PALAEOBIOGEOGRAPHY AND EVOLUTIONARY PATTERNS OF THE LARGER FORAMINIFER *BORELIS* DE MONTFORT (BORELIDAE)

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Abstract: The palaeobiogeography of the alveolinoid *Borelis* species reveals the evolutionary patterns leading to the two extant representatives, which occur in shallow-water tropical carbonate, coral reef-related settings. Type material and new material of fossil *Borelis* species, along with

Recent specimens were studied to assess their taxonomic status, species circumscriptions (based on proloculus size, occurrence of Y-shaped septula, and the index of elongation), palaeobiogeography and evolutionary dynamics. The species dealt with here are known from exclusively fossil (*B. pygmaea*, *B. inflata*, *B. philippinensis*, *B. melo*, *B. curdica*), and from fossil and modern (*B. pulchra*, *B. schlumbergeri*) specimens. For the first time, fossil and Recent *Borelis* specimens are illustrated via micro-computed tomography scanning images. Depending on the occurrence of Y-shaped septula, two lineages are distinguished. Deriving from the middle–upper Eocene *Borelis. vonderschmitti*, the first lineage includes *B. inflata*, *B. pulchra* and *B. pygmaea*, lacking Y-shaped septula. The first species bearing Y-shaped septula is the Rupelian *B. philippinensis* of the western Indo-Pacific. The westward migrants of *B. philippinensis* into the Mediterranean gave rise to *B. melo* (Aquitanian–Messinian) and *B. curdica* (Burdigalian–Tortonian). These two species became isolated from the Indo-Pacific by the Langhian eastern closure of the Mediterranean basin and disappeared during the Messinian Salinity Crisis. Since the Tortonian, *B. schlumbergeri*, which descended from *B. philippinensis*, has inhabited the Indo-Pacific along with *B. pulchra*. From the central Pacific Ocean, *B. pulchra* reached the Caribbean area before the early Piacenzian closure of the Central America seaway.

Key words: palaeobiogeography, evolutionary patterns, *Borelis*, biostratigraphy, Tethys, Pacific Ocean.

ALVEOLINOIDEANS are porcelaneous larger foraminifera thriving in the upper photic zone of tropical marine carbonate sedimentary systems. This foraminiferal group is particularly important in terms of abundance, taxonomic diversity and biostratigraphy in Upper Cretaceous and lower Cenozoic deposits (Hottinger 1982; Serra-Kiel *et al.* 1998). Alveolinoids represent biostratigraphic markers for the Upper Cretaceous, Paleocene and Eocene of the Western Tethys. Although the Cretaceous species are good biostratigraphic markers, Paleocene and Eocene species have more restricted stratigraphic ranges and are key elements of the standard Tethyan larger foraminiferal biozonations (shallow benthic zones SBZ; Cahuzac & Poignant 1997; Serra-Kiel *et al.* 1998).

The diagnostic characters at genus level are based on structural differences of the shell identifiable in non-oriented thin sections (Hottinger 1960, 1963; Parker 2017), whereas species circumscriptions are based on differences in the spire, shell shape and shell proportions observed in centered sections (Hottinger 1960, 1974). Two alveolinoid genera are extant in tropical shallow-marine settings in carbonate provinces: *Borelis* de Montfort, 1808 and *Alveolinella* Douvillé, 1906. The related extinct genus *Flosculinella* Schubert *in* Richarz, 1910 ranges from the Burdigalian to the Serravallian (BouDagher-Fadel 2018). Among these genera, *Borelis* first appeared in the middle Eocene (Loeblich & Tappan 1987).

Within his revision of the Alveolinidae, Reichel (1937, pp. 105–108, pl. 10, figs 8–9) studied a specimen of *Borelis melo* collected by Schlumberger from the Leitha-Kalk (middle Miocene, Langhian–early Serravallian) exposed 3 km north of Bujtur in Transylvania (Romania). The specimen studied by Reichel (1937) is deposited in the Schlumberger collection, Sorbonne, Paris (specimen number 2405-3). Reichel (1937) identified it as *Neoalveolina melo* (Fichtel & Moll, 1798) because he considered *Nautilus melo* Fichtel & Moll, 1798 as a senior synonym of *Neoalveolina bradyi* (Silvestri) (= *Alveolina bradyi* Silvestri, 1927). *Neoalveolina bradyi* (Silvestri) was designated before by Bakx (1932, p. 208) as the type species of *Neoalveolina* Silvestri, 1928. Reichel (1937) chose to use *Neoalveolina* because its more modern morphological description 'exclut toute erreur d'interpretation' ('excludes any misinterpretation') and he also believed that *melo* was a species that could be firmly identified.

The first designation of a neotype for *Nautilus melo* Fichtel & Moll (=*Borelis melonoides* de Montfort, 1808) was by Smout (1963, pp. 265–266, figured in Reichel 1937, pl. 10, fig. 8). This is the designation that is valid by ICZN (1985) Article 75e (Banner 1988). Based on the deviation of the gross test from a spheroidal shape, Reichel (1937, p. 107) distinguished three subspecies of *B. melo*: *B. melo melo* Fichtel & Moll, *B. melo haueri* d'Orbigny, 1846, and *B. melo curdica* n. subsp. Hottinger (1974) considered *B. curdica* (Reichel) and *B. melo* (Fichtel & Moll) as distinct species characterized by different proloculus size (30–50 μm, 60–65 μm respectively), number of streptospiral whorls (4–5, 3–4), and occurrence of Y-shaped septula (present in all whorls, more numerous in later whorls). Rögl & Hansen (1984, p. 71, pl. 30, figs 1–2) designated a new specimen from the Miocene of the Vienna Basin as the neotype for *B. melo*. However, their designation is invalid (Loeblich & Tappan 1987; Banner 1988) because the neotype had been already defined by Smout (1963).

Jones *et al*. (2006) re-assessed the stratigraphic and palaeobiogeographic occurrences of *B. melo*. They distinguished *B. melo melo* and *B. melo curdica,* concluding that *B. melo melo* spans the Miocene, while *B. melo curdica* is restricted to the Aquitanian–Langhian. Although a comprehensive taxonomic re-assessment is lacking, the *Borelis* species have been used very often as biostratigraphic markers for the Miocene, especially in the Middle East successions. Since their occurrence in shallow-water deposits is often related to coral-reef settings, palaeoecological models have been also proposed (e.g. Hottinger 1997; Beavington-Penney & Racey 2004).

Here we assess *Borelis* shell architecture and stratigraphic occurrences, which help to understand the species taxonomy and evolutionary relationships, as well as the Indo-Pacific and Mediterranean palaeobiogeographic dynamics of the genus. Analysing fossil and Recent material, we demonstrate two species groups separated by the occurrence of Y-shaped septula. These groups occur across a long range in the Western Tethys and the Indo-Pacific, from the late Eocene to the Recent. The genus diversified in the early Miocene and migrants from the Pacific moved westward into the Mediterranean area and eastward to Central America.

MATERIAL AND METHODS

This study was carried out on material preserved as thin sections in museum collections (Tohoku University, Sendai) and newly collected specimens from fossil and modern deposits. The studied fossil material, from northern Hungary, northwestern Italy and southeastern Spain, consists of specimens either matrix-free or within hard-cemented limestone. The present-day *Borelis* specimens were collected from the Florida Keys, Jarvis Island (Pacific Ocean) and the Red Sea.

The fossil and modern *Borelis* specimens were scanned at the Dipartimento di Fisica e Scienze della Terra of the University of Ferrara. 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 was100-110 uA. Rotation step ranges between 0.5° to 1°, with an exposure time of 1 second. The reconstructed voxel size was 5x5x5 um^3 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. The studied samples are stored in the same department. The shallow-water Eilat specimen was scanned with an X-ray phoenix|x-ray (v|tome|x s) of GE Measurement & Control at the Steinmann Institute, University of Bonn. Cross-section images were post-processed (rendering and segmentation) and a final 3D image was computed by using the visualization and analyses software Avizo 9 of the Visual Science Group (VGS).

Architectural and morphological terms are those used by Smout & Eames (1958), Hottinger (1960, 2006) and Hottinger *et al*. (1993). The suprageneric classification follows Loeblich & Tappan (1987) and Fleury & Fourcade (1990). The analysed *Borelis* species are listed in the systematic palaeontology chapter according to their stratigraphic appearance. References to published species and their records include only those which have described and illustrated architectural diagnostic features.

