



## A new species of the larger porcelaneous foraminifer *Borelis* provides novel insights into Neogene to Recent western Pacific palaeobiogeographical dispersal patterns

Davide Bassi<sup>a,\*</sup>, Yasufumi Iryu<sup>b</sup>, Shunichi Kinoshita<sup>c</sup>, Kazuhiko Fujita<sup>d</sup>, Johannes Pignatti<sup>e</sup>

<sup>a</sup> Dipartimento di Fisica e Scienze della Terra, Università di Ferrara, 44122 Ferrara, Italy

<sup>b</sup> Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Aobayama, Sendai 980-8578, Japan

<sup>c</sup> Department of Geology and Paleontology, National Museum of Nature and Science, 4-1-1, Amakubo, Tsukuba, Ibaraki 305-0005, Japan

<sup>d</sup> Department of Physics and Earth Sciences, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan

<sup>e</sup> Dipartimento di Scienze della Terra, Università 'La Sapienza', P.le A. Moro 5, 00185 Rome, Italy

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### ABSTRACT

Only three species of alveolinoidean larger foraminifera occur in present-day tropical shallow-water marine settings. *Alveolinella quoyi* thrives in the Central Indo-Pacific and Eastern Indo-Pacific, *Borelis pulchra* in the Central and Eastern Indo-Pacific and in the central Atlantic, whereas *Borelis schlumbergeri* inhabits the Indo-Pacific Ocean. The northernmost record is that of *Alveolinella quoyi* from the shallow-water settings in Okinawa (central Ryukyu Islands, Japan). A new porcelaneous larger foraminiferal species, *Borelis matsudai* sp. nov. (Alveolinoidea, Borelinae), is established herein, based on specimens discovered in present-day shallow-water sediments from Sekisei Lagoon, southern Ryukyu Islands (Japan). This is the northernmost record of the genus in the western Indo-Pacific Warm Pool. The architectural characters of this species suggest its phylogenetic relationship with the *Borelis pulchra* group. A comprehensive literature survey of fossil and modern records of *Borelis pulchra* over the past 30 million years shows that the Middle Miocene constriction of the Indonesian Seaway and the Late Miocene–Early Pliocene restriction of the Indonesian Throughflow impacted the species-level dispersal of this species in the Indo-Australian Archipelago. Driven by the Kuroshio dispersal route *Borelis matsudai* sp. nov. likely appeared in the southern and central Ryukyu Islands at least from the Chibanian (Middle Pleistocene). This species represents a marginal part of a population in significant contact with its ancestor (*B. pulchra*), which is widespread southward since the Oligocene (Philippines). With ongoing global warming possible occurrences of *Borelis matsudai* sp. nov. in the northern Ryukyu Islands, where it has not yet been found, are expected. The Sekisei Lagoon represents, therefore, a biogeographical stepping stone relay station in northward migration of the shallow-water benthic organisms along the Kuroshio dispersal route.

### 1. Introduction

Larger benthic foraminifera (LBF), symbiont-bearing unicellular organisms, have been important components of shallow-marine communities throughout the Cenozoic (e.g., Buxton and Pedley, 1989). LBF, often integral parts of the coral reef ecosystems, are widespread from the tropics to the warm regions within the euphotic zone (e.g., Hottinger, 1980, 1996, 1997; Hohenegger, 2018). Because of their high preservation potential, LBF have an excellent fossil record not only as carbonate producers (Narayan et al., 2022) but even as fossil markers (e.g., Serra-

Kiel et al., 1998). LBF show their peak in diversity during the middle Eocene, followed by a steady decrease up to today (e.g., Hottinger, 1998).

*Alveolinella* H. Douvillé, 1907 and *Borelis de Montfort*, 1808 are the only present-day alveolinoidean porcelaneous larger benthic foraminifera (pLBF) in tropical shallow marine settings (Hohenegger, 2000; Langer and Hottinger, 2000). *Alveolinella* is represented by a single species, *A. quoyi* (d'Orbigny, 1826), and *Borelis* by two species, *B. pulchra* (d'Orbigny, 1839) and *B. schlumbergeri* (Reichel, 1937). *Alveolinella quoyi* occurs in the Central Indo-Pacific and Eastern Indo-

\* Corresponding author.

E-mail addresses: [bsd@unife.it](mailto:bsd@unife.it) (D. Bassi), [yasufumi.iryu.d8@tohoku.ac.jp](mailto:yasufumi.iryu.d8@tohoku.ac.jp) (Y. Iryu), [skinokoscos@gmail.com](mailto:skinokoscos@gmail.com) (S. Kinoshita), [fujitaka@sci.u-ryukyu.ac.jp](mailto:fujitaka@sci.u-ryukyu.ac.jp) (K. Fujita), [johannes.pignatti@uniroma1.it](mailto:johannes.pignatti@uniroma1.it) (J. Pignatti).

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Pacific (from the Maldives to the Hawaii islands; Reiss and Hottinger, 1984; Bassi et al., 2022a). *Borelis pulchra* has been recorded from the Central Indo-Pacific to Central America (Cushman et al., 1954; Javaux and Scott, 2003; Förderer and Langer, 2018). *Borelis schlumbergeri* inhabits the Indo-Pacific Ocean (Hottinger et al., 1993). In the Pacific Ocean the northernmost record of *Alveolinella quoyi* is from the shallow-water settings in Okinawa (central Ryukyu Islands, Japan), whereas the northernmost *Borelis* has been found in the Sekisei Lagoon, southern Ryukyu Islands (Hatta and Ujiie, 1992; Ujiie and Hatta, 1995).

Located in the Kuroshio upstream region (i.e., southern Ryukyu Islands), the Sekisei Lagoon is the largest coral reef lagoon in Japan and is thought to help maintain coral reef ecosystems across the entire archipelago by supplying coral spawn and larvae to downstream sites (i.e., relatively northern regions of the archipelago; Takeda et al., 2021). Massive bleaching events impacted considerably on hermatypic corals thriving in this lagoon, which becomes, therefore, important for coral recovery as a first step toward the recovery of the entire Ryukyu Islands. The lagoon plays also an important ecological role in aiding poleward migrations of coral habitat under the influence of ongoing global climate change (Takeda et al., 2021).

The finding of *Borelis* in the Sekisei Lagoon by Hatta and Ujiie (1992), associated with *Alveolinella quoyi*, makes intriguing the palaeobiogeographical dynamics of the alveolinoideans since their highest diversity has been so far identified in the Indo-Australian Archipelago (IAA; Langer and Hottinger, 2000). The IAA, tropical and north-western Pacific region as far north as c. 20°N (Renema et al., 2008), comprises some of the world's highest levels of species richness and endemism (Bruyn de et al., 2014), for example, in bivalves, gastropods, corals and fishes (e.g., Hoeksema, 2007; Tittensor et al., 2010; Jablonski et al., 2013; Yasuhara et al., 2022).

The IAA biodiversity hotspot originated in the Early Miocene when species diversity was significantly enhanced also in mid-latitude southwestern Japan (Yasuhara et al., 2016, 2022). The northern expansion of the tropical high diversity zone into mid-latitudes has been seen in the present-day western Indo-Pacific Warm Pool (wIPWP) for several taxa (Renema et al., 2008; Jablonski et al., 2013). The wIPWP is the large body of water in the western Pacific denoted by sea-surface temperatures >28 °C (Sosdian and Lear, 2020). Western Indo-Pacific biodiversity is known to be high also in adjacent mid-latitude areas, such as the Ryukyu Islands (Fujikura et al., 2010), for example in larger benthic foraminifera, bivalves, ostracods and coastal fishes (Hohenegger, 1994, 2006; Tittensor et al., 2010; Jablonski et al., 2013; Yasuhara et al., 2016).

In the north-western Pacific the current intensity and position of the major warm Kuroshio current has varied markedly over millions of years with changing greenhouse (Pliocene) to icehouse (Pleistocene) conditions (Gallagher et al., 2015). These variable cooling and warm cycled conditions due to the Kuroshio current brought about the Ryukyu reef front advance and retreated in the last c. 2 Myr (Iryu et al., 2006; Gallagher et al., 2015; Cruz Salmeron et al., 2022).

