and those corresponding to the supplementary foramina in the attics f3. The attics ('mansardes' in Reichel, 1937) correspond to the outermost lateral or abaxial layer of tubiform chamberlets with smaller calibre/diameter than the less lateral or adaxial ones (f1, f2).

Genus *Flosculinella* Schubert in Richarz, 1910.

Type species: *Alveolinella bontangensis* L. Rutten, 1913, p. 221.

Diagnosis: Shell sub-spheroidal, ellipsoidal to fusiform in shape, up to 1.5 mm in diameter and up to 2.5 mm in length, no dimorphism, early whorls streptospiral, septula aligned, Y-shaped septula present, each chamber with one layer of main chamberlets and, in the adult stages, one layer of attics.

Remarks: *Flosculinella* species are exclusively known from fossil specimens (*F. globulosa*, *F. reicheli*, *F. bontangensis*; Figs. 1–2, 4, 7). Y-shaped septula occur in the whorls of adult stages (Figs. 1–2, 6; see also *F. globulosa* in Hottinger, 1974, pl. 103, fig. 4; *F. bontangensis* in Hottinger, 1974, pl. 104, figs. 1, 4). The length of the shell, the diameter of the proloculus, the number of whorls of the first attic occurrence, and the number of supplementary chamberlets in the attic layer per chamberlet in the main layer are reliable characters to distinguish the species (Table 1).

Flosculinella globulosa (Rutten, 1917).

Fig. 1A–E.

(see Supplementary data for the synonymy list)

Type reference and figures: *Alveolinella globulosa* Rutten, in Martin (1917), p. 277, pl. 5, figs. 140–141 (drawings), holotype not designated.

Lectotype of *F. globulosa*: In the original material illustrated as drawings Rutten (1917) did not designate a type. In accordance with Art. 74 of ICZN (1999), we designate hereby as lectotype the specimen originally illustrated by Rutten (1913, pl. 7, fig. 140), in order to clarify the application of this name.

Diagnosis: Sub-spheroidal to slightly sub-ellipsoidal shell 0.7–1.5 mm in diameter. Proloculus 35–50 µm in diameter with 2–3 streptospiral whorls. First attic occurs from the non-streptospiral second whorl. Less than 2 supplementary chamberlets in the attic (f3) per chamberlet in the basal layer (f1).

Studied material: The studied specimens are from the lower Burdigalian of the Taballar Limestone in the Mankalihat Peninsula (East Kalimantan, Indonesia; Fig. 1). Sub-spheroidal specimens 0.45–0.82 mm in length. Proloculus is *c.* 40 µm in diameter. Y-shaped septula occur in the whorls of adult stages (Fig. 1A). The first attic occurs in the second whorl with two supplementary chamberlets in the attic layer (f3) per chamberlet in the basal layer of chamberlets (f1).

Remarks: Two specimens were illustrated as drawings by Rutten (*in* Martin, 1917), representing tangential sub-axial and oblique sub-equatorial sections. The specimen illustrated in fig. 141 of Rutten *in* Martin (1917) shows the preseptal passage only and that in fig. 140 shows one layer of main chamberlets and one layer of attics, which are diagnostic characters for *Flosculinella*.

Flosculinella globulosa is separated from *F. reicheli* by having attics appearing from the second whorl and from *F. bontangensis* by its smaller size and by having less than two supplementary chamberlets in the attic per chamberlet in the basal layer of chamberlets (Table 1).

Stratigraphical distribution: Rutten's (*in* Martin, 1917) material was collected from the Burdigalian deposits of Kembang Sokkoh and Gunun Spolong, Yogyakarta, Java, Indonesia (Martin, 1911; Renema, 2008), which have been dated at 18.9 Ma (Reich et al., 2014). This species occurs from the late Chattian to the Langhian in Bikini Atoll, Midway Atoll, and the Philippines (Cole, 1954, 1969; Matsumaru, 2011, 2017), in the early Miocene (upper Te–lower Tf) of New Britain (Binnekamp, 1973), in the early Miocene of Indonesia (Hanzawa, 1957; Hottinger, 1974; Lunt and Allan, 2004; Renema, 2007, 2008; this study), in the late Aquitanian–Burdigalian of eastern and southwestern Australia (Haig et al., 2020) and in the late Langhian–early Serravallian of Western Australia (Chaproniere, 1984; Riera et al., 2019; Table 2, Fig. 7).

Flosculinella reicheli Mohler, 1949.

Fig. 2.

(see Supplementary data for the synonymy list)

Type reference and figures: *Flosculinella reicheli* Mohler, 1949 (p. 151; only description); Mohler (1950), pp. 524–525, text-fig. 2 (1–6; fig. 5, holotype).

Diagnosis: Spheroidal shell 0.4–0.6 (maximum 0.8) mm in diameter. Proloculus 35–40 µm in diameter with 3–4 streptospiral whorls. Adult whorls with attics and one to two supplementary chamberlet (f3) per chamberlet in the basal layer of chamberlets (f1).

Studied material: The studied specimens are from the early Burdigalian of the Taballar Limestone in the Mankalihat Peninsula (East Kalimantan, Indonesia; Fig. 2). Sub-spheroidal and tightly coiled specimens with length up to 0.48 mm. Proloculus is 35–40 µm in diameter. The first attic occurs in the third whorl with one supplementary chamberlet (f3) in the attic layer per chamberlet in the basal layer of chamberlets (f1).

Remarks: The holotype of *F. reicheli* is an unsectioned, isolated specimen that does not show inner shell structures (Mohler, 1949). The occurrence of only the preseptal passage, aligned septula, one layer of main chamberlets and one layer of attics per chamber in the paratypes of *F. reicheli* (Mohler, 1949, fig. 2/1–3) indicate that it belongs to *Flosculinella*. *Flosculinella reicheli* differs from *F. globulosa* and *F. bontangensis* in having the attics appearing in the third or fourth whorls with only one supplementary chamberlet in the attic layer per chamberlet in the basal layer of chamberlets (Table 1, Fig. 2).

Stratigraphical distribution: The types of *F. reicheli* are from the Aquitanian of Hulu-Sungei, southern Borneo (Mohler, 1949). This species has only been found in the early Miocene of Indonesia (Adams, 1965, 1970; Hottinger, 1974; BouDagher-Fadel and Lokier, 2005; Renema, 2007; this study; Table 2, Fig. 7). Poorly preserved specimens identified as *F. reicheli* by Matsumaru (1996, pp. 212, 214, pl. 84, figs. 1–2) from the Oligocene of the Ogasawara Islands (Japan) do not appear to be conspecific or even congeneric.