Northern Hungary

The studied *Borelis* specimens are from Letkés (western Börzsöny Mountains, northern Hungary), a well-known middle Miocene site in the Neogene Pannonian Basin. Since the 1840s the western Börzsöny Mountains have been famous for their Cenozoic molluscan and foraminiferal assemblages (Stache 1866; Csepreghy-Meznerics 1956).

The Börzsöny Mountains belong to the Miocene Inner Carpathian Volcanic Chain, which at its margins is overlain by shallow-marine sedimentary deposits (Leitha Limestone, Badenian Clay, Schlier, various sandy and marly deposits; e.g. Kovács & Vicián 2014).

The studied *Borelis* come from a new excavation located on the slope of the Bagoly Hill, eastward from the Letkés village (47°53'17.94" N, 18°47'4.73" E).

This locality is characterized by re-sedimented beds consisting of fossil-rich limonitic marly sand with andesite rock fragments, andesitic tuff and eroded coral reef blocks (Sámsonháza Formation; Kovács & Vicián 2014). The macrofauna includes colonial and solitary corals, serpulids, fragmented echinoids and decapods, bivalves, gastropods, scaphopods, polyplacophores, small brachiopods, bryozoans and rare fish teeth. Based upon molluscan assemblages, these beds are early Langhian (early Badenian) in age (Kovács & Vicián 2014; Harzhauser & Landau 2016; Harzhauser *et al*. 2017).

Southeastern Spain

Specimens examined from southeastern Spain span the middle to late Miocene. The Serravallian specimens occur in limestones in Sierra de Jimena (Jaén) at the southern margin of the Guadalquivir Basin, the Atlantic-linked foreland basin of the Betic Cordillera. The limestones are intercalated in marls with Serravallian planktonic foraminifera (Castillo-Guzmán 2016). The late Tortonian *Borelis* occur in coral patch-reefs in the Almanzora Corridor, a narrow intermontane Neogene basin in the Betic Cordillera (Braga & Martín 1988; Martín *et al*. 1989). *Borelis* specimens were reported by Betzler & Schmitz (1997) from Messinian reef limestones from Cabo de Gata, a volcanic province with Neogene deposits intercalated in and overlying volcanic rocks (Martín *et al*. 2003).

Northwest Italy

The studied material was collected in the Sant'Agata Fossili Marl Formation (i.e. Formazione delle Marne di Sant'Agata Fossili) cropping out in the Stazzano area (Alessandria, Piedmont, northwest Italy). This Tortonian–lower Messinian formation consists of two informal members: a lower silty-sandstone member (silty-sandstone and conglomerate beds) and an upper pelitic one (Ghibaudo *et al*. 1985; Dell'Angelo *et al*. 2014; Vercesi *et al*. 2014). This formation overlies the Serravallian Serravalle Sandstones (i.e. Arenarie di Serravalle) and is overlain by the Messinian Gessoso-solfifera Formation (Messinian; Ghibaudo *et al*. 1985). Four samples (numbered as 1, 2, 5, 11) yielding *Borelis* specimens were collected from chaotic lenticular bodies with re-sedimented material. Samples 1–2 and 5 were collected in the Rio di Bocca d'Asino (44°44'24" N, 08°53'21" E), a historic fossiliferous locality (Dell'Angelo *et al*. 2014), at the top of the lower member. Sample 11 was collected near Villa Monti (44°44'17" N, 08°52'221" E), at the base of the upper member. According to the stratigraphic position of samples, the studied material is Tortonian in age (Ghibaudo *et al*. 1985).

Florida Keys

The studied specimens were collected from the Molasses Reef (22°0'54" N, 80°22'42" QW), the upper Florida Keys. *Borelis* specimens were found on reef rubble at 3–20 m water depths (Hallock *et al*. 2006; Baker *et al*. 2009 and references therein).

Jarvis Island

Sediment samples for *Borelis* specimens were collected along the north-western coast of Jarvis Island in the South Pacific Ocean in 2010 at 8 m water depth (0°22'8.46" S, 160°0'29.49" W). Jarvis Island is an uninhabited coral island with average surface-water temperatures of *c*. 27° C. Sediments were collected by SCUBA diving by filling plastic bags with sediment from the top 2 cm. The sediments are coral carbonate medium sand with diverse and abundant benthic foraminifera.

Red Sea

Sediment samples yielding *Borelis* specimens were collected from Tur Yam, south of the port of Eilat (29°31'02.52" N, 34°55'35.40" E), and in front of the Interuniversity Institute for Marine Sciences at Eilat (IUI; 9 m water depth, 29°30'04.93" N, 34°55'02.79" E), Israel. The Tur Yam habitat is characterized by *Halophila stipulacea* seagrass meadows and the IUI collection site has narrow fringing reefs with carbonaceous coral rubble sediments. Specimens were collected from leaves at 5 m (Tur Yam) and from surface sediments at 9 m water depth. The Gulf of Eilat is a branch of the Red Sea located between the Sinai and the Arabian peninsulas, in a desert area characterized by high evaporation rates due to high temperatures and dry air (e.g. Reiss & Hottinger 1984). There are minor seasonal fluctuations in the SST (20.5–27.4 °C) and salinity (40.3–41.6).

SYSTEMATIC PALAEONTOLOGY

Superfamily ALVEOLINOIDEA Ehrenberg, 1839
Family BORELIDAE Fleury & Fourcade, 1990
Subfamily BORELINAE Schmarda, 1871

Genus BORELIS de Montfort, 1808

Type species. Borelis melonoides de Montfort, 1808 = *Nautilus melo* Fichtel & Moll, 1798, *varietas* β.

Diagnosis. Spherical to fusiform test with minor dimorphism. Early streptospiral whorls occurring in both generations. Septula aligned from chamber to chamber, which may appear Y-shaped in axial section resulting in alternately larger and smaller chamberlets. Only preseptal passage is present; apertures in a single row.

Remarks. In the Alveolinoidea *sensu* Fleury & Fourcade (1990) the chambers are subdivided by septula into parallel chamberlets. Chamberlets are laterally connected by a passage parallel to and immediately beneath the septum. This connection is called the preseptal passage (e.g. Hottinger 2006). Septula of successive chambers are either aligned or alternating (e.g. Hottinger 1974; Loeblich & Tappan 1987, p. 362).

The alveolinoid *Flosculinella* and *Alveolinella* differ from *Borelis* in having one layer of attics per chamber in the adult growth stage, and in having two or more layers of main chambers and one layer of attics per chamber in the adult growth stage, respectively (Loeblich & Tappan 1987; Hottinger 1974).

Borelis de Montfort, 1808 (with *Nautilus melo* Fichtel & Moll, 1798 as type species; see Banner 1988) is defined by the architecture of its spheroidal to fusiform shell characterized by preseptal passage and septula, possibly Y-shaped, aligned from chamber to chamber. The proposed diagnostic characters to separate *Borelis* species have been so far the diameter of the megalosphere, the number of streptospiral whorls, the frequency of Y-shaped septula, the number of chambers in the last whorl (e.g. Hanzawa 1930; Reichel 1937; Schweighauser 1951; Adams 1965), and the index of elongation (ratio of the coiling axis length to the diameter at the equator; Hottinger 1974, 2006). However, the number of streptospiral whorls and the number of the chambers in the last whorl are characters related to the ontogenetic stage of the studied specimens. Moreover, since many fossil *Borelis* species have been described from thin sections of hard cemented limestone, the recognition of these characters is strongly influenced by random sections. For these reasons, only the diameter of the megalosphere, the frequency of the Y-shaped septula, and the index of elongation are reliable characters to distinguish the species (Table 1, Fig. 1).

The presence of the only preseptal passage and the alignment of septula in the herein assessed species permit their assignment to *Borelis* de Montfort (Smout 1963, p. 265; Loeblich & Tappan 1987, p. 362).

The World Register of Marine Species (Hayward *et al.* 2018) lists fiftheen *Borelis* species. Among them, eight are discussed here. Regarding the other seven, *B. jamaicensis* Vaughan, 1929 has been considered synonym of *Pseudofabularia matleyi* (Vaughan) Robinson, 1974, and *B. palaeosphaera* Ehrenberg, 1854 has been ascribed to the fusulinid *Staffella* Ozawa, 1925 (Thomson 1935). *B. clarionensis* McCulloch, 1977, *B. peybernesi* De Castro & Peybernès, 1983, *B. pilus* Serova, 1955, and *B. reicheli* Souaya 1963*a* were not sufficiently described and illustrated to assess their status as separate species. In particular, no key information about Y-shaped septula is given in their protologues. *B. hottingeri* Vicedo, Berlanga & Serra-Kiel, 2014 is similar to *B. floridanus* Cole, 1941 (not listed in WoRMS 2018). The latter only shows pre-septal passage, and no post-septal passage can be observed. Maybe it belongs to a new genus of alveolinoid. In fact Vicedo *et al.* (2013) called it "*Quasiborelis*" *floridanus*. Vicedo *et al.* (2014) stated that *hottingeri* differs from *floridanus* in being larger in size.