From the late Oligocene to the Early Miocene, biogeographical studies showed that the Indonesian Seaway became effective for surface water transport (Kuhnt et al., 2004). The Middle Miocene tectonic closure of the Indonesian Seaway was as a trigger for invigoration of tropical surface ocean circulation systems (Kennett et al., 1985). This pivotal role for the Indonesian Seaway in setting the climate budget of the Indo-Pacific region, proximal seas, and distal outflow locations in the Miocene tropical Indian Ocean can be assessed by checking the palaeobiogeographical dynamics of the LBF species which thrived in shallow-water carbonate settings.

Here, we document palaeobiogeographic pLBF dynamics in the tropical and north-western Pacific region through the Oligocene–Recent. After introducing a new species of *Borelis* from the present-day southern and central Ryukyu Islands representing the northernmost record of this genus in the Pacific Ocean, we use the fossil records of the ancestor species as a model system because it is a common component of

shallow-marine benthic communities and because precise species-level identification is possible based on fossil specimens (Bassi et al., 2021a). Studies on smaller benthic foraminifera and LBF from the Ryukyu Islands date back to Yabe and Hanzawa (1925), Hanzawa (1948) and Matsumaru and Matsuo (1976). Since then, no *Borelis* species has been identified and illustrated.

Our main aims are (1) to assess the taxonomic status of the new *Borelis* species from the southern and central Ryukyu Islands, (2) to discuss the IAA palaeobiogeographical constraints that impacted species-level dispersal even in well-dispersed taxa such as *Borelis pulchra* over the past 30 Myr, and (3) to investigate when the new *Borelis* species plausibly appeared in this region. Data from a comprehensive literature survey show that the new species descends from *Borelis pulchra*, which first appeared in the Oligocene of the western Pacific Ocean. This record of a new *Borelis* species in southern and central Ryukyu Islands suggests that monitoring the northward migrations of the pLBF via the Kuroshio dispersal route may improve our understanding of current behaviour with future climate change.

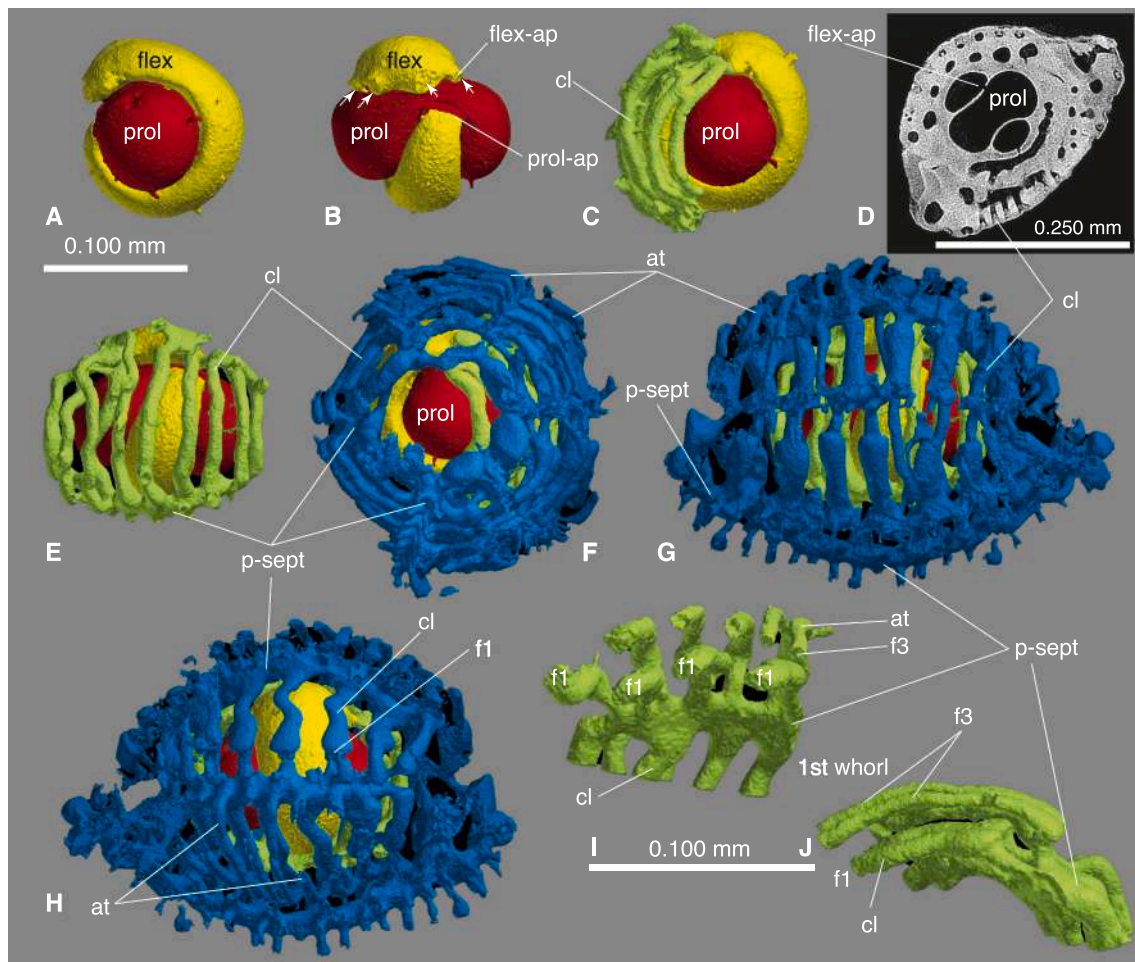
## 2. Material and methods

This study was carried out on fossil and present-day *Borelis* specimens from Minatogawa Formation and from modern coral-reef related settings in the Sekisei Lagoon (Sekisei-sho). The studied fossil material, from the Minatogawa (Horikawa) quarry at Tamagusuku, Nanjo City, in the southern part of Okinawa Island (Fujita et al., 2018), consists of specimens within hard-cemented limestone. This well-sorted detrital and coral limestone representing the Minatogawa Formation (Chibanian), part of the younger limestone in the central Ryukyu Islands, deposited on a ramp with patch reefs and/or fringing reefs (Fujita et al., 2018).

The present-day *Borelis* was collected from Sekisei Lagoon (southern Ryukyu Islands) and Sesoko Jima (Okinawa, central Ryukyu islands). The Sekisei Lagoon specimens occur in the sediment samples collected by Hatta and Ujiie (1992; see also Ujiie and Hatta, 1995 and Ujiie and Ono, 1995). This lagoon, about 30 km wide (East–West) and 15 km long (North–South), lies between the southwestern coast of Ishigaki Jima and the eastern coast of Iriomote Jima (central Yaeyama Islands, Ryukyu Islands; 24°15'47.9622"N, 123°57'57.3048"E). The lagoon provides various ecosystem services (i.e., conservation and management areas), including a national park, a program to exterminate crown of thorns starfish (*Acanthaster planci*) run by a non-profit organization, regulation of fisheries gear by Okinawa Prefecture, and temporary marine reserves for spawning aggregations of fisheries species (Sato et al., 2020). The lagoon, surrounded by a semi-barrier reef, is characterized by sandy substrates and many patch reefs at a maximum depth of c. 20 m (Ujiie and Hatta, 1995; Ujiie and Ono, 1995). The outer slopes of the northern and southern semi-barrier reefs are rocky stretches and reach a water depth of 25 m, then fine to very fine sandy substrates spread to deeper-water depths (Okamoto et al., 2005; Sato et al., 2020). Surface water temperature has an annual mean of 26 °C (Japan Oceanographic Data Center; <http://www.jodc.go.jp/>). The studied specimens have been collected from two medium-sand samples, at 19 (sample 46) and 44 (sample 57) m water depth (sample numbers after Hatta and Ujiie, 1992; see also Ujiie and Ono, 1995).

The Sesoko specimens occur in the bioclastic gravelly sandy sediment samples dredged at around 60 m water depth off north of Sesoko Jima (24°40'21.5"N 127°50'48.1"E), a small island situated to the west of Motobu Peninsula (Okinawa, central Ryukyu Islands). Sesoko Jima, surrounded by a fringing reef, is separated from Motobu Peninsula by a 800 m-narrow channel, 10 m deep. Marine geomorphology of Sesoko Jima is described in Hohenegger et al. (1999).