Flosculinella bontangensis (Rutten, 1913).

Figs. 1F, 3–5.

(see Supplementary data for the synonymy list)

Repository data of *F. cucumoides*: Thin sections labelled ‘*Alveolina cucumoides* Chapman, New Hebrides pl. 38 f. 5, 6. 108’ and ‘*Flosculinella cucumoides* (Chapman, 1908) Topotype Bartaleppe, Malekula, New Hebrides, Sample 108. P134790’, ‘*Flosculinella cucumoides* (Chapman, 1908) Topotype Bartaleppe, Malekula, New Hebrides, Sample 108. P134791’, ‘*Flosculinella cucumoides* (Chapman, 1908) Topotype Bartaleppe, Malekula, New Hebrides, Sample 108. P134792’, and ‘*Flosculinella cucumoides* (Chapman, 1908) Topotype Bartaleppe,

Malekula, New Hebrides, Sample 108. P134793'; housed at the Museum Victoria, Melbourne, Australia.

Type reference and figures of *F. cucumoides*: *Alveolina cucumoides* Chapman, 1908, pp. 754–755, pl. 38, figs. 5–6.

Type locality and horizon of *F. cucumoides*: Laleppe (Lalemba), along the track Laleppe Amil–Bartaleppe, northern Malakula Island, Vanuatu, Pacific Ocean. Miocene limestone and tuffs (Chapman, 1908, p. 746).

Diagnosis of *F. cucumoides* (modified from Chapman, 1908): Ellipsoidal to fusiform shell. Equatorial diameter of *c.* 1 mm and 1.8–2.5 mm in length. Proloculus *c.* 80 µm in diameter and 1–2 streptospiral whorls. Two supplementary chamberlets in the attic layer (f3) per chamberlet in the basal layer of chamberlets (f1).

Lectotype of *A. cucumoides*: Chapman (1908) did not designate a holotype. The original material illustrated by Chapman (1908, pl. 38, figs. 5–6) occurs in the same thin section. In accordance with Art. 74 of ICZN (1999), we designate hereby as lectotype (Fig. 3A) the specimen in thin section '*Alveolina cucumoides* Chapman, New Hebrides pl. 38 f. 5, 6. 108', originally illustrated by Chapman (1908) in pl. 38, fig. 5, with the purpose of clarifying the application of this name. The specimen illustrated by Chapman (1908) in pl. 38, fig. 6 becomes a paralectotype (Fig. 3B).

Type reference and figure: *Alveolinella Bontangensis* Rutten, 1913, pp. 221–224, text-figs. 1–2; pl. 14, figs. 1–3, holotype not designated.

Syntypes of *F. bontangensis*: Sample number RGM.17691 and labelled as '*Alveolinella bontangensis* Rutten; Bontang Borneo; Burdigalien; Rutten, Samml. Bd9, S221'. The type locality is *c.* 5 km to the North of the 3D-reef described in Novak et al. (2013) and dated as 15.6–16.0 Ma (Renema et al., 2015).

Studied material: The specimens are from the upper Burdigalian of the Bontang area in the Kutai Basin (East Kalimantan, Indonesia; Fig. 1F), from the early Langhian of Wailawi (East Kalimantan, Indonesia; Fig. 4), late Langhian- early Serravallian marls in Mankalihat (East Kalimantan; published before in van der Vlerk 1929), and from Serravallian carbonates drilled in the western Kardiva Channel in Maldives (Site U1465, International Ocean Discovery Program (IODP) Expedition 359; Reolid et al., 2020; Fig. 5). Sub-ellipsoidal specimens *c.* 0.65–1.0 mm in diameter and *c.* 1.1–2.3 mm in length. Proloculus, only observed in the isolated specimens from East Kalimantan, ranges from *c.* 75 to 85 µm in diameter. The proloculus is elliptical, with a ratio of 0.95/1/1.05 (minimum diameter, max diameter, height). The orientation of the flexostyle, enveloping the proloculus for *c.* 270°, is variable with respect to the direction of the elongation axis

of the shell. This increases the variability in observed proloculus size in oriented thin sections. The flexostyle is followed by $1\frac{1}{3}$ – $2\frac{1}{3}$ streptospiral whorls (1–8 streptospiral chambers) (Fig. 4A–B). The first attic occurs in the 14th–17th chamber equal to the fourth to fifth whorl with one or two supplementary chamberlets (f3) per chamber (f1) in the basal layer, whereas in the later whorls with two supplementary chamberlets (f3) in the attic layer per chamberlet (f1) in the basal layer. From the second whorl the chambers (with two chamberlets or more each) increase in number at *c.* one chamber per whorl; the fourth whorl shows six chambers with six–seven chamberlets each (f1). This increase in number of chambers can be irregular. In the fourth whorl the chamber axis is at *c.* 60° angle to the previous chamber (Fig. 4E). In the fifth whorl this axis is at *c.* 30° (Fig. 4F), the chamberlets are *c.* eleven with up to eighteen supplementary chamberlets (f3). From the fifth whorl onwards the chamber axis becomes increasingly more parallel to the elongation axis of the test, and number of chamberlets increases to up to 20 f1 and 40 f3 per chamber. Up to $9\frac{1}{3}$ whorl in the Wailawi population, up to 11 whorls in the larger specimens in the Bontang and Mankalihat population. The number of chambers per whorl is highly variable from 8–11. Damage and repair is frequent in the Wailawi population (Fig. 4G).

Remarks: The occurrence of the preseptal passage only and aligned septula in the lectotype of *A. cucumoides* indicates that it belongs to *Flosculinella* (Fig. 3A, C–D).

The lectotype of *A. cucumoides* illustrated in pl. 38, fig. 5 (Chapman, 1908) represents a sub-equatorial section showing the proloculus, the preseptal passages and the attics (Fig. 3A). The first attic occurs in the second whorl. The paralectotype (pl. 38, fig. 6) is a sub-axial section, nearly tangential to the nepionic apparatus, showing preseptal passages, aligned septula, the basal layer of chamberlets and two supplementary chamberlets in the attic layer per chamberlet in the basal layer of chamberlets (Fig. 3C–D).