The species dealt with here are known from either exclusively fossil (*B. pygmaea*, *B. inflata*, *B. philippinensis*, *B. melo*, *B. curdica*), or from fossil and Recent specimens (*B. pulchra*, *B. schlumbergeri*; Fig. 2).

Borelis inflata (Adams, 1965)

Figure 3

1947 *Neoalveolina haueri* (d'Orbigny); Bursch, p. 26, pl. 1, fig. 20, pl. 2, figs 8–11, text-figs 7–8.
1965 *Neoalveolina inflata* Adams, p. 325, pl. 25, figs d, i.
1974 *Borelis inflata* Adams; Hottinger, p. 68, pl. 101, figs 1–6.
1987 *Borelis pygmaea* Hanzawa; De Castro, p. 119, pl. 4, fig. 2.
2003 *Borelis inflata* Adams; Sirel, p. 299, pl. 11, figs 10–13.
2010 *Borelis inflata* Adams; Benedetti, p. 201, pl. 1, fig. 6.
2010 *Borelis inflata* (Adams); Di Carlo *et al.*, p. 62, pl. 9, figs 1–2.
v. 2011 *Borelis inflata* Adams; Braga & Bassi, fig. 5B.
2011 *Borelis pygmaea*; Seyrafian *et al.*, fig. 10q.

Type reference and figure. *Neoalveolina inflata* Adams, 1965, p. 325, pl. 25, fig. i.

Holotype. Figured in Adams (1965, pl. 25, fig. i), megalospheric form.

Diagnosis. Sub-spheroidal, tightly coiled shell 0.5–1.5 mm in diameter and 0.4–1.2 mm long. Proloculus 30–70 μm in diameter and 3–4 streptospiral whorls. Thin basal layer with occasional axial thickening. Index of elongation 0.95–1.56. No Y-shaped septula (Table 1).

Repository data. Not indicated.

Studied material. The studied specimens are from the Tortonian of Stazzano (Fig. 2). Subglobular and tightly coiled specimens with diameter up to 0.8 mm. Proloculus is 30–45 µm in diameter with 3–4 streptospiral whorls. The index of elongation is 1.25. No Y-shaped septula are present.

Remarks. Adams (1965) assigned his specimens to the genus *Neoalveolina* Silvestri, 1928 without comments as to this systematic ascription. No formal subsequent systematic ascription of *inflata* to the genus *Borelis* de Montfort has been made. The occurrence of only preseptal passage and aligned septula in the holotype of *inflata* (Adams 1965, pl. 25, fig. i) indicates that it belongs to *Borelis*.

Adams's (1965) type material consists of the holotype (pl. 25, fig. i) and six paratypes (pl. 25, figs d–h, j). Among the paratypes the specimen illustrated in pl. 25, fig. h shows possible Y-shaped septula (upper top of the photo, in the third last and last whorls). If this is the case, the specimen can be ascribed to *B. melo* rather than to *B. inflata* and, consequently, the specimens in figures e–g and j are *B. melo* as well. The taxonomic status of these specimens requires, therefore, further study. Adams (1965) reported younger specimens from Sarawak, which are slightly more elongated than *B. inflata* and comparable to *B. philippinensis* (Adams 1965, p. 325). This latter species, however, possesses Y-shaped septula separating it from *B. inflata*. Hanzawa (1949) reported *B. philippinensis* from the early Miocene (Tertiary e) of Luzon, Philippines. Hottinger (1974) recorded and illustrated *B. inflata*, remarking that *B. philippinensis* Hanzawa, 1949 and *B. parvulus* Hanzawa, 1957 resemble *B. inflata* but provided no further comment.

B. inflata differs from *B. philippinensis* in having a lower index of elongation (0.95–1.56 *versus* 1.3–1.8), and from *B. parvula* in having a larger proloculus (Table 1, Fig. 1). Considering its possible affinity with *B. inflata*, the exclusively Turkish species *B. arpati* Sirel & Gündüz, 1981, known only from Turkey, needs further study to assess its status as a separate species (Table 1).

Stratigraphic distribution. The types of *B. inflata* are from the Oligocene–lower Miocene of Sarawak (Borneo) in the Indo-Pacific area (Adams 1964, 1965; Matsumaru 1974*a*). In the Oligocene of the western Tethys, this species has been recorded from Apulia (southern Italy, De Castro 1987), eastern Turkey (Sirel 2003), southeastern Spain (Braga & Bassi 2011), Zakynthos (Greece; Di Carlo *et al.* 2010), and Sicily (Benedetti 2010). In these areas *B. inflata* occurs in the SBZ 21–23 as defined by Cahuzac & Poignant (1997; Figs 1–2). This taxon is herein first recorded from the Tortonian in Stazzano (northwest Italy, Fig. 2), extending the stratigraphic range of *B. inflata* to the upper part of SBZ 26.

Borelis pygmaea Hanzawa, 1930

1929 *Borelis* sp. indet., Yabe & Hanzawa, p. 181, pl. 15, figs 12–13, pl. 23, fig. 7.
1930 *B.* (*Fasciolites*) *pygmaea* sp. nov., Hanzawa, pp. 94–95, pl. 26 (1), figs 14–15.
1932 *Nealveolina pygmaea*; Bakx, p. 237, pl. 3, figs 18–19.
1937 *Neoalveolina pygmaea* (Hanz.) Reichel, pp. 112, 138.
1947 *Neoalvaolina pygmaea* (Hanzawa); Bursch, p. 28, pl. 1, figs 11, *non* 15, *non* 19.
1957 *Borelis pygmaea*; Hanzawa, p. 55, pl. 34, figs 8–9.
1965 *Neoalveolina pygmaea* (Hanzawa); Adams, p. 334, pl. 25, fig. 25 a–c.
1969 *Borelis melo* (Fichtel & Moll); Cole, pp. C5–C7, pl. 4, figs 8–23, pl. 5, figs 1–3, 6–8.
1974 *Borelis pygmaeus* Hanzawa; Adams & Belford, pp. 488–489, pl. 71, figs 9–14.
1974*b Borelis pygmaeus* (Hanzawa); Matsumaru, p. 113, pl. 19, figs 1, 5–6, 8–11.
1987 *Borelis pygmaea* Hanzawa; De Castro, pp. 119–121, pl. 3, figs 1–6, pl. 4, figs 1–6.
non 1987 *Borelis pygmaea* Hanzawa; De Castro, pp. 119–121, pl. 4, fig. 2 (= *B. inflata*).
1996 *Borelis pygmaeus* Hanzawa; Matsumaru, p. 210, pl. 83, figs 3–4.
2003 *Borelis pygmaea*; Sirel, p. 298, pl. 11, fig. 1–7.
2016 *Borelis pygmaea* Hanzawa; Serra-Kiel *et al.*, p. 344, figs 18 (3–8).
2017 *Borelis pygmaea* (Hanzawa, 1930); Gedik, p. 282, fig. 6P.
2017 *Borelis pygmaeus* (Hanzawa); Ma *et al.*, fig. 7 G-H.
2017 *Borelis pygmaeus* (Hanzawa 1930); Matsumaru, p. 234, pl. 41, figs 11–15.

Repository data. Unfortunately, the original material described by Hanzawa (1930) could not be located.

Diagnosis. Sub-spheroidal, tightly coiled shell 0.5 mm in diameter and 1.3 mm long. Proloculus 41–82 μm in diameter. Index of elongation 2.2–3.2. No Y-shaped septula (Table 1).