The studied fossil specimens occur in thin sections housed in the Department of Physics and Earth Sciences, University of the Ryukyus, Nishihara, Okinawa (Japan). The studied isolated specimens, picked out from the Hatta and Ujiie (1992) samples, housed in the Department of



**Fig. 1.** *Alveolinella quoyi* (d'Orbigny, 1826); megalospheric specimen (A-form); Hatta and Ujiie (1992, pl. 15, fig. 1, sample 57) collection, National Museum of Nature and Science, Tsukuba (Ibaraki, Japan); Sekisei Lagoon, southern Ryukyu Islands; Recent. Micro-computed tomographic scanning 3-D rendered models with shell removed (rendering by S.K.).

A–H. Sub-ellipsoidal proloculus (prol; prol-ap, proloculus aperture) enveloped by the flexostyle (flex) with multiple apertures (flex-ap). Chamberlets (cl) are connected by the preseptal passage (p-sept). D. Axial section.

I–J. Details of the chamber in the first whorl with one layer of chamberlets (f1, foramina in the basal layer of chamberlets) and one layer of attics (at; f3, supplementary foramina in the attic).

Physics and Earth Sciences, University of the Ryukyus (Okinawa), are stored in the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University (Sendai), labelled as IGPS Coll. Cat. nos. 11,257–112,766. The single specimen illustrated by Hatta and Ujiie (1992, pl. 15, fig. 1) is stored in the National Museum of Nature and Science, Tsukuba (Ibaraki, Japan), labelled as MPC-43003. The specimens were micro-computed tomographic scanned in the Tohoku University Museum, Sendai. Imaging analyses collected at 100 $\times$ , 200 $\times$ , 400 $\times$  and 1.000 $\times$  by scanning electron microscopy (SEM), done at the Institute of Geology and Paleontology (Tohoku University), were performed with a Keyence VE-8800 SEM at the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, with an accelerating voltage of 10 kV. 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 methods performed on LBF have been described by Kellner et al. (2019) and Macher et al. (2021). The micro-computed tomographic system ScanXmate-D160TSS105/11000 (Comscantecno Co. Ltd., Kanagawa, Japan) was used. This system consists of a Hamamatsu L10711–02 X-ray microfoc tube with a Hamamatsu E9014–01 LaB6 filament. The source voltage used was 80 and 90 kV, and current was 80 and 150  $\mu$ A. Rotation step range was 0.18 $^\circ$ , with

an exposure time of 1.5 s. The reconstructions were performed by ConeCTexpress (White Rabbit Corp., Tokyo, Japan), and direction sizes of a voxel were 0.658  $\mu$ m and 0.801  $\mu$ m.

Architectural and morphological terms are those used by Smout and Eames (1958), Hottinger (1960, 2006), Hottinger et al. (1993) and Bassi et al. (2022b). Species taxonomic and biostratigraphical assessments have been provided by Bassi et al. (2021a). References to published species and their records include only those which have described and illustrated architectural diagnostic features.

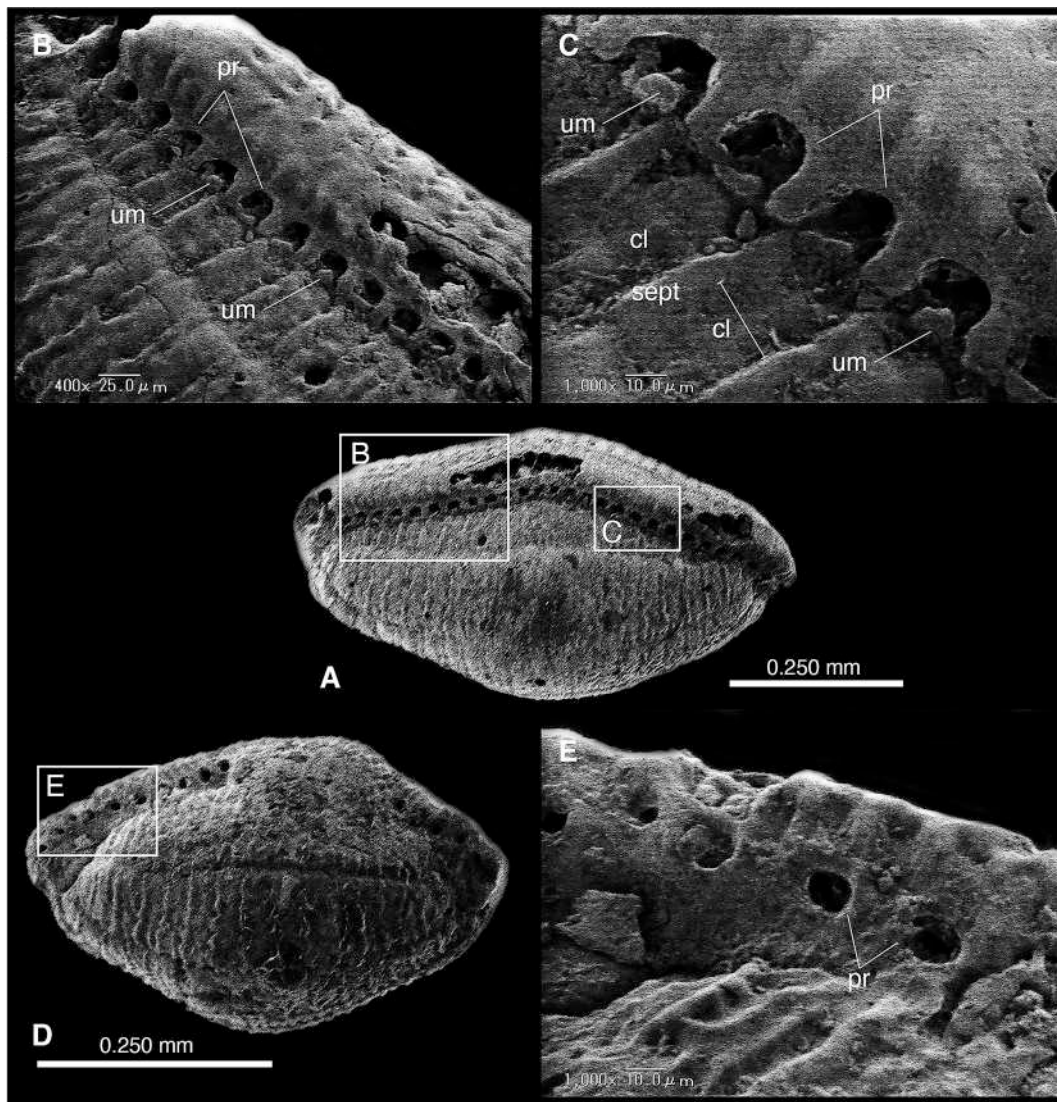
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### 3. Results

#### 3.1. Systematic description

Superfamily Alveolinoidea Ehrenberg, 1839.  
Family Borelidae Schmarda, 1871.





**Fig. 2.** SEM photos of *Borelis matsudai* sp. nov.; megalospheric specimens (A-forms), paratypes; Sekisei Lagoon, southern Ryukyu Islands; Recent. Institute of Geology and Paleontology, Graduate School of Science, Tohoku University (Sendai, Japan).

The apertural face is characterized by a single row of rimmed apertures (pr, peristomal rim) with upright masks (um). Septula (sept), dividing the chamberlets (cl), are aligned from chamber to chamber.

Subfamily Borelinae [Schmarda, 1871](#).

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 (with foramina f1–f2) and one layer of attics (with foramina f3) per chamberlet in later whorls.

**Remarks:** The *Alveolinella* shell structure is characterized by superimposed layers of chamberlets whose foramina have been suitably/conveniently named according to their succession. The chamberlets in the basal layer have foramina named f1, those of the second layer f2, and those corresponding to the attics f3 ([Bassi et al., 2022a](#)).

*Alveolinella quoyi* (d'Orbigny, 1826).