Rutten (1913) introduced the name *Alveolinella bontangensis* from the Burdigalian of Bontang (East Kalimantan, Borneo) with no mention of Chapman's species (see also Keijzer, 1940, p. 628). The name *cucumoides* has been rarely quoted in literature. Crespin (1955, p. 74, no illustration) recorded *F. cucumoides* from the middle Miocene Trealla Limestone (Cape Range area, Western Australia). Adams (1970, p. 115) incorrectly stated that *A. cucumoides* is a junior synonym of *F. bontangensis* Rutten, 1913, as noted by Chaproniere (1984). The name *cucumoides* is, actually, a senior subjective synonym of *bontangensis*.

In contrast, *Flosculinella bontangensis* is a name that has been widely used in systematic and stratigraphical studies, having been used in at least twenty-five works by twenty authors in the immediately preceding fifty years. Thus, *Flosculinella cucumoides* precedes *F. bontangensis*, but priority is suppressed under Arts. 23.91.1 and 23.9.1.2 of the ICZN (1999). The younger valid name

is *F. bontangensis* (*nomen protectum*) and the invalid, but older, name is *F. cucumoides* (*nomen oblitum*).

Flosculinella bontangensis differs from *F. globulosa* and *F. reicheli* in being ellipsoidal to fusiform in shape and in having the attics appearing from the third whorl with two supplementary chamberlets in the attic layer per chamberlet in the basal layer (Table 1).

Hashimoto and Matsumaru (1975) described *Flosculinella fusiformis* from the Aquitanian–Burdigalian of the Philippines and separated it from *F. bontangensis* by its different growth rate. The single illustrated specimen is the holotype (Hashimoto and Matsumaru, 1975, pl. 14, fig. 8) showing a tangential section of a proloculus (34–36 µm in diameter in Hashimoto and Matsumaru 1975) and about two supplementary chamberlets (f3) in the attic layer per chamberlet (f1) in the basal layer of chamberlets. The shell length (2.20 mm in length in Hashimoto and Matsumaru, 1975) and the number of supplementary chamberlets in the attic floor per chamberlet in the basal layer suggest that it cannot be separated from *F. bontangensis*.

Stratigraphical distribution: Chapman (1908) attributed his material from Malekula, New Hebrides, Vanuatu to the Miocene (1908, p. 758). *Flosculinella bontangensis* occurs in the early–middle Miocene of the Pemba Island (Kenya; Eames et al., 1962), Philippines (Matsumaru, 2011, 2017), Indonesia, Malaysia and Java (Hottinger, 1974; Barberi et al., 1987; Lunt and Allan, 2004; BouDagher-Fadel and Lokier, 2005; Renema, 2007; Renema et al., 2015; BouDagher-Fadel, 2018; Novak and Renema, 2018), southwestern Australia (Haig et al., 2020), and in the middle Miocene of the Maldives (Reolid et al., 2020; this study), Northern and Western Australia (Chaproniere, 1984; Riera et al., 2019), and Marion Plateau in northeastern Australia (Hallock et al., 2006; Table 2, Fig. 7).

Genus *Alveolinella* H. Douvillé, 1907.

Type species: *Alveolina quoyi* d’Orbigny, 1826 (= *Alveolina quoyi*, *nom. imperf.*).

Diagnosis: Prolate, fusiform shell with dimorphism. Early streptospiral whorl occurring in both generations. Septula aligned, Y-shaped septula in axial sections. Only preseptal passage present. Two or three layers with chamberlets (i.e. with foramina f1–f2) and one layer of attics (i.e. with foramina f3) per chamberlet in later whorls.

Remarks: The species dealt with here are known from exclusively fossil (*A. borneensis*) and from fossil and Recent (*A. quoyi*) specimens (Figs. 6–9). Y-shaped septula occur in the whorls of adult stages (Fig. 7C–D), marking even Y-shaped chamber sutures on the shell surface (Figs. 7–8). These septula are randomly distributed in the shell development. The index of elongation (I.E.), the number of floors and the whorl number of the attic first occurrence are reliable characters to separate species (Table 3).

Alveolinella borneensis and *A. quoyi* belong to the same evolutionary lineage and, therefore, represent successive chronospecies within the same lineage. The scattered stratigraphical data available prevent us from choosing a well-defined morphometric limit between these two chronospecies and instead we refer to a combination of characters. By definition (Drooger, 1993, p. 26), in every geological sample no more than a single chronospecies within a lineage is represented. Populations or specimens showing characters intermediate between the two chronospecies may be referred to either as *exemplum intercentrale* (*ex. interc.*) following the conventions set forth by Drooger (1993, p. 31) according to the biometrical approach, or as transitional specimens between *A. borneensis* and *A. quoyi* according to a typological approach.

Alveolinella borneensis Tan, 1936.

Fig. 6.

(see Supplementary data for the synonymy list)

Neotype of *A. borneensis*: Tan (1936) introduced the new name *Alveolinella borneensis* for van der Vlerk's (1929, fig. 24) material, but no holotype nor lectotype have been designated. Although Hottinger (1974, p. 70) considered as the type the specimen illustrated by van der Vlerk (1929, fig. 24), he did not properly designate a neotype (ICZN, Art. 75.3.1). In accordance with Art. 75 of ICZN (1999), we designate herein the specimen illustrated in Fig. 6 as the neotype in order to clarify the taxonomic status of this species. The neotype is stored in the micropalaeontological collections of the Naturalis Biodiversity Center of Leiden (The Netherlands).

Diagnosis: Fusiform (prolate) shell (I.E. 3.4–4.2; Table 3) with early two whorls with one basal layer of chamberlets (f1) and one layer of supplementary chamberlets (f3) in the attic, later whorls with two layers of main chamberlets (f1, f2) and one layer of supplementary chamberlets (f3) in the attic per chamberlet. Slight polar torsion. The proloculus is globular (60–80 µm in diameter) with a flexostyle enveloping for 265°–280° and ending in a single aperture.