Remarks. Hanzawa (1930) studied Upper Oligocene material collected from the Rajamandala limestones between Bogor (then Buitenzorg) and Bandung (Te1 in Lunt & Allan 2004; p. 12, Lunt & Renema 2014). The author designated neither a holotype nor paratypes. No information about the collection storage was provided and the specimens illustrated by Hanzawa (1930) were not found. Three specimens were illustrated by Hanzawa (1930), representing axial and sub-axial sections. The specimen illustrated in fig. 15 (Hanzawa 1930) shows septula in alignment and preseptal passage only, characters diagnostic for *Borelis*. No Y-shaped septula are present in the three illustrated specimens (figs 14–15). *Borelis pygmaea* is separated from *B. schlumbergeri* by its smaller size, less elongated shape, and absence of Y-shaped septula (Table 1, Fig. 1). The taxonomic ascriptions of *B. pygmaea* to *Neoalveolina pygmaea* var. *schlumbergeri* (Reichel 1937) and to *Borelis melo* (Cole 1969; see Adams & Belford 1974 and Jones *et al*. 2006) cannot be, therefore, accepted.

Borelis pygmaea shows affinities with *B. inflata* in having comparable proloculus and shell diameter size, but differs in the elongation index (Table 1).

Among the specimens illustrated by De Castro (1987) from the Oligocene of southern Italy, the specimen in pl. 4, fig. 6 shows Y-shaped septula (central right-hand side of the shell; see also pl. 3, fig. 4), suggesting a possible ascription to *B. philippinensis* rather than to *B. pygmaea*.

Stratigraphic distribution. Hanzawa's material was collected from Oligocene–lower Miocene deposits (e.g. Adams 1965; Matsumaru 1974*a*; Fig. 2). In southeast Asia this species occurs from the late Eocene to late Oligocene (Tb–Te4, Philippines; Matsumaru, 2017), in the Rupelian–latest Burdigalian (uppermost Upper Te; Boudagher-Fadel & Banner 1999) and in Borneo from Tc to Te5 (Bakx 1932; Adams 1965). Adams & Belford (1974) illustrated specimens of *B. pygmaea* from the Chattian (Lower Te) of Christmas Island (eastern Indian Ocean). In the Philippines Matsumaru (2011 and references therein) recorded the species range as Priabonian–Chattian. In the Western Tethys, De Castro (1987) described specimens of *B. pygmaea* from the Oligocene of Santa Cesarea (Salentine Peninsula, Apulia, Southern Italy), Cahuzac & Poignant (1997) reported *B. pygmaea* from the Rupelian in the Mediterranean area, Sirel (2003) and Gedik (2017) illustrated this species from the Rupelian of Turkey, and Serra-Kiel *et al*. (2016) from the Early Oligocene of Oman and Yemen (Figs 1–2).

Borelis pulchra (d'Orbigny, 1839)

Figure 4

1839 *Alveolina pulchra* d'Orbigny, in de la Sagra, p. 70, pl. 8, figs 19–20.
1930 *Borelis pulchra* (d'Orbigny); Cushman, p. 55.
1957 *Borelis parvulus* n. sp., Hanzawa, p. 56, pl. 23, figs 3a–c.
1957 *Borelis primitivus* n. sp. Cole, pp. 766–767, pl. 240, figs 3–10.
1959 *Neoalveolina pulchra*; Graham & Militante, p. 65, pl. 10, fig. 13.
1974 *Borelis pulchra* (d'Orbigny); Hottinger, p. 69, pl. 102, figs 1–9.
1974*b* *Borelis globosa* n. sp. Matsumaru, p. 113, pl. 19, figs 2–4, 7.
1996 *Borelis boninensis* n. sp. Matsumaru, pp. 208–210, pl. 83, figs 1–2, pl. 85, fig. 5.

2003 *Borelis pulchra* (d'Orbigny); Javaux & Scott, fig. 2 (10–11).
2003 *Borelis pulchra* (d'Orbigny); Langer & Lipps, p. 152.
2017 *Borelis globosa* Matsumaru; Matsumaru, p. 232, pl. 41, figs 6–9.
2017 *Borelis melo* (Fichtel & Moll 1798); Matsumaru, p. 236, pl. 41, fig. 10.
2017 *Borelis schlumbergeri* (Reichel); Fajemila & Langer, figs 7(34).
2017 *Borelis schlumbergeri* (Reichel); Thissen & Langer, pl. 9, figs 22–23.
? 2018 *Borelis melo* (Fichtel & Moll); Boudagher-Fadel, pl. 7.1, fig. 18.
non 2018 *Borelis pulchra* (d'Orbigny); Boudagher-Fadel, pl. 7.1, fig. 17.
2018 *Borelis pulchra* (d'Orbigny); Förderer & Langer, p. 62, pl. 31, figs 22–23.

Diagnosis. Spheroidal shell *c*. 0.5 mm in diameter and *c*. 0.5 mm long. Streptospiral early whorls and proloculus 25–30 µm in diameter. Index of elongation 1. No Y-shaped septula (Table 1).

Repository data. Not indicated. The possible types, supposedly housed in the Museum of Natural History of Paris, could not be found.

Studied material. The analysed specimens are present-day materials from Florida Keys and Jarvis Island. The shell is spheroidal with aligned septula. The streptospiral nepionic stage occurs around a proloculus of *c*. 25 µm in diameter. No Y-shaped septula. The index of elongation is 1 (Table 1, Fig. 4).

Remarks. *B. pulchra* was described from present-day sands of Cuba (d'Orbigny 1839) and the West Indies (Cushman 1930). Cushman (1930) recorded a single specimen, illustrated by drawings, and no information about the shell architecture was provided. The studied material from Florida and from Jarvis Island corresponds to what Hottinger (1974), Javaux & Scott (2003), Langer and Lipps (2003), and Förderer & Langer (2018) named as *B. pulchra*.

Four fossil species described from the Pacific area show no distinctive characters to be separated from *B. pulchra*. *B. parvula* Hanzawa (Aquitanian–early Burdigalian), *B. primitiva* Cole (Chattian–early Miocene), *B. boninensis* Matsumaru (early Miocene), and *B. globosa* Matsumaru (Aquitanian–?Serravallian) (Figs 1–2) are subglobular in shape as are *B. melo* and *B. pulchra*. They differ from *melo* in lacking Y-shaped septula (Table 1).

The original material of *B. parvula* described by Hanzawa (1957, p. 56, pl. 23, fig. 3a–c) from the Tagpochau limestone, Aquitanian–lower Burdigalian in age (Saipan; Cole & Bridge 1953; Hanzawa 1957) cannot be located. Matsumaru (2011, 2017 and references therein) considered *B.*

parvula as ranging from the Priabonian to the Rupelian in the Philippines.

Stratigraphic distribution. *Borelis primitiva* has been described from Upper Oligocene limestone from Eniwetok (Cole, 1957). The Rupelian *Borelis globosa* Matsumaru, 1974*b* (Matsumaru 2011, 2017) and *Borelis boninensis* Matsumaru, 1996 (Matsumaru 2017; both species emended here) have been described respectively from east Mindanao (Matsumaru 2011) and from the Ogasawara Islands (Bonin Islands). Boudagher-Fadel (2018) reported as *B. melo* a specimen from the middle Miocene (Serravallian) of Australia. The absence of Y-shaped septula and the proloculus size in this illustrated specimen suggest its ascription to *B. pulchra*.

Borelis philippinensis Hanzawa, 1949

Figures 5–6

v. 1949 *Borelis philippinensis* n. sp., Hanzawa, p. 156, pl. 4, figs 1–7.
1981 *Borelis meriçi* Sirel & Gündüz, pp. 73–74, pl. 1, figs 9–13.
2017 *Borelis philippinensis* Hanzawa; Matsumaru, pp. 232–233, pl. 42, figs 1–3.

Repository data. Thin sections labelled 'Borelis philippinensis Hanz. Sagada Mountain Prov. Luzon P. Coll. H. Okutsu 66274' (Fig. 5A) and 'Borelis 66274 philippinensis Hanzawa Sagada Mountain Prov. Luzon 9.I Coll. H. Okutsu' (Fig. 5B); housed at the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Sendai, Japan.

Diagnosis. Sub-spheroidal shell with an index of elongation of 1.3–1.8. Proloculus ranges from 38 to 50 µm in diameter (Table 1). Y-shaped septula occurring only in adult growth stages.

Lectotype. Hanzawa (1949) did not designate a type. The original material illustrated by Hanzawa (1949) occurs in two thin sections (Fig. 5). Only the specimen illustrated in pl. 4, fig. 3 was not found. In accordance with ICZN Art. 74, we designate here as lectotype the specimen in thin section 'Borelis 66274 philippinensis Hanzawa Sagada Mountain Prov. Luzon 9.I Coll. H. Okutsu' (Fig. 5B), originally illustrated by Hanzawa (1949, pl. 4, fig. 2), with the purpose of clarifying the application of this name. The thin section illustrated in Fig. 5A thus becomes a paralectotype.