(see [Bassi et al., 2022a](#) for the synonymy list)

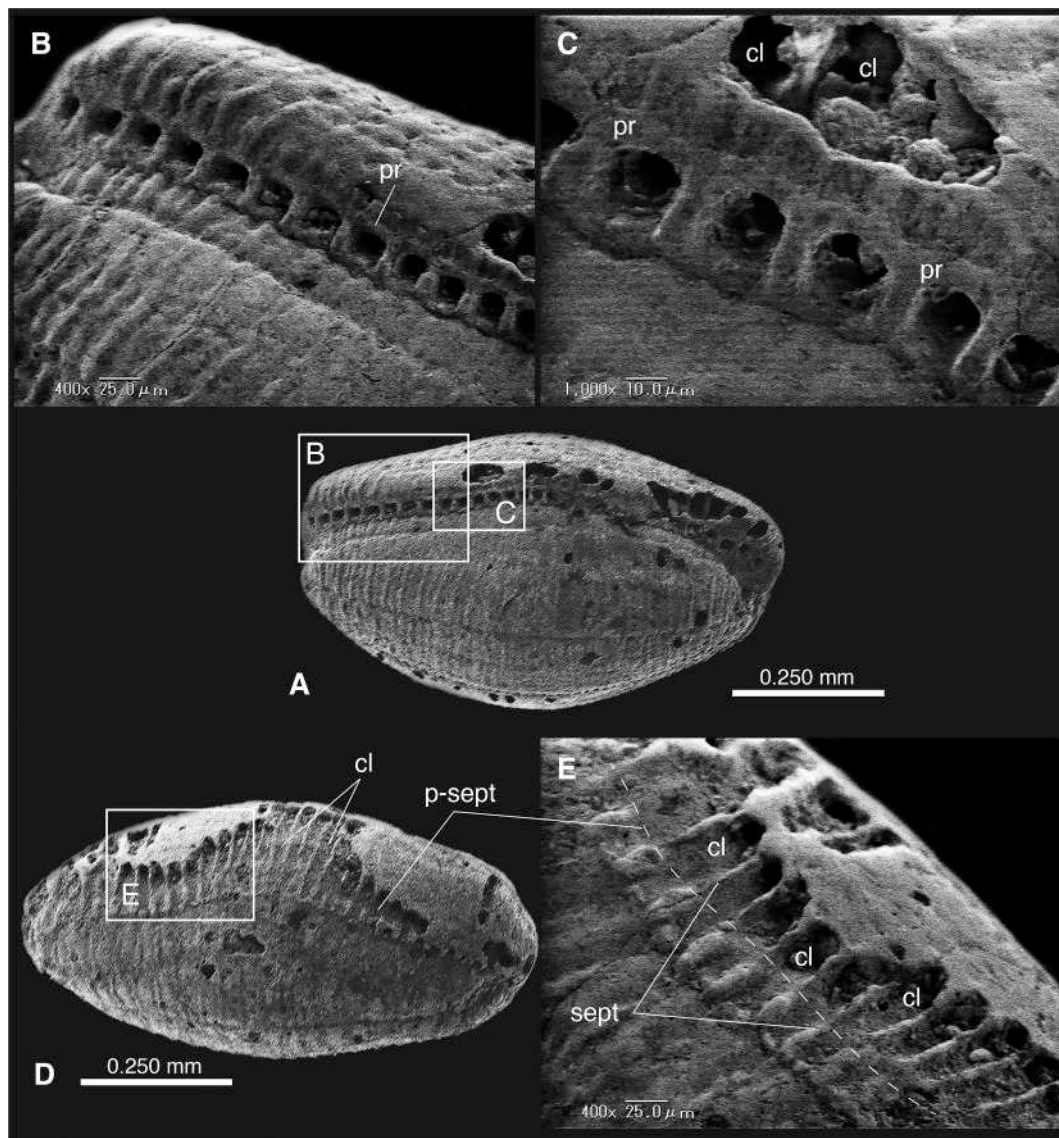
v. 1992 *Borelis pulchra* (d'Orbigny); [Hatta and Ujiie, pl. 15, fig. 1](#).

**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 (index of elongation > 5), the

first whorl with one basal layer of main chamberlets (with apertures f1) and one layer of attic per chamberlet (with apertures 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 sub-ellipsoidal (up to c. 80 µm in diameter and 160 µm in length) with its longest axis in the direction of the coiling axis and constrained at the position of the flexostyle. The flexostyle envelopes the proloculus for 330° in the Recent specimens, 300°–320° in the Upper Miocene specimens, and ends in multiple apertures.

**Studied material:** The single analyzed specimen, illustrated by [Hatta and Ujiie \(1992, pl. 15, fig. 1, sample 57\)](#), is sub-spheroidal (0.35 mm long and 0.25 mm in diameter) in shape with aligned septula. The sub-ellipsoidal proloculus is 70 µm in diameter and 120 µm in length with its longest axis in the direction of the coiling axis and constrained at the position of the flexostyle (about 70 µm width and 30 µm high; [Fig. 1A–D](#)). Flexostyle with multiple apertures ([Fig. 1B](#)). Y-shaped septula are absent. Shell consists of 3 whorls. The index of elongation is 1.35. The first whorl shows one basal layer of main chamberlets (f1) and one layer of attic per chamberlet (f3). In the second and third whorls two layers of main chamberlets (f1, f2) are overlain by one layer of attic (f3);



**Fig. 3.** SEM photos of *Borelis matsudai* sp. nov.; megalospheric specimens (A-forms), paratypes; Sekisei Lagoon, southern Ryukyu Islands; Recent. Institute of Geology and Paleontology, Graduate School of Science, Tohoku University (Sendai, Japan).

In these specimens the rimmed apertures (pr, peristomal rim), arranged in a single row, do not bear upright masks (um) which were resorbed in subsequent growth stages (D). The chamberlets (cl) are connected to each other by the pre-septal passage (p-sept) occurring beneath the septal wall (sept, septulum).

Fig. 11–J) per chamberlet (Fig. 1F–H).

**Remarks:** The occurrence of 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 indicates that the studied specimen belongs to *Alveolinella* (Fig. 1). The analyzed specimen represents a juvenile megalospheric A-form, which is architecturally concordant with *Alveolinella quoyi* (Hottinger, 1974, pl. 1; Parker, 2009, fig. 59c; Bassi et al., 2022a, table 5).

Genus *Borelis* de Montfort, 1808.

**Type species:** *Borelis melonoides* de Montfort, 1808 = *Nautilus melo* Fichtel and Moll, 1798, *varietas* b.

**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 pre-septal passage is present; apertures in a single row.

*Borelis matsudai* Bassi and Iryu sp. nov.

**LSID:** urn:lsid:zoobank.org:act:8B0C8C13-F73C-41D7-B06A-4DE8 AEA9210E.

? 1948 *Borelis pygmaeus schlumbergeri* Reichel; Hanzawa, p. 86.