Studied material: The studied specimens are from the Serravallian–Langhian boundary of the Stadion stratigraphic section near Samarinda (East Kalimantan, Indonesia), from the Serravallian of Pacitan (Java) and the Tortonian of the Kutai basin (East Kalimantan, Indonesia). Fusiform (prolate) shell with globular proloculus (*c.* 70 µm in diameter) with the main axis not parallel to the coiling axis. Flexostyle, enveloping the proloculus by *c.* 270°, shows a single aperture. The first and second chambers with multiples apertures (f1) are followed by the third chamber characterised by one layer of supplementary chamberlets (f3) in the attics (Fig. 6A–D). Later whorls with two layers of chamberlets (f1, f2) and one layer of supplementary chamberlets (f3) in the attic per chamberlet (Fig. 6E–F). The supplementary chamberlets (f3) in the attics are larger than in *A. quoyi*.

Remarks: Verbeek and Fennema (1896) described and illustrated two alveolinoids from the Miocene of south Sindagsari (p. 1141, pl. 2, fig. 42) and Bautarguebang (p. 1142, pl. 2, fig. 43) in Java with no taxonomic ascription. Because their drawings do not show the earlier whorls with layers of chamberlets and related foramina, these specimens cannot be ascribed with any certainty to *Alveolinella*. In a footnote Checchia-Rispoli (1909, pp. 67–68) introduced two new names for Verbeek and Fennema's (1896) alveolinoid specimens: *Alveolina Verbeeki* and *Alveolina Fennemai*. These taxa, although insufficiently figured by Verbeek and Fennema (1896), were validly established, being species names by indication (ICZN, 1999, Art. 12.2).

Van der Vlerk (1922) recorded *Alveolinella boscii* Defrance (pp. 68–69) and *Alveolinella fennemai* (Checchia-Rispoli) (p. 69) from the Miocene of Sumbawa (Indonesia). The two figured specimens ascribed to *A. boscii* (pl. 2, fig. 10) are tangential sub-axial sections showing two layers of main chamberlets (f1, f2) and one layer of supplementary chamberlets (f3) in the attics. No features of the early whorls can be observed. However, van der Vlerk (1922, p. 70) states that the early whorls of *A. boscii* are comparable to those of *F. bontangensis*. Therefore, van der Vlerk's (1922) specimens can be ascribed to *Alveolinella* based upon the characteristics of the early whorls (Table 3). The specimen named as *A. fennemai* and illustrated in pl. 2, fig. 11 is a tangential sub-axial section which does not show clear diagnostic characters, hampering its generic ascription.

Tan (1936, p. 178, no illustration) introduced the new species *Alveolinella borneensis* for the Miocene specimen of van der Vlerk (1929, fig. 24 as *Alveolinella boscii*), recognising that 'it corresponds to the *bontangensis* type due to the chamber structure' (p. 178, transl. from German). Van der Vlerk's (1929, fig. 24) specimen, c. 1.6 mm long, shows one floor of chamberlets (f1) and supplementary chamberlets (f3) in the attic. Therefore, it cannot be ascribed to *Alveolinella* and, based upon the occurrence of first attic in the second whorl with two supplementary chamberlets (f3) in the attic layer per chamberlet in the basal layer of chamberlets (f1; Table 1), it belongs to *F. bontangensis*.

Hottinger (1974, pl. 105, figs. 1–2, pl. 106, fig. 5) named *A. borneensis* Miocene specimens from the Moluccas and Mangkalihat (Indonesia) with early whorls with one basal layer of chamberlets (f1) and one layer of supplementary chamberlets (f3) in the attic. The later whorls are characterised by two layers of main chamberlets (f1, f2) and one layer of supplementary chamberlets (f3) in the attic per chamberlet. The occurrence of chamberlets in more than two layers (f1, f2) in the neotype of *Alveolinella borneensis* (Fig. 5; compare with van der Vlerk, 1922, pl. 2, fig. 10) supports that it belongs to *Alveolinella*. Its status as a distinct species is confirmed by the occurrence of one layer of main chamberlets in the first two whorls along with the characters of the proloculus and the flexostyle (Table 3).

Based on material from the early to middle Miocene (Tf1–Tf2) of the Central Highlands, Papua New Guinea, Wonders and Allan (1991) introduced *Alveolinella praequoyi*. Wonders and Allan (1991, p. 173) did not rule out the possible synonymy of *A. praequoyi* and *A. fennemai*, the latter being a possible senior synonym. However, they mentioned neither *A. verbeeki* (Checchia-Rispoli) nor *A. borneensis* Tan. Wonders and Adams (1991) separated *A. praequoyi* from *A. quoyi* based on a distinct juvenile stage with only a single layer of chamberlets and attic, followed by an adult stage with two layers of chamberlets and one attic (p. 173, holotype figured in fig. 5a–b; see also BouDagher-Fadel, 2018, pl. 7.4, fig. 20). As described and illustrated by Hottinger (1974), these characters are in fact typical of *A. borneensis* which, therefore, is likely to be a senior synonym of *A. praequoyi*. However, detailed analysis of the early whorls are necessary to clarify its status as distinct species. These middle Miocene forms can be, therefore, referred as to *Alveolinella ex. interc. borneensis* Tan *et quoyi* (d’Orbigny) (Table 4).

Stratigraphical distribution: *Alveolinella borneensis* has been recorded from the late Burdigalian–early Tortonian of Indonesia, Papua New Guinea and northern Australia (Hottinger, 1974, 2006a; Wonders and Adams, 1991; Lunt and Allan, 2004; see Supplementary data, Table 4, Fig. 10).

The Langhian–Tortonian records of *A. quoyi* in Bikini (Todd and Post, 1954), Eniwetok (Cole, 1957) and *A. praequoyi* in Papua New Guinea (Wonders and Adams, 1991) show characters attributable to *A. borneensis* rather than to *A. quoyi sensu stricto* (see Tables 3–4).

Alveolinella quoyi (d’Orbigny, 1826).

Figs. 7–9.

(see Supplementary data for the synonymy list)

Type reference and figures: *Alveolinella quoyi* (d’Orbigny) Hofker, 1930, 166–170; d’Orbigny, 1826, pl. 17, figs. 11–13 (fig. 11, lectotype).

Diagnosis: Fusiform (prolate) shell (I.E. higher than 5; Table 3), the first whorl with one basal layer of main chamberlets (f1) and one layer of attic per chamberlet (f3). In the later whorls up to three layers of main chamberlets (f1, f2, f2) with one layer of attic (f3) per chamberlet. Polar torsion twisted/convoluted. Proloculus is sub-ellipsoidal (up to *c.* 80 µm in diameter and 160 µm in length) with the longest axis of the proloculus in the direction of the coiling axis and constrained at the position of the flexostyle (Fig. 9). The flexostyle envelopes the proloculus for 330° in the Recent specimens, 300°–320° in the upper Miocene specimens, and ends in multiple apertures.