Remarks. The occurrence of preseptal passage only and septula in alignment in the specimens of *philippinensis* provide clear evidence that the species belongs to *Borelis*. In the analysed Hanzawa's specimens, Y-shaped septula occur only in the last whorls (Fig. 6). Its status as a distinct species is confirmed by the combination of its index of elongation, which is different from the other *Borelis* species, and the occurrence of Y-shaped septula (Table 1, Figs 1–2). Based on *Borelis* specimens from Midway drill holes, Cole (1969) considered *B. pygmaea* Hanzawa and *B. philippinensis* Hanzawa as synonyms of *B. melo* because shell size, shape, number of whorls and the number of chamberlets per whorl are variable, whilst the internal architecture is constant (p. C7). This synonymy cannot be accepted due to the different shell characteristics of these species (Table 1). *Borelis merici* Sirel & Gündüz, 1981 (as *meriçi*), described from the early–mid Oligocene of the Palu (eastern Turkey), has been considered a separate species from *B. philippinensis* essentially by having a different index of elongation '1.35–1.56 instead of 1.5–1.8' (Sirel & Gündüz 1981, p. 74). However, after checking the type of *B. philippinensis* (Table 1), the overlapping range of the indices of elongation of *B. philippinensis* and *B. merici*, together with the possible occurrence of Y-shaped septula in the latter question the separation of these species.

Stratigraphic distribution. Hanzawa attributed his material to the Aquitanian Te (1949, p. 155; Fig. 2). In the updated stratigraphy of the Luzon area the reef limestone (i.e. Kennon Limestone, Luzon Island) from which presumably Hanzawa's material originated, is considered early–middle Miocene in age, lying unconformably on Oligocene deep-water limestone (Peña 1998; Matsumaru 2011). Adams (1965, p. 325) noted that specimens comparable to *B. philippinensis* occur in coeval limestones in Sarawak. *B. philippinensis* ranges, therefore, from the Rupelian to the late Burdigalian (Figs 1–2).

Borelis melo (Fichtel & Moll, 1798)

Figure 7

1798 *Nautilus melo* Fichtel & Moll, pp. 118–123, pl. 24.
1928 *Alveolina bradyi* Silvestri, p. 21, pl. 1.
1937 *Neoalveolina melo* (Fichtel & Moll) Reichel, p. 105, pl. 10, figs 8–9.
1962 *Borelis melo* (Fichtel & Moll); Eames *et al.*, pl. 7, fig. F.
1966 *Borelis melo melo* (Fichtel & Moll); Reiss & Gvirtzman, pl. 1, figs 1–7.
1968 *Borelis melo* (Fichtel & Moll); Azema *et al.*, pl. 1.
1974 *Borelis melo* (Fichtel & Moll), 1803; Hottinger, p. 68, pl. 100, figs 1–7.

1978 *Borelis melo melo* (Fichtel & Moll); Karim, pl. 2, figs 2–4.

1985 *Borelis melo melo* (Fichtel & Moll); Al-Hashimi & Amer, pls 145, 148.

1997 *Borelis melo* (Fichtel & Moll); Betzler & Schmitz, pp. 2011–2012, fig. 3f–g.

1998 *Borelis melo melo* (Fichtel & Moll); Cicha *et al*., pl. 19, fig. 13, pl. 20, figs 1–2.

1999 *Borelis melo* (Fichtel & Moll); Abdulsamad & Barbieri, pl. 3, fig. 6.

2001 *Borelis melo* (Fichtel & Moll); Popescu & Crihan, p. 379, pl. 10, figs. 4–7.

2001 *B. roegli* n. sp.; Popescu & Crihan, p. 380, pl. 10, fig. 8.

2006 *Borelis melo haueri sensu* Chicha *et al*., 1998; Jones *et al*., pl. 1, figs 2–3.

2006 *B. melo*; BouDagher-Fadel & Clark, pl. 5, figs 6–7.

2007 *Borelis melo* (Fichtel & Moll) *curdica* (Reichel); Daneshian & Ramezani Dana, fig. 5(4).

2011 alveolinid foraminifera; Bucur *et al*., pl. 2, figs 3, 5.

2014 *B. melo curdica*; Saleh, fig. 2(17).

2016 *B. melo*; Brandano *et al*., fig. 7C.

2016 *B. melo curdica*; Kakemem *et al*., fig. 5e.

2016 *Borelis melo* (Fichtel & Moll 1798), *curdica* (Reichel 1937); Roozpeykar & Maghfouri Moghaddam, fig. 10E.

Diagnosis. Spheroidal shell *c*. 1 mm in diameter and *c*. 1 mm long. Proloculus 60–65 μm in diameter. Index of elongation 1. Rare Y-shaped septula only in adult whorls (Table 1).

Studied material. The analysed specimens are from Serravallian limestones of Sierra de Jimena (Jaén), in southern Spain (Castillo-Guzmán 2016), from the Tortonian of the Almanzora Corridor and from the Messinian of Cabo de Gata (southeastern Spain; Fig. 2). The shell is spheroidal with aligned septula. The streptospiral nepionic stage around a proloculus is *c*. 60 μm in diameter. Y-shaped septula occur only in the adult stage. The index of elongation is 1 (Table 1, Figs 1, 7).

Remarks. There are four species bearing Y-shaped septula: *B. philippinensis*, *B. melo*, *B. curdica* and *B. schlumbergeri* (Table 1). *Borelis melo* is clearly different from these other species due to its spheroidal shape and larger proloculus (Table 1, Fig. 1). Moreover, in *B. melo* the Y-shaped septula occur only in the adult growth stage (Fig. 7) and are rarer than in *B. curdica*.

Assessing the lower Miocene material collected in drill holes in Midway atoll (Hawaii), Cole (1969) considered *B. pygmaea* Hanzawa, *B. philippinensis* Hanzawa, *B. primitiva* Cole, and *B. parva* Hanzawa as heterotypic synonyms of *B. melo* (Fichtel & Moll). His conclusions were based on dimensions of the test, shape, number of whorls, and in the number of chamberlets per whorl

(Cole 1969, p. C7). He did not mention the Y-shaped septula, which do not appear in the illustrated specimens. Therefore, Cole's (1969) specimens cannot be ascribed to *B. melo* and, based upon the index of elongation and proloculus size, they probably belong to *B. pulchra*.

Stratigraphic distribution. This species occurs only in the Western Tethys (e.g. Adams *et al*. 1983; Jones *et al*. 2006; Figs 1–2). The first appearance is in the Aquitanian from the Middle East to the western Mediterranean area. After being rare in the Serravallian (Fig. 8), the species was reported in the Tortonian of the western Mediterranean but with no illustrations (Grasso *et al*. 1982; Moisette & Saint-Martin 1995; Franseen *et al*. 1997; Pomar *et al*. 1996) and in the Tortonian of the Central Apennines (Brandano *et al*. 2016). The Messinian records are from southeastern Spain (Betzler & Schmidt 1997 and this study; Fig. 8).

Borelis curdica (Reichel, 1937)

Figures 9–11

1937 *Neoalveolina melo curdica* Reichel, p. 108, pl. 10, figs 4–7.
1909 *Alveolina sphaerica* (Fortis) Osimo, figs 2–6.
1960 *Neoalveolina melo* (F. & M.); Hottinger, p. 227.
1966 *Borelis melo curdica* (Reichel); Reiss & Gvirtzman, pl. 1, fig. 8; pl. 2, fig. 1.
1974 *Borelis curdica* (Reichel), 1937; Hottinger, pp. 67–68, pl. 99, figs 1–8.
1976 *B. curdica*; Bignot & Guernet, pl. 2, figs 1–10.
1993 *B. melo melo*; Buchbinder *et al*., fig. 2E.
1993 *Borelis melo curdica*; Buchbinder *et al*., fig. 2F.
1998 *Borelis melo curdica* (Reichel); Cicha *et al*., pl. 19, fig. 8.
?2004 *B*. cf. *curdica*; Cahuzac & Poignant, pl. 2, fig. 3.
2006 *Borelis melo curdica*; Jones *et al*., pl. 1, figs 4–5.
2011 *B. melo curdica*; Seyrafian *et al*., fig. 9f.
2018 *Borelis curdica* (Reichel); Boudagher-Fadel, pl. 7.1, fig. 19.
2018 *Borelis melo curdica* (Reichel); Yazdi-Moghadam *et al*., p. 236, fig. 11A–B.

Syntype. Figured in Reichel (1937, pl. 10, fig. 4), megalospheric form.