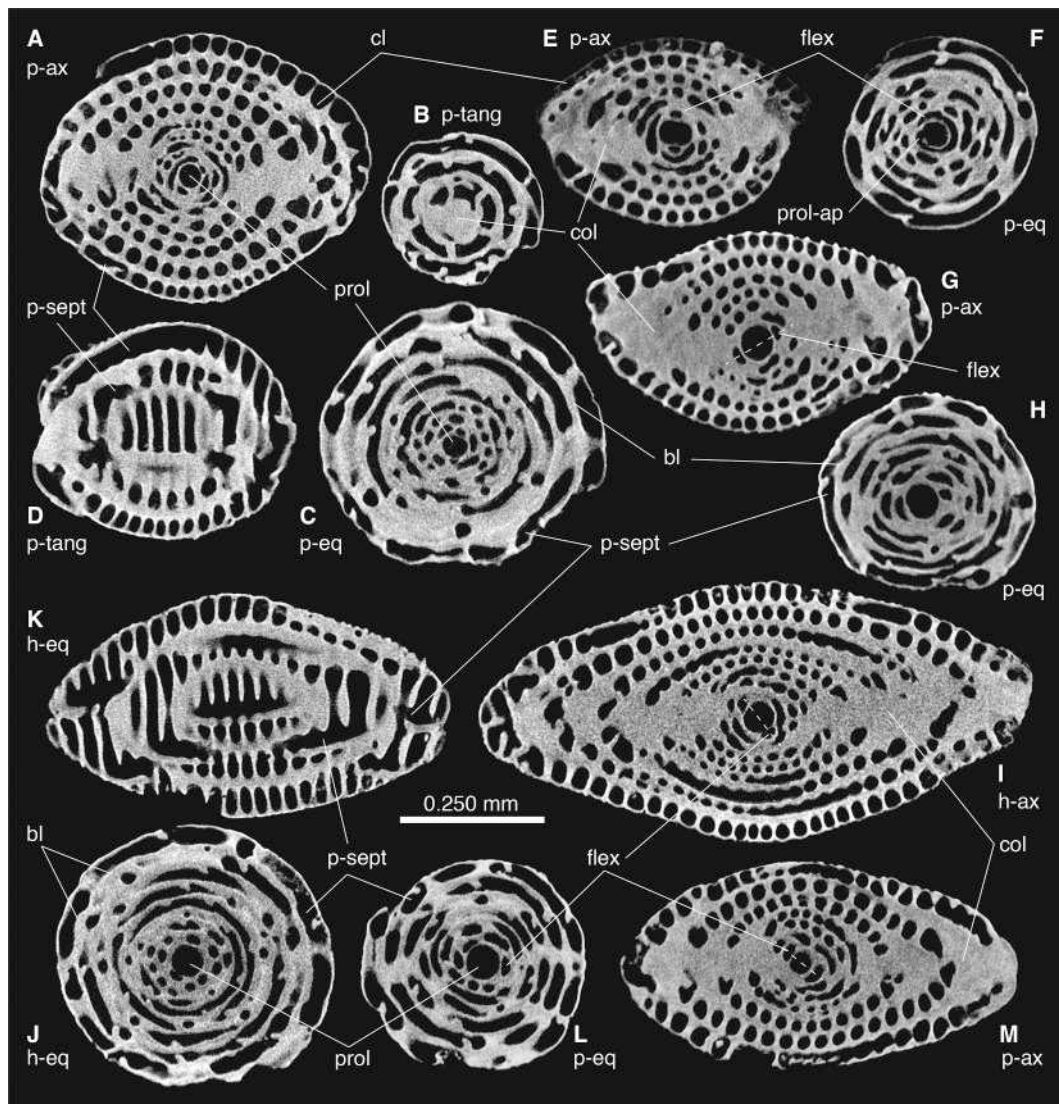
? 1978 *Borelis pulchra* (d'Orbigny); Cheng and Zheng, pl. 18, fig. 1a–c.

**Derivation of name:** The specific name honours Professor Shinya Matsuda (University of the Ryukyus, Okinawa Prefecture, Japan) for his outstanding contributions to marine geology and palaeontology of the Ryukyu Islands, especially taxonomical and ecological studies on non-geniculate coralline algae and sedimentological research on modern and Pleistocene reef deposits. According to ICZN (1999) Art. 31.1.2, because the personal name is that of a man, an -i was added to the stem of that name (i. e., Matsuda).

**Holotype:** The holotype is the specimen illustrated in Figs. 4I–J, 5, stored at the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Sendai, Japan, with register number IGPS Coll. Cat. No. 112751. The holotype is from sample 46, collected by Hatta and Ujjié (1992).

**Dimensions of the holotype:** Megalospheric sub-ellipsoidal shell, 0.450 mm in diameter and 0.950 mm long (ICZN (1999), Recommendation 73C.1).





**Fig. 4.** *Borelis matsudai* sp. nov.; Sekisei Lagoon, southern Ryukyu Islands; Recent. Institute of Geology and Paleontology, Graduate School of Science, Tohoku University (Sendai, Japan). A–H, L–M, paratypes; I–J, holotype. Micro-computed tomography of megalospheric specimens (A-forms) showing the preseptal passages (p-sept) and the large flexostyle (flex). Note the thickening of the basal layer in the polar regions making up the axial columella. Abbreviations: bl, basal layer; cl, chamberlet; col., columella; h-ax, axial section of the holotype; h-eq, equatorial section of the holotype; h-tang, tangential section of the holotype; p-ax, axial section of the paratype; p-eq, equatorial section of the paratype; prol, proloculus; prol-ap, proloculus aperture.

**Paratypes:** The specimens illustrated in Figs. 2–4A–H, 4L–M (sample 46; Hatta and Ujiie, 1992); conserved at the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Sendai, Japan, with register number IGPS Coll. Cat. No. 112752–112770.

**Material:** Twenty-five specimens from the sample 46, collected at 19 m water depth at the Sekisei Lagoon (Hatta and Ujiie, 1992). Recent.

**Type locality:** 24°15'47.9622"N, 123°57'57.3048"E; Sekisei Lagoon between Ishigaki and Iriomote islands in the Ryukyu Islands, Japan (ICZN, 1999, Recommendation 73C.2). The specimens have been collected from sandy substrate at 19 m water depth (ICZN, 1999, Recommendation 73C.9).

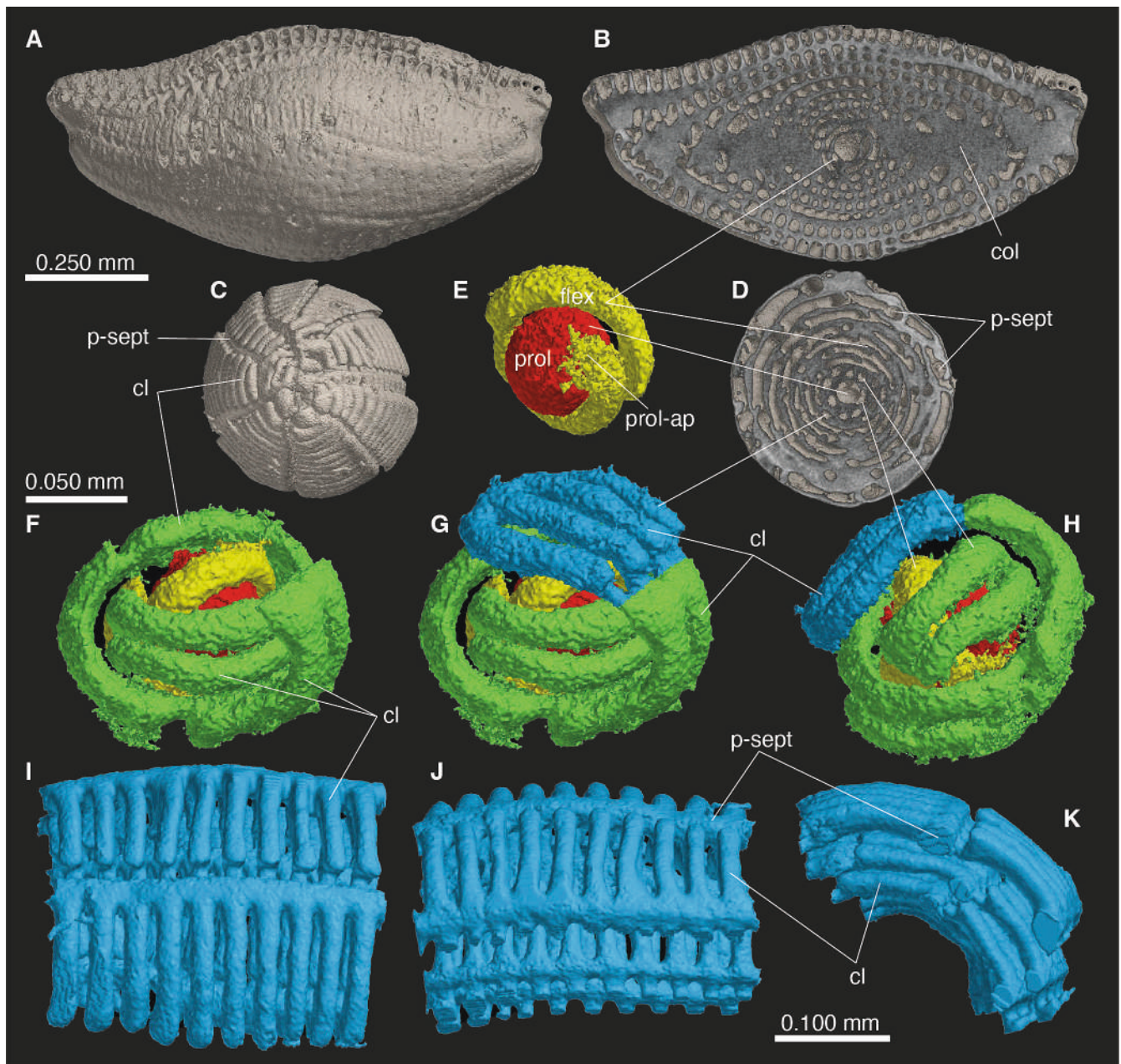
**Diagnosis:** *Borelis* with megalospheric sub-ellipsoidal shell, 0.350–0.450 mm in diameter and 0.450–0.950 mm long. Proloculus 40–60 µm in diameter with flexostyle. Index of elongation 1.2–2. Y-shaped septula absent.