Lectotype: In the original material illustrated as drawings d’Orbigny (1826) did not designate a type. In accordance with Art. 74 of ICZN (1999), we designate hereby as lectotype the specimen originally illustrated by d’Orbigny (1826, pl. 17, fig. 11).

Studied material: Late Tortonian of Sangatta (Kalimantan; Renema et al., 2015), Messinian of Bengalon (Kalimantan), Pliocene of Malaysia and Waigeo (West Papua New Guinea) and Pleistocene of Cebu (Philippines). These isolated specimens show proloculus shapes, flexostyle and initial chambers very similar in shape to those of Recent studied specimens. Most specimens are characterised by the occurrence of two or three layers with chamberlets (f1, f2, f2) and one layer of attics (f3) per chamberlet in later whorls.

Calabrian–Chibanian Kourijima (Pleistocene) Formation, Motobu Peninsula, Okinawa-jima, Ryukyu Islands (samples M62, 167 Tobaru Core 12B-4–13.0 m, 16 Tobaru Core 13B-7–5.98 m, N1-2, N1-3) and Calabrian–Chibanian Sobe Formation, Yomitan to Onna area of Okinawa-jima (sample 362). The fossil specimens occur as random sections in thin sections from a hard-cemented limestone. Specimens, *c.* 1.0 mm in diameter and *c.* 4.0 mm in length, show two to three layers of chamberlets (f1, f2, f2) and one layer of attic with supplementary chamberlets (f3; Fig. 6). The studied Recent specimens are from coral rubble on a fore-reef slope (15 m water depth) at Kushibaru, Aka-jima, Okinawa-jima, Japan (Fig. 8), and from Vanuatu (Fig. 9). Prolate specimens with a diameter up to 1.0 mm and *c.* 3.8 mm long. Sub-ellipsoidal proloculus, up to *c.* 160 µm in diameter, with the flexostyle enveloping by *c.* 330° and multiple apertures (Fig. 9). Y-shaped septula present (Fig. 8). Later whorls with three layers of chamberlets (f1, f2, f2) and one layer of attics (f3) per chamberlet (Figs. 8A, 9G–H). Sinusoidal reverse masks in the apertural face (Fig. 8H).

Remarks: The analysed material is morphometrically and architecturally concordant with *Alveolinella quoyi* (Reichel, 1937; Hottinger, 1974; Table 5).

Alveolinella quoyi differs from *A. borneensis* in being longer (I.E. up to 5.4) and in having two layers of chamberlets (two layers with superposed foramina f1, f2) and one layer of attic (f3) per chamber from the first whorl (Table 3).

Stratigraphical distribution: This species has been identified exclusively in the CIP area, from the Tortonian to the Recent (Todd and Post, 1954; Hottinger, 1974, 1980; Hohenegger, 1994; Langer and Hottinger, 2000; Yordanova and Hohenegger, 2002; Renema et al., 2015; Table 5, Fig. 10). *A. quoyi* is reported from the late Langhian–Tortonian of Java with no illustrations (BouDagher-Fadel and Lokier, 2005, fig. 3).

4. Implications of Y-shaped septula for phylogeny

The early streptospiral whorls, the only preseptal passage and septula which are continuous in adjacent chambers (i.e. aligned) are diagnostic characters shared by *Borelis*, *Flosculinella* and

Alveolinella (Reichel, 1937, 1964; Hottinger, 1974; Loeblich and Tappan, 1987). *Flosculinella* and *Alveolinella* differ from *Borelis* in having two or more layers of main chamberlets and one layer of attic per chamber in the adult growth stage (Hottinger, 1974; Loeblich and Tappan, 1987; Parker, 2009; Tables 1, 3).

In *Borelis* the occurrence of Y-shaped septula is a diagnostic character (Bassi et al., 2021a) for the species lineage of *Borelis philippinensis* (*B. melo*, *B. curdica*, *B. schlumbergeri*). After the first occurrence of this shell feature in the Rupelian (early Oligocene) *Borelis* in the CIP area (e.g. Lunt and Allan, 2004; Matsumaru, 2011), westward migrants occur in the Mediterranean Miocene (*B. melo*, *B. curdica*; Bassi et al., 2021a; Fig. 10). In the Eastern Indo-Pacific area, the present-day *B. schlumbergeri* appeared in the late Miocene (Eniwetok and Bikini; Hanzawa, 1940; Cole, 1954, 1957; Adams, 1970; Matsumaru, 1974; Lunt and Allan, 2004), probably descendant from the Rupelian–Burdigalian *B. philippinensis* (Bassi et al., 2021a).

Borelis schlumbergeri, *Flosculinella* (*F. globulosa*, *F. reicheli*, *F. bontangensis*) and *Alveolinella* (*A. borneensis*, *A. quoyi*) are the only alveolinoids with Y-shaped septula in the Indo-Pacific area, and, therefore, they all are probably descendants from the common ancestor *B. philippinensis*.

The temporal ranges of *Flosculinella* species and *Alveolinella* species partially overlap and succeed each other in the Indo-Pacific. These temporal range setting supports the inference that Y-shaped septula are not a homoplastic character that independently appeared in separate lineages but a synapomorphy of the *Borelis philippinensis*+*Flosculinella*+*Alveolinella* clade, which originated with the ancestral species (Fig. 10).

The appearance of two floors with chamberlets and one with attics is a synapomorphy of the *Flosculinella*+*Alveolinella* clade, whereas the occurrence of more than one chamberlet per chamber is an autapomorphy of *Alveolinella*.