Diagnosis. Spheroidal shell *c*. 1 mm in diameter and *c*. 1 mm long, exceptionally reaching 1.6 mm. Proloculus 30–60 μm in diameter. Index of elongation 1. Frequent Y-shaped septula in all whorls (Table 1).

Studied material. The analysed specimens are from the Langhian of Letkés and the Tortonian of Stazzano (Ghibaudo *et al*. 1985; Kovács & Vicián 2014; Fig. 2). The shells are spheroidal in shape with aligned septula. Only A-forms were recorded (Figs 9–11). The proloculus, with a streptospiral nepionic stage, is *c*. 40 μm in diameter. Y-shaped septula occur throughout the growth stages, especially in the adult ones. Index of elongation is *c*. 1 (Table 1, Fig. 1).

Remarks. According to Reichel (1937, p. 109), *B. curdica* shows an alternation of large and small apertures, sometimes disarranged. Hottinger (1974, p. 68) distinguished *B. melo* and *B. curdica* by the rare and common occurrence of Y-shaped septula, respectively. Jones *et al*. (2006, p. 179) stated that *B. melo* is characterized by 'chamberlets of same chamber of equal or nearly equal size', while in *B. curdica* 'chamberlets of later chambers alternately large and small… result in the development of incipient attic chamberlets separated by Y-shaped septula'.

X-ray micro-tomographic analysis shows that number of Y-shaped septula increases in the adult stages (Figs 10–11). The frequency of occurrence of the Y-shaped septula can actually be high in some specimens as those recorded from Letkés (see also Hottinger 1974, pl. 99, figs 1–2). The rarity of these septula in the nepionic stages can be due to the smaller dimensions of the chamberlets and, therefore, of the Y-shaped septula. In addition, the ordinary thin sections randomly cut the specimens and the early stages are rarely sectioned.

Most of the *B. curdica* records are inadequately illustrated since they do not show the possible Y-shaped septula and the proloculus considered diagnostic characters in separating the two subspecies (e.g. Daneshian & Ramezani Dana 2007; Saleh 2014; Kakemem *et al*. 2016; Tables 2–3).

Stratigraphic distribution. Reliable records of *B. curdica* are restricted to the Mediterranean area, including the Anatolian peninsula (where its type locality Garzan is), and range from the Burdigalian to the uppermost Tortonian (Figs 2, 8). Only one record occurs in the Serravallian and possibly in the Tortonian in the eastern Mediterranean (Reiss & Gvirtzman 1966; Buchbinder *et al*. 1993); records from Iran are sparse. The present record from Hungary is the first from the Paratethys (Fig. 8).

Borelis schlumbergeri (Reichel, 1937)

Figures 12–13

1880 *Alveolina boscii* Defrance; Möbius, p. 79, pl. 3, fig. 1.

1937 *Neoalveolina pygmaea schlumbergeri*, Reichel, p. 110, pl. 10, figs 1–3, pl. 11, fig. 6b.

1950 *Borelis pygmaea* (Hanzawa) *schlumbergeri* Reichel; Said, p. 26, pl. 3, fig. 6.

1954 *Borelis schlumbergeri* (Reichel); Cole, pl. 209, figs 10–18.

1957 *Borelis schlumbergeri* (Reichel); Cole, p. 767.

1966 *Borelis schlumbergeri* (Reichel); Reiss & Gvirtzman, p. 444, pl. 2, figs 3–8.

1974 *Borelis schlumbergeri* (Reichel); Hottinger, pp. 68–69, pl. 102, figs 10–13.

1977 *Borelis schlumbergeri* (Reichel); Hottinger, p. 93, figs 29 A–H.

1984 *Borelis schlumbergeri*; Reiss & Hottinger, fig. G.10.

1987 *Borelis schlumbergeri* (Reichel); Loeblich & Tappan, pl. 375, fig. 1.

1993 *Borelis schlumbergeri* (Reichel); Hottinger *et al.*, p. 68, pl. 75, figs 1–17.

2011 *Borelis schlumbergeri* (Reichel); Makled & Langer, pl. 7, fig. 35.

2013 *Borelis schlumbergeri* (Reichel); Langer *et al.*, pl. 7, fig. 14.

Diagnosis. Sub-ellipsoidal megalospheric forms *c*. 0.8 mm in diameter and up to 2 mm long. Spheroidal proloculus 40–80 μm in diameter followed by a streptospiral nepionic stage. Index of elongation 2.2–4.0. Sub-ellipsoidal microspheric forms *c*. 1 mm in diameter and up to 2.4 mm long. Y-shaped septula occurring only in the adult growth stages (Table 1).

Repository data. Not indicated.

Studied material. The studied specimens are from the south of the port of Eilat and in front of the IUI, Israel. Sub-ellipsoidal megalospheric specimens with a diameter up to 0.85 mm and *c*. 1.6 mm long. Proloculus is *c*. 60 μm in diameter. The index of elongation is *c*. 3. Rare Y-shaped septula (Figs 12–13).

Remarks. The analysed material is morphologically and architecturally concordant with *Borelis schlumbergeri* (see Reichel 1937; Reiss & Gvirtzman 1966; Hottinger 1977, 1980; Reiss & Hottinger 1984; Hottinger *et al.* 1993). Present-day *Borelis* species are represented by *B. pulchra* and *B. schlumbergeri* (Fig. 2). *B. schlumbergeri* differs from *pulchra* in being fusiform in shape and having rare Y-shaped septula, usually located in the adult growth stages (e.g. Hottinger 1974;

Hottinger *et al*. 1993; Debenay 2012). *Borelis schlumbergeri* occurs in the Red Sea, in the Indian Ocean and in the Pacific Ocean (Reiss & Hottinger 1984; Hottinger *et al*. 1993; Makled & Langer 2011; Langer *et al*. 2013) and in the area in between these oceans (Jakarta, Pulau Pari; Renema 2008). Debenay (2012) considered *B. pulchra* as a junior synonym of *schlumbergeri* with no description and discussion of the shell architecture of the studied specimens recorded in New Caledonia. The occurrence of the Y-shaped septula (Figs 12–13) discards this interpretation.

Stratigraphic distribution. This species has been identified exclusively in the Indo-Pacific area, from the Tortonian to the Recent (e.g. Cole 1954; Reiss & Gvirtzman 1966; Matsumaru 1974*a*; Hottinger *et al*. 1993).

PALAEOBIOGEOGRAPHIC DISTRIBUTION AND EVOLUTIONARY DYNAMICS

Seven *Borelis* species can be distinguished by means of the proloculus diameter, the index of elongation and the occurrence of Y-shaped septula (Table 1). Four species (*B. philippinensis*, *B. melo*, *B. curdica*, *B. schlumbergeri*) are characterized by rare to common Y-shaped septula (Fig. 1), while this feature is absent in three species (*B. inflata*, *B. pulchra*, *B. pygmaea*). The proloculus size range of *B. inflata* falls within that of *B. pygmaea* but the index of elongation is markedly different in these two species.

In the Eocene, *Borelis* is represented by the spheroidal *B. vonderschmitti* (Schweighauser, 1951), which was widespread throughout the middle–late Eocene in the Western Tethys (e.g. Bassi & Loriga Broglio 1999; Drobne *et al*. 2000). The single record of this species in the Pacific area is from Saipan (Matsumaru 1974*a*, p. 291, no illustration). In the Indo-Pacific province Lunt & Allan (fig. 6, 2004) considered the first appearance of *Borelis* as upper Eocene in age (upper Tb).

The Pacific *Borelis inflata, B. pulchra* and *B. pygmaea* show morphological affinities with *B. vonderschmitti*. *B. pulchra* and *B. pygmaea* appear in the Priabonian whereas *B. inflata* first occurs in the Rupelian (Figs 2, 14). It is likely that these species are descendants of *B. vonderschmitti*. Except for Adams's (1965) record from the Oligocene of Sarawak, *B. inflata* has been only recorded from the Western Tethys. *B. pygmaea* occurs from the Oligocene of Dhofar and Socotra Island (Serra-Kiel *et al*. 2016). During the Rupelian the *Borelis* species diversified with the appearance of Y-shaped septula in the Pacific *B. philippinensis,* which remained the single Pacific species with Y- shaped septula until its disappearance in the Burdigalian (Fig. 14; uppermost Te5 in fig. 6 of Lunt & Allan 2004).