**Description:** All specimens from the sample 46 of Hatta and Ujiie (1992) are megalospheric (A-forms). The sub-ellipsoidal A-forms are 0.330–0.480 mm in diameter and 0.450–0.960 mm long (Figs. 2–3). Sub-spheroidal proloculus is 40–60 µm in diameter enveloped by a

flexostyle 13–20 µm in diameter for c. 310° with a single aperture (Figs. 4F, 5). The first and second whorls are streptospiral (Fig. 5F–H). Only the preseptal passage is present with apertures of the chamberlets in a single row and aligned septula (Fig. 5I–K). The thin basal layer coating the bottom of the chambers of the previous whorl thickens at the polar regions producing an axial columella (Fig. 4). The chamberlets in the last whorl are 20–40 µm high. Shells consist of 6–8 whorls. Upright masks were found in the apertural face (Fig. 2A–C), resorbed in subsequent growth stages (Fig. 2D–E). No Y-shaped septula are present. Index of elongation ranges from 1.2 to 2. No B-forms were identified.

The fossil specimens, identified in the hard-cemented limestone of the Minatogawa Formation (Chibanian), occur as random sections in thin sections. Specimens, c. 0.380 mm in diameter and c. 0.560 mm in length, show only the preseptal passage with apertures of the chamberlets in a single row (Fig. 6). Index of elongation is c. 1.5. No Y-shaped septula are present.

**Remarks:** *Borelis matsudai* sp. nov. possesses all structural and architectural characters considered diagnostic of *Borelis* as delimited by Loeblich and Tappan (1987, p. 362) and Bassi et al. (2021a): (1) septula



**Fig. 5.** *Borelis matsudai* sp. nov.; holotype, megalospheric specimen (A-form); Sekisei Lagoon, southern Ryukyu Islands; Recent. Institute of Geology and Palaeontology, Graduate School of Science, Tohoku University (Sendai, Japan); IGPS Coll. Cat. No. 112751. Micro-computed tomographic scanning 3-D rendered models with shell removed (rendering by S.K.).

A–E. The sub-ellipsoidal megalospheric shell showing the large proloculus (prol; prol-ap, proloculus aperture) enveloped by the flexostyle (flex). Note the thick columella (col) in the axial region. F–H. The first and second whorls (green) are streptospiral. I–K. Chamberlets (cl) are aligned from chamber to chamber with apertures in a single row and only preseptal passage (p-sept) present. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

aligned from chamber to chamber, (2) only preseptal passage present, (3) apertures in a single row. The investigated *B. matsudai* sp. nov. specimens show upright masks on the apertural face as described for *B. schlumbergeri* (Hottinger et al., 1993; Bassi et al., 2022b).

The absence of Y-shaped septula in *Borelis matsudai* sp. nov. places the species into the group of *B. inflata* (only fossil), *B. pulchra* (fossil and Recent) and *B. pygmaea* (only fossil), all deriving from the middle–late Eocene *B. vonderschmitti* (Bassi and Loriga Broglio, 1999; Bassi et al., 2021a). Differences in the diameter of the megalosphere, the frequency of the Y-shaped septula, and the index of elongation were considered diagnostic of species by Hottinger (1974) and Bassi et al. (2021a; Fig. 7).

*Borelis matsudai* sp. nov. differs from *Borelis pulchra* in having a larger proloculus (40–60  $\mu\text{m}$  in diameter versus 25–30  $\mu\text{m}$ ; see table 1 in Bassi et al., 2021a) and a higher index of elongation. *Borelis inflata* (Adams, 1965) has a proloculus of 30–70  $\mu\text{m}$  in diameter (Bassi et al., 2021a), comparable to that of *B. matsudai* sp. nov. However, this latter species differs in having a basal layer with a considerable axial thickening producing a columella (Fig. 4A, G, M). The taxonomic status of *Borelis matsudai* sp. nov. as a distinct species is, therefore, confirmed by the combination of the diameter of its megalosphere and its index of elongation, which are different from the other *Borelis* species (Bassi et al., 2021a, table 1; Fig. 7).



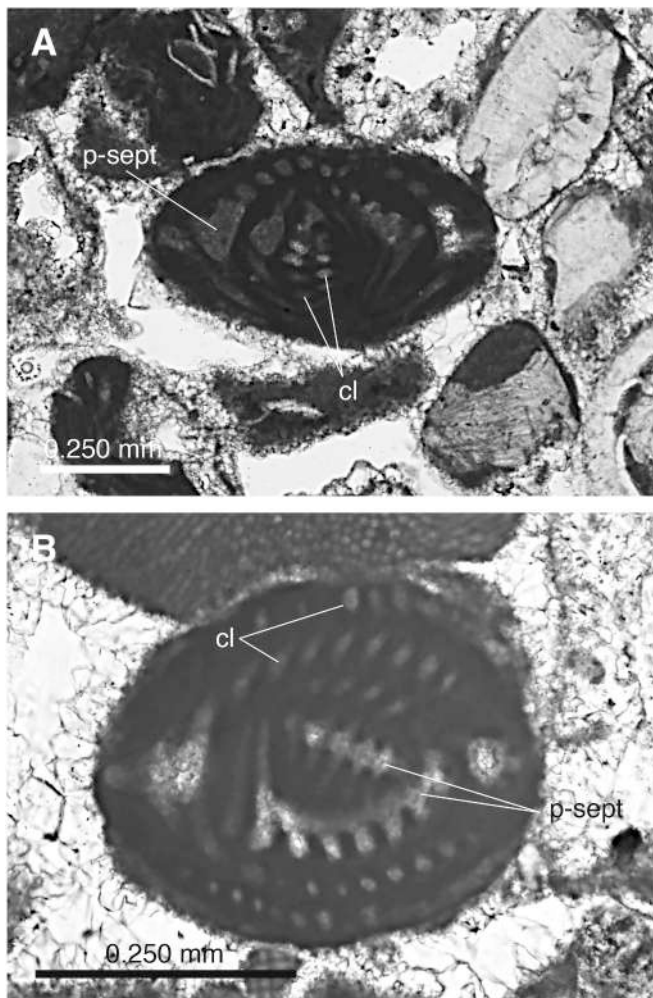


Fig. 6. *Borelis matsudai* sp. nov.; Minatogawa (Horikawa), Nanjo City, central Ryukyu Islands; Minatogawa Formation, Chibanian. Department of Physics and Earth Sciences, University of the Ryukyus, Nishihara, Okinawa (Japan). A, tangential section nearly parallel to the equatorial plane showing the pre-septal passage. B, tangential-oblique section showing the aligned septula and the pre-septal passage; no Y-shaped septula are present.