Flosculinella appeared in the latest Oligocene of the CIP with *F. globulosa* (Lunt and Allan, 2004; Hallock et al., 2006; Renema et al., 2015; Table 3, Figs. 10–11). The single record of *F. bontangensis* in eastern Africa (Pemba Island) is Burdigalian in age (Eames et al., 1962). Often found together with *B. philippinensis* (Adams, 1965; Lunt and Allan, 2004; Renema, 2007; Matsumaru, 2011), *Flosculinella reicheli*, *F. bontangensis* and *Alveolinella borneensis* appeared in the CIP in the early Miocene (Tables 2, 4). This area corresponds to the Coral Triangle, the most important centre of marine biodiversity whose diversification started in the early Miocene (Renema et al., 2008; Veron et al., 2009; Förderer et al., 2018; Reuter et al., 2019; Fig. 11). As other larger porcelaneous forms such as *Borelis* and *Austrotrillina*, *Flosculinella* and *Alveolinella* thrived in shallow-water carbonate settings above the fair-weather wave base (Buxton and Pedely, 1989;

Hottinger, 1997; Beavington-Penney and Racey, 2004; Haig et al., 2020; Simmons, 2020). From the late Oligocene the seagrass settings expanded (Brasier, 1975; Teske and Beheregaray, 2009) including vast areas of shallow-water habitats between Indonesia and Australia (Wilson and Rosen, 1998). Via these settings, *Flosculinella bontangensis* likely reached the Langhian seagrass habitats off northeastern Australia (Hallock et al., 2006), whilst *A. borneensis* and *Alveolinella ex. interc. borneensis et quoyi* the middle Miocene of Indonesia, Bikini and Eniwetok (Table 4). A similar eastward dispersion route has been found for the shallow-water larger porcelaneous foraminifer *Austrotrillina* (Bassi et al., 2021b) and the brown macroalga *Sargassum* (Yip and Quek, 2020).

Alveolinella quoyi has been identified from the Tortonian of Indonesia (Renema et al., 2015) to the Pliocene–Pleistocene of Palau (Hanzawa, 1957). The northernmost occurrence of the species is in Okinawa-jima (Pleistocene–Recent; this study; Fig. 11). A Burdigalian record of *A. quoyi* needs further confirmation, since no illustrations were published (Matsumaru, 2011).

The present-day *Alveolinella* records from the Indian Ocean are inadequately illustrated since they often do not show the septula in alignment, two or more layers of main chamberlets and one layer of attics per chamber, considered to be diagnostic characters of this genus (e.g. Rana et al., 2007, fig. 2D; Mazumder et al., 2012, pl. 1, fig. 6; Panchang and Nigam, 2014, pl. 15, figs. 1–2; Sreenivasulu et al., 2017; Ranju et al., 2019, fig. 2f; Symphonia and Senthil, 2019, fig. 22(15)). In this area *Alveolinella quoyi* has been found only in the Maldives (Hottinger, 1980, p. 11; Parker and Gischler, 2011, pl. 3, figs. 16–17). The Maldives is considered the western limit of several Indo-Pacific larger foraminiferal taxa (Parker and Gischler, 2011). Because there are no fossil occurrences of this species in the Indian Ocean, the single occurrence in the Maldives may reflect a recent migration from the western CIP.

5. Concluding remarks

According to the species circumscriptions of latest Oligocene–middle Miocene *Flosculinella*, *F. globulosa* and *F. reicheli* are sub-spheroidal in shape, whereas *F. bontangensis* is ellipsoidal to fusiform and has the largest proloculus. *Flosculinella bontangensis* also differs from the other two species in having two supplementary chamberlets in the attic per chamberlet in the basal layer of chamberlets. *Flosculinella bontangensis* is considered a valid junior synonym of the *nomen oblitum* *F. cucumoides*.

The occurrence of the preseptal passage only (i.e. the lack of the postseptal passage) and Y-shaped septula in *Flosculinella* and *Alveolinella* are traits of phylogenetic significance. These shell

characters can be considered as inherited from the common ancestor *Borelis philippinensis*, whose present-day descendant in the *Borelis* lineage is *B. schlumbergeri*.

Alveolinella borneensis appeared in the late Burdigalian of the Central Indo-Pacific area and disappeared in the Serravallian, whereas *A. quoyi* appeared in the Tortonian in the same area. Specimens with characters intermediate between *A. borneensis* and *A. quoyi*, referred to as *Alveolinella ex. interc. borneensis et quoyi*, range from the late Serravallian to the Tortonian.

The Coral Triangle in Southeast Asia was the centre of early Miocene *Flosculinella* and *Alveolinella* speciation. The south-eastward migrants of *F. bontangensis* and *A. borneensis* reached northeastern Australian and Bikini coral reef settings in the Langhian.

In modern coral reefs *Borelis schlumbergeri* occurs from the Western to the Central Indo-Pacific, and *Alveolinella quoyi* is widespread from Central to the Eastern Indo-Pacific areas. The northernmost occurrence of *A. quoyi* is in the Ryukyu Islands.

Author statement

All authors have contributed to data curation and interpretation, and critically reviewed the manuscript.

Declaration of Competing Interest

None.

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Supplementary data

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

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Figure and table captions

Fig. 1. *Flosculinella globulosa* (Rutten, 1917); A–E, early Burdigalian, Tallabar Limestone, Mankalihat Peninsula, East Kalimantan, Indonesia.

A, sub-equatorial section showing preseptal passages, the basal layer of chamberlets overlain by attics (sample SA220c).

B, tangential section showing alignment of septula and chamberlets with a single attic layer (sample SA220d).

C–E, sub-axial sections showing the Y-shaped septula, basal layer of chamberlets and attics; note that there are more than 2 supplementary chamberlets in the attic layer per chamberlet in the basal layer (samples SA220f, SA220i, SA221g).

Flosculinella bontangensis (Rutten, 1913); late Burdigalian, Kutai Basin, East Kalimantan, Indonesia.

F, tangential sub-axial sections showing preseptal passage, aligned septula and chamberlets with attic (sample SA117).

Abbreviations: at, attic; cl, chamberlet; f1, foramina in the basal layer of chamberlets; f2, foramina in the second layer of chamberlets; f3, supplementary foramina in the attic; prol, proloculus; p-sept, preseptal passage; sept, septula; Y-sept, Y-shaped septula. Scale bars represent 0.20 mm (A–E) and 0.50 mm (F).

Fig. 2. *Flosculinella reicheli* Mohler, 1949; A–C, early Burdigalian, Tallabar Limestone, Mankalihat Peninsula, East Kalimantan, Indonesia.

A–B, nearly axial sections showing the proloculus, single layer of chamberlets (cl) with attics (at) and Y-shaped septula (samples SA218, SA215).

C, oblique tangential section showing attics (at); note more than 2 supplementary chamberlets in the attic (f3) per chamberlet in the basal layer of chamberlets (f1; sample SA216).

Abbreviations: at, attic; cl, chamberlet; f1, foramina in the basal layer of chamberlets; f3, supplementary foramina in the attic; prol, proloculus; p-sept, preseptal passage; sept, septum. Scale bar represents 0.20 mm.