Borelis pulchra (Priabonian–Recent) has been recorded from the middle Miocene of the western Pacific (Australia; BouDagher-Fadel 2018), although there are no records from the Middle East (e.g. Jones *et al*. 2006; Renema 2007). Confirmed *B. schlumbergeri* appeared in the late Miocene of the Pacific (i.e. Eniwetok and Bikini; e.g. Hanzawa 1940; Cole 1954, 1957; Adams 1970; Matsumaru 1974*a*; Lunt & Allan 2004). Chattian–Burdigalian records of *B. schlumbergeri* need further confirmations, since no illustrations were published (Hanzawa 1940; Cole 1957; Matsumaru 1974*a*). In the Mediterranean, the Aquitanian *B. melo* likely represents the descendant of westward migrants of *B. philippinensis* (Fig. 14). Considering that *Borelis schlumbergeri* is not present in the Mediterranean, and that this species occurs in the present-day Red Sea, the westward *B. philippinensis* migrants moved into the Red Sea before the progressive closure of the Indonesian gateway at *c*. 14 Ma, which re-organized the palaeoceanic circulation (see the strong westerly oceanic surface current MIOJet of Gourlan *et al*. 2008).

The present-day Indo-Pacific *Borelis* records have been so far ascribed to *B. schlumbergeri* (e.g. Hottinger 1974; Hottinger *et al*. 1993; Haig 1997; Angel *et al*. 2000; Holzmann *et al*. 2001; Debenay 2012; Fajemila *et al*. 2015), which is the descendant of the Rupelian–Burdigalian *B. philippinensis* in the Indo-Pacific area (Fig. 14). However, the studied specimens from Jarvis Island belong to *B. pulchra*. The attribution of *pulchra* as an exclusively Caribbean species is here rejected (see also Langer & Hottinger 2000). The Pacific *B. pulchra* is a long-lasting species ranging from the Priabonian (Fig. 2). Pliocene (as *B. melo*, in Matsumaru 2011, p. 249) and Pleistocene (Adams 1970; Matsumaru 1974*a*; Iryu *et al*. 2006) records are documented. Althought in *B. pulchra* shape and proloculus size remain relatively constant through time, its record in Indo-Pacific shallow-water settings has two gaps in the Langhian and in the Tortonian–Messinian (Fig. 14; see also Lunt & Allan 2004). In southeast Asia, an evolutionary lineage of three genera, *Heterostegina–Tansinhovella–Spiroclypeus,* appears twice in the fossil record with a temporal gap between the two observed ranges. The coeval re-appearance in the second development of the three-genera morphologies in geographically separated areas has been interpreted as the result of iterative evolution (Lunt & Renema 2014). In contrast to the patterns shown by these three genera, the *Borelis* species do not show iterative apperance of diagnostic characters. Y-shaped septula appeared in a Rupelian taxon (i.e. *B. philippinensis*) and still persist in the extant *B. schlumbergeri*, while proloculus size and the index of elongation change through time. The temporal gaps in the *B. pulchra* distribution in the Indo-Pacific are probably due to taphonomic bias caused by selective destruction of the weak porcelaneous spheroidal tests within the fair-weather wave base (Yordanova & Hohenegger 2007). The rarity of Pacific *Borelis* in middle–late Miocene shallow-water settings, in which *Alveolinella* is rather common, may also be related to a higher ecological tolerance of this latter taxon (Hohenegger 2000; Langer & Hottinger 2000). This can be the case of

Okinawa where modern *Alveolinella* is commonly reported in coral-reef related settings (e.g., Hohenegger 2000), whereas there is only one record of *Borelis* (Hatta & Ujiie 1992).

With regard to its occurrence in the Caribbean, considering that the species does not occur in the Mediterranean, the migrants probably followed an eastwards path from the Pacific through the Central America Seaway (CAS) before its closure in the Pliocene (O'Dea *et al*. 2016; Fig. 14). From the western Atlantic coasts *B. pulchra* colonized the eastern Atlantic (see biogeographic distribution in Langer & Hottinger 2000).

Extant Archaiasinae, which are predominantly found in the Caribbean, apparently underwent a similar biogeographic migration. Sequencing the complete SSU rDNA gene, Holzmann *et al*. (2001) concluded that the Archaiasinae originated in the Indo-Pacific and migrated later to the western Atlantic. An analogous pathway was suggested for the coralline algae of the *Lithophyllum pustulatum* species group (Bassi *et al*. 2009).

The largest extant benthic foraminifer *Cycloclypeus*, represented today by a single species, appeared in the early Rupelian of Java and Kalimantan. After speciation in the Indo-Pacific and reaching the Mediterranean area, this species now is restricted to the Pacific Ocean (Renema 2015).

In the Mediterranean area *B. curdica* ranges from the Burdigalian to the uppermost Tortonian (Figs 8, 14). The connections between the Mediterranean Sea and the Indian Ocean were closed during the late Langhian by the emergence of the 'the area extending from Iraq to south-eastern Turkey' (Harzhauser & Piller 2007). The isolation of the Mediterranean Sea from the Indian Ocean separated the Mediterranean *Borelis* populations from the Indo-Pacific area. In the Mediterranean area, *B. inflata*, *B. curdica* and *B. melo* co-existed until the late Tortonian when *Borelis inflata* disappeared (Fig. 14). *B. melo* disappeared in the Messinian.

The Serravallian–Tortonian records of *B. melo* are restricted to the western Mediterranean (Sierra Espuña, Hottinger 1974; this study) and Central Apennines (Brandano *et al*. 2016) with a single Serravallian record from Lebanon (BouDagher-Fadel & Clark 2006; Fig. 8). *B. curdica* occurs in the Serravallian–Tortonian of Israel (Reiss & Gvirtzamn 1966; Buchbinder *et al*. 1993) and in the Tortonian of northwestern Italy (Fig. 8).

The studied Tortonian–Messinian *Borelis* specimens come from shallow-water reef-related settings (Martín *et al*. 1989; Betzler & Schmidt 1993; Kovács & Vicián 2014). The Messinian coral reef settings were the refugia of *B. melo* and its last appearance datum in the Mediterranean (Figs 8, 14).

Borelis sp. has recently been documented along the Levantine coast in the eastern Mediterranean off Israel (Hyams *et al.* 2002; Hyams-Kaphzan *et al.* 2008; Langer 2008). The Mediterranean specimens recorded are subglobular in the juvenile stage and more elongate in the adult forms. They resemble *B. pulchra* (Hyams-Kaphzan *et al.* 2008) but their species designation requires further study. To date, Y-shaped septula have not been documented in *Borelis* sp. and the size range of the proloculus is not known. The current biogeographic appearance in the Mediterranean Sea suggests a relatively recent and current driven dispersal along the coast of Israel (Langer, 2008) and the minimum sea surface temperature required for the presence of this taxon is at around 18° C. Three potential mechanisms may be responsible for the biogeographic range expansion of this species of *Borelis* into the eastern Mediterranean: (1) Lessepsian migration from the Red Sea via the Suez Canal into the Mediterranean as a result of the opening of the Suez Canal in 1869; (2) anthropogenic introduction via ballast waters from the Red Sea or the Atlantic; and (3) natural invasion of propagules via the Atlantic.

CONCLUDING REMARKS

After studying fossil and modern isolated shells in thin sections and through micro-computed tomography scanning of seven *Borelis* species, the species circumscriptions were circumscribed in terms of proloculus size, occurrence of Y-shaped septula and index of elongation.

The new records of *B. inflata* from the Tortonian deposits (northwestern Italy) and of *B. curdica* from the early Langhian (northern Hungary) and the Tortonian (northwestern Italy) extend the stratigraphic range of these species from the Rupelian to the Tortonian, and from the Burdigalian to the Tortonian, respectively.

For the first time the shell architectures of *B. melo*, *B. curdica* and *B. pulchra* are illustrated via micro-computed tomography scanning images. Although known from the early Miocene and in the Messinian, *B. melo* was identified for the first time in the Serravallian of southern Spain, filling the gap of previous reports.

The absence or presence of Y-shaped septula permits to distinguish two species groups in the Priabonian–Burdigalian of the Tethyan ocean. *Borelis inflata*, *B. pulchra* and *B. pygmaea*, which lack Y-shaped septula, belong to the first group, deriving from the middle–upper Eocene *B. vonderschmitti*. The first species bearing Y-shaped septula is *B. philippinensis* which appeared in the Rupelian of the Indo-Pacific.