From present-day material Hanzawa (1948) reported *Borelis pygmaeus schlumbergeri* Reichel from south of Tarara-jima (southern Ryukyu Islands) at 82 m water depth, without illustrating it. However, this species name is a younger synonym of *Borelis pygmaea* Hanzawa, 1930 whose stratigraphical range is Priabonian–Burdigalian (Bassi et al., 2021a). Hanzawa's (1948) record needs further confirmation, since no illustration was published. Matsumaru (1977, table 1-2) recorded *Borelis* (referred to as *Borelis pulchrus*) from the Middle Pleistocene of Tokunoshima and Yoron (Ryukyu Islands), but provided no further comment and illustration. A drawn single specimen ascribed to *Borelis* sp. from sandy beach of Tokara Islands (northern Ryukyu Islands) does not show the apertural face (Kuwano, 1956, pl. 29, fig. 1) making this record unreliable. Cheng and Zheng (1978) described and illustrated a possibly single specimen of *Borelis pulchra* (d'Orbigny) from the China Sea (pl. 18, fig. 1a–c). Although the illustrated sub-spheroidal specimen is about 0.450 mm in diameter, with a size comparable to that of *Borelis matsudai* sp. nov., their drawings do not show the apertural face with layers of chamberlets and related foramina. Thus, these specimens cannot be ascribed reliably to any species of *Borelis*.

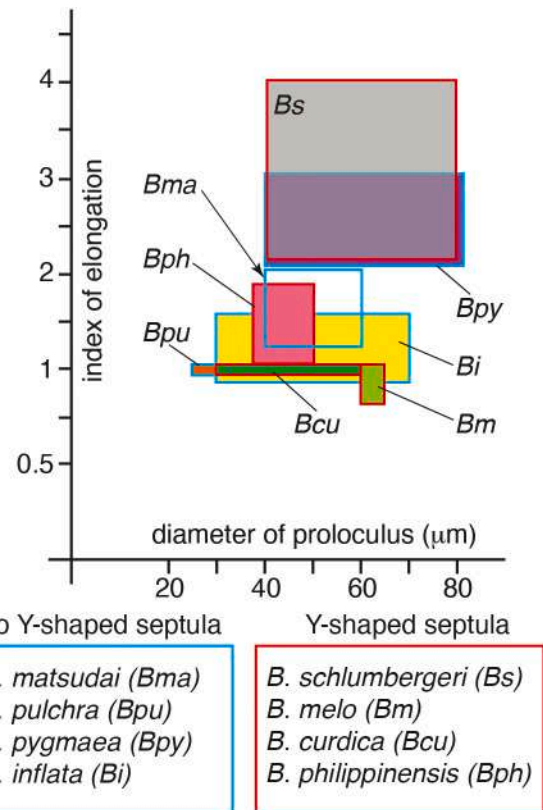


Fig. 7. Plot of proloculus diameter and index of elongation for the Oligocene–Miocene *Borelis* species. Numerical data from Bassi et al. (2021a). *Borelis matsudai* sp. nov. belongs to the group of *Borelis* species without Y-shaped septula.

#### 4. Discussion: palaeobiogeographical constraints and patterns

In this study, we (1) introduced a new species of pLBF found in the southern-central Ryukyu Islands, (2) reviewed the available records of fossil and modern *Borelis pulchra* in the wIPWP areas, and (3) assessed the phylogenetic relationship of *Borelis matsudai* sp. nov. with *Borelis pulchra*. Stratigraphically as well as oceanographically assessed dispersal routes revealed that *Borelis matsudai* sp. nov. represents a population adapted to a new zone (i.e., southern and central Ryukyu Islands), in a marginal part in significant contact with its ancestor (i.e., *B. pulchra* in the Philippines and Indonesia). The adaptive zone of these islands became contemporaneous with the *A. quoyi* zone widespread up to Okinawa Jima (central Ryukyu Islands).

##### 4.1. Late Eocene–Middle Miocene dispersal pattern

The first appearance datum of *Borelis pulchra* is in the Priabonian (late Eocene) of the Philippines (referred to as *B. globosa* in Matsumaru, 2011; Bassi et al., 2021a). The middle Eocene record of *Borelis* (referred to as *Borelis* sp.; Cotton et al., 2019, fig. 5.5), offshore western India, needs further confirmation, since the single published illustration does not show diagnostic characters for the taxonomic identification.

During the Oligocene *Borelis pulchra* occurs in the Rupelian of the Ogasawara Islands (Matsumaru, 2017) and in the Chattian of Eniwetok (Cole, 1954, 1957; Table 1, Fig. 8). The Lower Miocene records are restricted to the Philippines (Matsumaru, 1974), the Ogasawara Islands (Matsumaru, 1996, 2017), Eniwetok and Bikini (Cole, 1954, 1957), and Saipan (Hanzawa, 1957; Table 1). These occurrences, often associated with the alveolinoid *Flosculinella* species and *Alveolinella borneensis* (e.g., Lunt and Allan, 2004; Renema, 2007; Bassi et al., 2022a), are in the Coral Triangle area, the Early Miocene centre of marine biodiversity (e.