Fig. 3. *Flosculinella cucumoides* (Chapman, 1908), thin sections of types; Chapman's collection; Museum Victoria, Melbourne, Australia.

A, sub-equatorial section showing the proloculus and basal layer of chamberlets (f1) with attics (f3) (Chapman, 1908, pl. 38, fig. 5); lectotype of *Alveolina cucumoides* Chapman, 1908, designated herein; note that the first attic occurs in the second whorl.

B, sub-axial section of the fusiform shell (Chapman, 1908, pl. 38, fig. 6); paralectotype.

C–D, magnifications of the lectotype showing pre-septal passages, basal layer of chamberlets (f1) with two supplementary chamberlets in the attic (f3) per chamberlet in the basal layer.

E–F, sub-axial sections showing the basal layer of chamberlets and attics (topotypes; E, ‘*Flosculinella cucumoides* (Chapman, 1908) Topotype Bartaleppe, Malekula, New Hebrides, Sample 108. P134791’; F, ‘*Flosculinella cucumoides* (Chapman, 1908) Topotype Bartaleppe, Malekula, New Hebrides, Sample 108. P134792’).

Abbreviations: at, attic; cl, chamberlet; f1, foramina in the basal layer of chamberlets; f2, foramina in the second layer of chamberlets; f3, supplementary foramina in the attic; prol, proloculus; p-sept, preseptal passage; sept, septum. Scale bars represent 0.20 mm (A, C–F) and 0.50 mm (B).

Fig. 4. *Flosculinella bontangensis* (Rutten, 1913); Langhian, Wailawi. Micro-computed tomographic scanning 3-D rendered models with shell removed (rendering by W.R.).

A–B, the sub-spherical proloculus is enveloped by the flexostyle followed by two streptospiral whorls.

Third whorl (C) with four chamberlets (f1) and fourth whorl (D–E) with six chamberlets (f1). The chamber axis is at *c.* 60° (dashed white line) to the previous chamber.

Fifth whorl (F) with six chamberlets and up eleven supplementary chamberlets (f3).

Chamber axis is at *c.* 30° (dashed white line) to the previous chamber.

Six whorl (G) shows a thickening of the chamber shell whose coiling axis is unparallel to elongation axis.

H, chamber 43 of the sixth whorl.

I, last chamber of the sixth whorl. J, chamber 44 of the seventh whorl. K, chamber 52 of the eighth whorl. L, chamber 64 of the eighth whorl.

Abbreviations: d&r, damaged and repaired; f1, foramina in the basal layer of chamberlets; f3, supplementary foramina in the attics; flex, flexostyle; flex-ap, flexostyle aperture; p-sept, preseptal passage; prol, proloculus; prol-ap, proloculus aperture; strept, streptospire. Scale bars represent 0.10 mm in A–F and 0.20 mm in G–K.

Fig. 5. *Flosculinella bontangensis* (Rutten, 1913); Serravallian, Maldives.

A, sub-equatorial section (sample IODP 359, Site U1465, Hole B, Core 2, Section 1, at 17cm).

B, tangential sub-equatorial section (sample IODP 359, Site U1465, Hole A, Core 10, Section CC, at 1 cm).

Abbreviations: at, attic; fl, foramina in the basal layer of chamberlets; f3, supplementary foramina in the attis; prol, proloculus; p-sept, preseptal passage; sept, septum. Scale bar represents 0.20 mm.

Fig. 6. *Alveolinella borneensis* Tan; Serravallian, Pacitan, East Java. Micro-computed tomographic scanning 3D-rendered models with shell removed (rendering by W.R.).

A–D, The sub-ellipsoidal proloculus (prol) is followed by the flexostyle (flex). The first (1st) and second (2nd) chambers show the basal layer of chamberlets (fl). The supplementary chamberlets in the attics (f3) occur from the third (3rd) chamber (D).

E–F, Chambers in the penultimate (E) and last (F) whorls with two layers of chamberlets (fl, f2) and one layer of supplementary chamberlets (f3) in the attic.

Scale bar represents 100 μ m.

Fig. 7. *Alveolinella quoyi* (d’Orbigny, 1826); Calabrian–Chibanian Ryukyu Group, Okinawa-jima. A–B, Nakijin; C–E, Tobaru; Motobu peninsula; Kourijima Formation (Yamamoto et al., 2006). F, Maeda, Yomitani–Onna; Sobe Formation (Muraoka et al., 2005).

A–B, tangential and oblique sub-equatorial sections (samples N1-3-5, N1-2-5).

C, tangential sub-axial section (sample 167_12B-4–13.0 m).

D–F, sub-equatorial section (samples 16_13B-7–5.98 m, M62_5, 362).

Abbreviations: at, attic; cl, chamberlet; fl, foramina in the basal layer of chamberlets; f2, foramina in the second layer of chamberlets; f3, supplementary foramina in the attic; prol, proloculus; p-sept, preseptal passage; sept, septula; Y-sept, Y-shaped septula. Scale bar represents 0.50 mm.

Fig. 8. *Alveolinella quoyi* (d’Orbigny, 1826); Recent material from coral rubble on a fore-reef slope (15 m water depth) at Kushibaru, Aka-jima, Okinawa-jima, Japan. Micro-computed tomographic analysis (A–G) and SEM details of the apertural face H–I) of a specimen illustrating the foramina in the basal and second layers of chamberlets (fl, f2) and the attics (f3).

Abbreviations: at, attic; cl, chamberlet; fl, foramina in the basal layer of chamberlets; f2, foramina in the second layer of chamberlets; f3, supplementary foramina in the attic; potort, polar

torsion; prol, proloculus; p-sept, preseptal passage; rm, reverse masks; sept, septula; Y-sept, Y-shaped septula. Scale bars represent 1 mm (A–E), 0.5 mm (F–H) and 0.1 mm (I).

Fig. 9. *Alveolinella quoyi* (d’Orbigny, 1826); Recent material from Vanuatu. Micro-computed tomographic scanning 3D-rendered models with shell removed (rendering by W.R.).

A–E, sub-ellipsoidal proloculus (prol) enveloped by the flexostyle (flex) and the first (1st) and second (2nd) chambers. The flexostyle shows multiple apertures.

F, growth stage with four chambers showing the complicated superposition of layers of chamberlets and related attics.