In the Indo-Pacific the long-lasting *B. pulchra* persists until today, whereas the westward migrants of *B. philippinensis* gave rise to *B. melo* (Aquitanian–Messinian) and *B. curdica* (Burdigalian–Tortonian). These two species became isolated from the Indo-Pacific by the eastern closure of the Mediterranean basin in Langhian times.

Before the early Piacenzian closure of the Central America Seaway, from the central Pacific

Ocean *B. pulchra* reached the Caribbean area from where it colonized the western Atlantic coasts.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://datadryad.org/review?doi=doi:10.5061/dryad.st65n12 (*Borelis curdica* micro-computed tomography scanning images).

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Figure and table captions

FIG. 1. Plot of proloculus diameter (μm) and index of elongation for the Oligocene–Miocene *Borelis* species. Numerical data from Table 1. Black bordered ranges point to Y-shaped septula-bearing taxa. Bi, *B. inflata*; Bpy, *B. pygmaea*; Bpu, *B. pulchra*; Bm, *B. melo*; Bcu, *B. curdica*; Bs, *B. schlumbergeri*; Bp, *B. philippinensis*.

FIG. 2. Stratigraphic distributions of the taxonomically re-assessed Oligocene–Miocene *Borelis* species. Dashed lines point to absence of record in that stratigraphic interval; for details see text. a, Cahuzac & Poignant (1997), Jones *et al*. (2006). b, Adams (1965), Hottinger (1974). c, Hanzawa (1957). d, Hanzawa (1930), Hottinger (1974). Numbers refer to the studied samples: 1, Hanzawa's (1949) material; 2, Letkés village, Hungary; 3, Sierra de Jimena; 4, Piedmont; 5, Almanzora Corridor; 6, Cabo de Gata. SBZ, Shallow Benthic Zonation (Cahuzac & Poignant 1997). Serravall., Serravallian.

FIG. 3. *Borelis inflata* (Adams, 1965). Tortonian, Sant'Agata Fossili Marl Formation cropping out in the Stazzano area (northwestern Italy). Micro-computed tomographic analysis of a megalospheric specimen illustrating the pre-septal passages (pre-sept) and the proloculus (prol). Note the absence of Y-shaped septula. Scale bar represents 0.50 mm.

FIG. 4. *Borelis pulchra* (d'Orbigny, 1839). Recent material. Micro-computed tomographic analysis of megalospheric specimens. Note that no Y-shaped septula occur throughout the shell growth stages. A–J, upper Florida Keys, 10–30 m water depth. K–P, Jarvis Island. Scale bar represents 0.50 mm.

FIG. 5. *Borelis philippinensis* Hanzawa, 1949, thin sections of types; Hanzawa's collection; Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Sendai, Japan. Scale bar represents 2 cm. A, '*Borelis philippinensis* Hanz. Sagada Mountain Prov. Luzon P. Coll. H. Okutsu 66274'. B, '*Borelis* 66274 *philippinensis* Hanzawa Sagada Mountain Prov. Luzon 9.I Coll. H. Okutsu'. Scale bar represents 2 cm.

FIG. 6. *Borelis philippinensis* Hanzawa, 1949; Hanzawa's collection; Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Sendai, Japan. A, axial section

showing the fusiform text characterized by a high number of whorls (Hanzawa 1949, pl. 4, fig. 1). B, axial section showing Y-shaped septula in the last three whorls (Hanzawa 1949, pl. 4, fig. 2). C, tangential section illustrating the pre-septal passages (Hanzawa 1949, pl. 4, fig. 7). Y-sept, Y-shaped septula; p-sept, pre-septal passage. Scale bar represents 0.50 mm.

FIG. 7. *Borelis melo* (Fichtel & Moll, 1798); A–B, D–G, Messinian, Cabo de Gata; C, late Tortonian, Almanzora Corridor; southeastern Spain. A, oblique section near to the equatorial plane showing the streptospiral nepionic stage (sns); B, tangential section showing the pre-septal passage (p-sept). C, axial section showing the chamber (ch). D–G, oblique sections near the equatorial plane showing the proloculus (prol), the chambers (ch) and the Y-shaped septula (Y-sept). Scale bar represents 0.50 mm.

FIG. 8. Location of *Borelis melo* (A–C) and *B. curdica* (D–F) records in palaeomaps proposed by Rögl (1998) for the Early Oligocene–early Miocene (A–B, E–D), and by Harzhauser & Piller (2007) for the middle–late Miocene (C, F). Numbers refer to Tables 2–3 in which detailed information on each record can be found.

FIG. 9. *Borelis curdica* (Reichel, 1937). Isolated specimens from (A) early Langhian, Bagoly Hill, Letkés village (Hungary), and (B) Tortonian, Stazzano area (northwestern Italy, Sant'Agata Fossili Marl Formation). Scale bar represents 1 mm.

FIG. 10. *Borelis curdica* (Reichel, 1937); early Langhian, Bagoly Hill, Letkés village, Hungary. Micro-computed tomographic analysis of microspheric specimen showing tangential to axial sections. The Y-shaped septula occur from the early to the adult growth stages. Y-sept, Y-shaped septula; p-sept, pre-septal passage; prol, proloculus. Scale bar represents 0.50 mm.

FIG. 11. *Borelis curdica* (Reichel, 1937); Tortonian, Sant'Agata Fossili Marl Formation cropping out in the Stazzano area (northwestern Italy). Micro-computed tomography of a megalospheric specimen showing pre-septal passage (p-sept) and the Y-shaped septula (Y-sept) which occur from the early to the last growth stages. prol, proloculus. Scale bar represents 0.50 mm.

FIG. 12. *Borelis schlumbergeri* (Reichel, 1937); Recent material from the south of the port of Eilat, Israel. Micro-computed tomography of microspheric (A) and megalospheric (B–C) specimens

(prol, proloculus) showing the pre-septal passages (p-sept) and the Y-shaped septula (Y-sept). Scale bars represent 0.50 mm.

FIG. 13. *Borelis schlumbergeri* (Reichel, 1937); Recent material collected at 9 m water depth in front of the IUI, Eilat, Israel. Micro-computed tomographic scanning 3D-rendered model with shell removed, note the Y-shaped septula (Y-sept**).** Scale bar represents 0.50 mm.

FIG. 14. Major events in the palaeobiogeographic history of the Oligocene–Miocene *Borelis* species. The two present-day *Borelis* species (i.e. *B. pulchra*, *B. schlumbergeri*) represent the descendants of two species groups distinguished by the occurrence of Y-shaped septula. The *B. philippinensis*-related migrants from the Pacific presumably reached the Mediterranean area in the Aquitanian (1) giving rise to *B. melo* and *B. curdica*. In the Mediterranean *B. inflata*, *B. melo* and *B. curdica* disappeared by the MSC. In the Indo-Pacific *B. philippinensis* and *B. pygmaea* disappeared in the late Burdigalian. The Pacific *B. pulchra* is a long-lasting species ranging from the Priabonian. Before the CAS (2), *B. pulchra* migrated into the Caribbean area, where is still thriving. Time scale after ICS website (2018; www.stratigraphy.org). For details see text. MIOJet, Miocene Indian Ocean Equatorial Jet (Gourlan *et al*. 2008).

TABLE 1. Comparison of diagnostic shell characteristics of *Borelis* species and related stratigraphical setting.
Species are listed according to their first appearance reported in literature; compare with Figure 2.
Numbers in brackets point to the maximum size range.
I.E., index of elongation; Oligo, Oligocene; Tort, Tortonian; Rup, Rupelian; Mioc, Miocene; Chat, Chattian; Burd, Burdigalian; Aquit, Aquitanian; Serr, Serravallian; Tort, Tortonian; Mess, Messinian

Based on data from:
1, Adams (1965), Hottinger (1974), this study; 2, Hanzawa (1930), Hottinger (1974); 3, Cole (1957); 4, Hanzawa (1957); 5, Matsumaru (1974*b*, 2017); 6, Hanzawa (1949), this study; 7, Hottinger (1974), Jones *et al*. (2006), this study; 8–9, Sirel & Gündüz (1981); 10, Cushman (1930), Hottinger (1974), this study; 11, Reichel (1937), Reiss & Gvirtzman (1966), Hottinger *et al*. (1993).

TABLE 2. Stratigraphical and palaeogeographical distribution of *Borelis melo*. For the palaeogeographical locations see Figure 8A–C.

TABLE 3. Stratigraphical and palaeogeographical distribution of *Borelis curdica*. For the palaeogeographical locations see Figure 8D–F. *SEM illustration of an isolated specimen; **equivalent to Langhian–middle Serravallian in Piller *et al*. (2007).