G–H, detail of the chamber in last whorl with three layers of chamberlets (f1, f2, f2) and one layer of attics (f3) per chamberlet.

f1, foramina in the basal layer of chamberlets; f2, foramina in the second layer of chamberlets; f3, supplementary foramina in the attic; p-sept, preseptal passage.

Scale bar represents 0.1 mm.

Fig. 10. Major events in the palaeobiogeographical history of the latest Oligocene–Miocene *Borelis* (*B.*), *Flosculinella* (*F.*) and *Alveolinella* (*A.*) species. The two present-day *B. schlumbergeri* and *A. quoyi*, both having only preseptal passages and bearing Y-shaped septula, are descendants of the Oligocene–early Miocene *B. philippinensis*. The Mediterranean *B. melo* and *B. curdica* also descended from *B. philippinensis* (1) and disappeared by the Messinian Salinity Crisis (MSC; Bassi et al., 2021a). *Flosculinella* appeared in the latest Oligocene giving rise to three early–middle Miocene species (*F. globulosa*, *F. reicheli*, *F. bontangensis*; 2). *Alveolinella* presumably appeared in the latest Burdigalian as *A. borneensis*, and *A. quoyi* in the late Tortonian (3). From the Central Indo-Pacific *F. bontangensis* and *A. borneensis* migrated southward reaching Western and Northern Australia and Bikini and Eniwetok in the Langhian. See text for details. This study: a, East Kalimantan, Indonesia; b, Maldives; c, Samarinda (East Kalimantan), Pacitan (Java); d–e, Sangatta (East Kalimantan); f, Bangalon (Kalimantan), g, Togopi (Malaysia), h, Cebu (Philippines); i, k, Okinawa-jima, Ryukyu Islands; j, Vanuatu. CT, Miocene Coral Triangle; ecMS, eastern closure of the Mediterranean Sea. Time scale after Cohen et al. (2021, updated). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article)

Fig. 11. Palaeogeographical locations of *Flosculinella* (*F.*) species and *Alveolinella* (*A.*) species in the Central Indo-Pacific. *Flosculinella* and *Alveolinella* speciation was in the Coral Triangle

of Southeast Asia. *F. globulosa* appeared in the Chattian–Aquitanian of Bikini (1), Midway Atoll (2) and Philippines (3), whereas *F. reicheli* in the Aquitanian of Indonesia (4), and *F. bontangensis* in the Burdigalian of Philippines (3), Indonesia (4) and Pemba Island (5). The first and last appearances of *A. borneensis* are in the Burdigalian (6, Hottinger, 1974) and Serravallian (3, Mohler, 1949; 6, Hottinger, 2006a), whereas *A. ex. interc. borneensis et quoyi* first occurs in the Langhian of Bikini (1, Todd and Post, 1954). The short-lasting *F. reicheli* disappeared in the Burdigalian (4, this study), whilst *F. globulosa* (4, this study; 7, Riera et al., 2019) and *F. bontangensis* (4, this study) in the Langhian and Serravallian respectively. The present-day *A. quoyi* appeared in the Tortonian of Indonesia (Renema et al., 2015; see text). Occurrences refer to citations in Tables 2, 4 in which detailed information on each record can be found. Compare with Fig. 9. Palaeogeographical maps modified from Rögl (1998), Meulenkamp and Sissingh (2003) and Kocsis and Scotese (2021).

Numbers refer to localities: 1, Cole (1954; Aq, Fg, Bikini), Todd and Post (1954; Ab, Bikini); 2, Cole (1969; Fg, Midway Atoll); 3, Matsumaru (2017; Fb, Fg, Philippines); 4, Mohler (1949; Ab, Fr, Borneo), Adams (1965; Fr, Sarawak), Hottinger (1974; Fr, Borneo), Renema et al. (2015; Aq, Indonesia); Leupold and van der Vlerk (1921; Fb, Borneo), Barberi et al. (1987; Fb, Indonesia), this study (Fb, Pacitan; Ab, Samarinda, East Kalimantan); 5, Eames et al. (1962; Fb, Pemba Island); 6, Hottinger (1974, 2006a; Ab, Moluccas); 7, Riera et al. (2019; Fg, W Australia). Ab, *A. borneensis*; Aq, *A. quoyi*; FAD, first appearance datum; Fb, *F. bontangensis*; Fg, *F. globulosa*; Fr, *F. reicheli*; LAD; last appearance datum. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article)

Table 1.

Comparison of diagnostic shell characteristics of *Flosculinella* species and related stratigraphical distribution.

Species are listed according to their first appearance reported in literature.

Based on data from: 1, Chapman (1908), Rutten (1913), Mohler (1949, 1950), Hanzawa (1957), Hottinger (1974), Hashimoto and Matsumaru (1975), Matsumaru (1996, 2017), this study; 2, Cole (1954), Chaproniere (1984), this study; 3, Adams (1965), this study.

attics, (number of whorl of their first occurrence) number of supplementary chamberlets in the attic floor per chamberlet in the main floor; flexost, flexostyle; L, length (max); prol, proloculus diameter (min); strsp, streptospiral whorls

Table 2.

Stratigraphical and palaeogeographical distribution of *Flosculinella* species.

Table 3.

Comparison of diagnostic shell characteristics of *Alveolinella* species and related stratigraphical distribution. Species are listed according to their first appearance reported in literature.

Based on data from:

1, Tan Sin Hok (1936); Mohler (1949); Binnekamp (1973); Hottinger (1974); Wonders and Adams (1991, as *A. praequoyi*).

2, Hofker (1930); Cole (1957); Hottinger (1974); Zheng (1979); Matsumaru (2017); this study.

I.E., index of elongation; f (wh), number of layers of chamberlets (whorl number of the attic first occurrence); f1, foramina in the basal layer of chamberlets; f2, foramina in the second layer of chamberlets; f3, supplementary foramina in the attic; flexost, flexostyle; prol, proloculus diameter; prol sh, proloculus shape (length, μm); pt, polar torsion; Rs, Recent specimens; uMs, upper Miocene specimens.

Table 4.

Stratigraphical and palaeogeographical distribution of *Alveolinella borneensis* Tan.

* *Alveolinella ex. interc. borneensis* Tan *et quoyi* (d'Orbigny)

** see Remarks in the text for further details.

Table 5. Stratigraphical and geographical distribution of *Alveolinella quoyi* (d'Orbigny).