**Table 1**  
Stratigraphical and geographical distribution of *Borelis pulchra* (d'Orbigny, 1839).

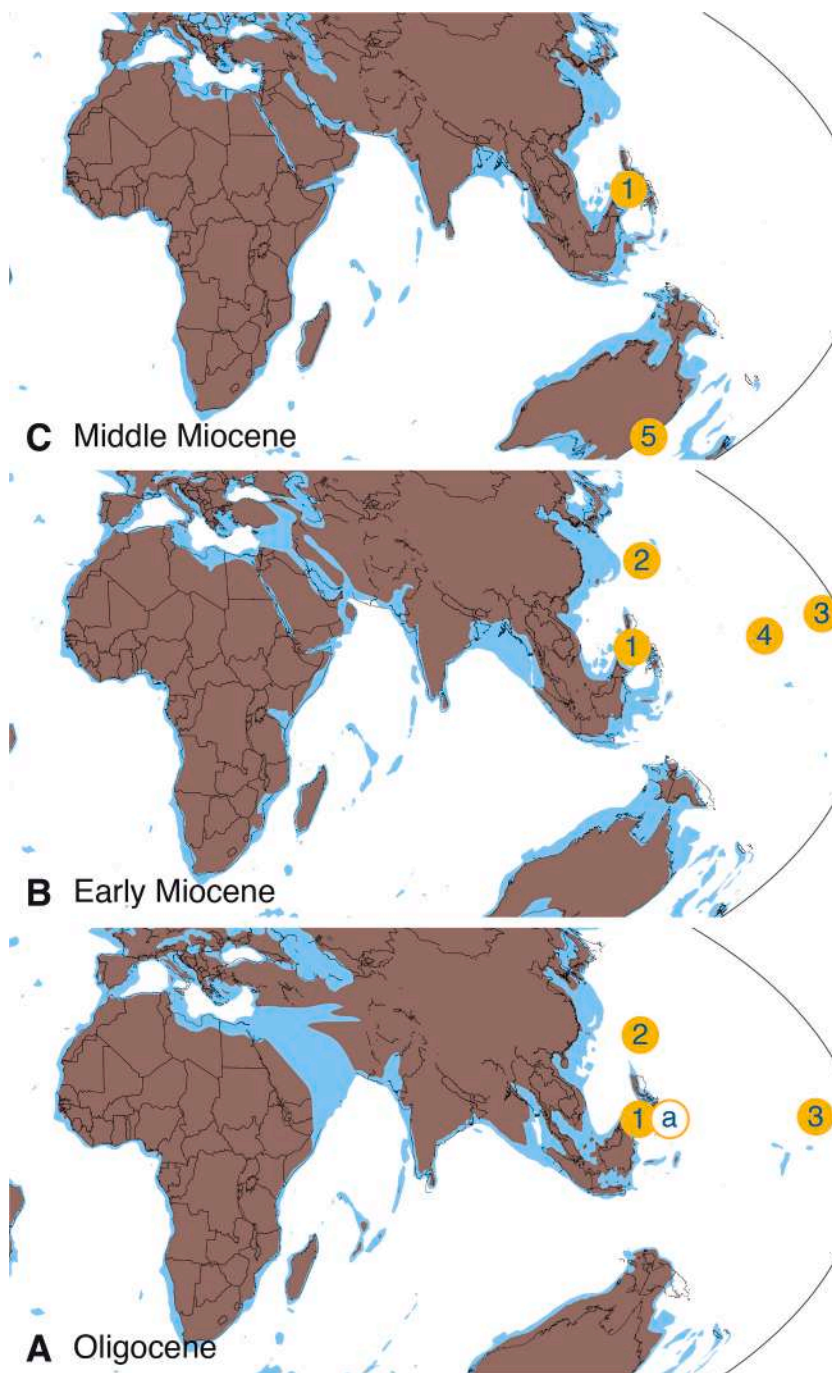
References	Referred to as	Age	Locality	Illustrations
Matsumaru (2011)	<i>B. globosa</i>	Priabonian	Philippines	no illustration
Cole (1957)	<i>B. primitiva</i>	late Oligocene	Eniwetok	pl. 23, fig. 3a–c
Matsumaru (1974)	<i>B. globosa</i>	Rupelian	Mindanao, Philippines	pl. 19, figs. 2–4, 7.
Matsumaru (2017)	<i>B. globosa</i>	Rupelian–Early Miocene	Ogasawara Islands	pl. 41, figs. 6–9
	<i>B. melo</i>			pl. 41, fig. 10
Matsumaru (1996)	<i>B. boninensis</i>	Early Miocene?	Ogasawara Islands	pl. 83, figs. 1–2, pl. 85, fig. 5
Cole (1957)	<i>B. primitivus</i>	Chattian–Early Miocene	Eniwetok	pl. 240, figs. 3–10
Cole (1954)	<i>B. schlumbergeri</i>	Miocene	Bikini Atoll	pl. 209, fig. 10–18
Cole (1969)	<i>B. melo</i>	Early Miocene	Hawaii	pl. 4, figs. 8–23; pl. 5, figs. 1–3, 6–8
Hanzawa (1957)	<i>B. parvulus</i>	Aquitanian–early Burdigalian	Saipan	pl. 23, fig. 3a–c
Ma et al. (2018)	<i>B. pygmaeus</i>	Early Miocene	South China Sea	
Matsumaru (1974)	<i>B. globosa</i>	Aquitanian–? Serravallian	Mindanao	pl. 19, figs. 2–4, 7
BouDagher-Fadel (2018)	<i>B. melo</i>	Serravallian	Barden, Australia	pl. 7.1, fig. 18
Todd and Post (1954)	<i>B. pulchra</i>	Pliocene–Pleistocene	Bikini Atoll	pl. 10, fig. 13
Matsumaru (2011)	<i>B. melo</i>	Pliocene–Recent	Philippines	no illustration
BouDagher-Fadel (2018)	<i>B. pulchra</i>	Holocene	Mauritius	pl. 7.1, fig. 17
Chapman (1901)	<i>Alveolina boscii</i>	Recent	Funafuti Atoll	no illustration
Chapman (1902)	<i>Alveolina boscii</i>	Recent	Funafuti Atoll	no illustration
Heron-Allen and Earland (1914)	<i>Alveolina boscii</i>	Recent	Kerimba Archipelago	no illustration
Cushman (1917)	<i>Alveolina melo</i>	Recent	Marshall Islands	no illustration
Cushman (1930)	<i>B. pulchra</i>	Recent	Bahamas, Cuba, Jamaica	pl. 15, figs. 9–10
Hofker (1952)	<i>Nealveolina pulchra</i>	Recent	West Indies	figs. 58–60
Cushman et al. (1954)	<i>Nealveolina pulchra</i>	Recent	Marshall Islands	pl. 87, fig. 8
Todd (1957)	<i>B. pulchra</i>	Recent	Saipan	no illustration
Graham and Militante (1959)	<i>B. pulchra</i>	Recent	Philippines	pl. 10, fig. 13
Todd (1961)	<i>B. pulchrus</i>	Recent	Onotoa Atoll, Gilbert Islands	no illustration
Hofker (1964)	<i>Nealveolina pulchra</i>	Recent	Netherland Antilles, West Indian Islands	fig. 161
Betjeman (1969)	<i>Alveolinella boscii</i>	Recent	Exmouth	no illustration
Cheng and Zheng (1978)	<i>B. pulchra</i>	Recent	Xisha Islands, China	pl. 18, fig. 1a–c
Li and Wang (1985)	<i>B. pulchra</i>	Recent	China Sea	no illustration
Hatta and Ujiie (1992)	<i>B. pulchra</i>	Recent	Ryukyu Islands	pl. 15, fig. 1
Whittaker and Hodgkinson (1995)	<i>B. pulchrus</i>	Recent	Pitcairn Islands	no illustration
Javaux and Scott (2003)	<i>B. pulchra</i>	Recent	Bermuda	fig. 2 (10–11)
Langer and Lipps (2003)	<i>B. pulchra</i>	Recent	Madang, Papua New Guinea	no illustration
Liu (2008)	<i>B. pulchra</i>	Recent	China Sea	no illustration
Zheng and Fu (2008)	<i>B. pulchra</i>	Recent	China Sea	no illustration
Fajemila and Langer (2017)	<i>B. schlumbergeri</i>	Recent	Gulf of Guinea	figs. 7 (34)
Thissen and Langer (2017)	<i>B. schlumbergeri</i>	Recent	Zanzibar, Tanzania	figs. 22–23
Förderer et al. (2018)	<i>B. pulchra</i>	Recent	Carolines, Gilbert Islands, Irian Jaya, Jakarta, Madang, Maldives, Marianas, Saipan, Marshall Islands, New Caledonia, Raja Ampat, Solomon Islands, South China Sea, Western Australia, Ningaloo Reef	geographic list
Förderer and Langer (2018)	<i>B. pulchra</i>	Recent	Irian Jaya, Indonesia	pl. 31, figs. 22–23

g., Renema et al., 2008; Reuter et al., 2019; Yasuhara et al., 2022).

During the late Oligocene–Early Miocene, the IAA area was characterized by several shallow-water carbonate platforms (de Bruyn et al., 2014) representing the largest suitable habitats for the LBF available in the region at that time (Fig. 9).

The Oligocene–Miocene pLBF (*Alveolinella*, *Austrotrillina*, *Borelis*, *Flosculinella*, *Praebullaalveolina*) have been identified in shallow-water carbonate deposits formed above the fair-weather wave base (e.g., Hottinger, 1983, 1997; Haig et al., 2020). In Indonesia and Australia shallow-water seagrass settings expanded from the late Oligocene

(Wilson and Rosen, 1998). The pLBF migrants (i.e., *Austrotrillina* species, *Flosculinella bontangensis*, *Alveolinella borneensis* and *A. ex. interc. borneensis* et *quoyi*) followed eastward the seagrass expansion (Bassi et al., 2021a, 2021b, 2022a). Only *Borelis pygmaea* Hanzawa, 1930 has been reported from the upper Oligocene of Western Australia (Chaproniere, 1984, pl. 14, figs. 16–17; Riera et al., 2019). The occurrences of *Borelis* in the Early–Middle Miocene of the Queensland Plateau (Betzler and Chaproniere, 1993, no illustration) and *Borelis pulchra* in the Middle Miocene of eastern Australia (BouDagher-Fadel, 2018; Table 1) may lend support to a southward species dispersal route from Indonesia



**Fig. 8.** Palaeogeographical locations of Oligocene–Middle Miocene *Borelis pulchra* (d’Orbigny, 1839) in the Central Indo-Pacific. After appearing in the Priabonian of the Philippines (a), *Borelis pulchra* occurs in the Oligocene of the IAA. The Lower Miocene records are in several shallow-water carbonate platforms of the IAA. The occurrences of *Borelis* in the Middle Miocene of eastern Australia (5) may lend support to a southward species dispersal from Indonesia.

Occurrences refer to citations in Table 1 in which detailed information on each record can be found. Palaeogeographical maps modified from Rögl (1998), Meulenkamp and Sissingh (2003) and Kocsis and Scotese (2021). Numbers refer to localities: a, Philippines (late Eocene, Priabonian; Matsumaru, 2011); 1, Philippines (Matsumaru, 1974, 2011); 2, Ogasawara Islands (Matsumaru, 2017); 3, Bikini, Eniwetok (Cole, 1954, 1957); 4, Saipan (Hanzawa, 1957); 5, Barden, Australia (Bou-Dagher-Fadel, 2018).

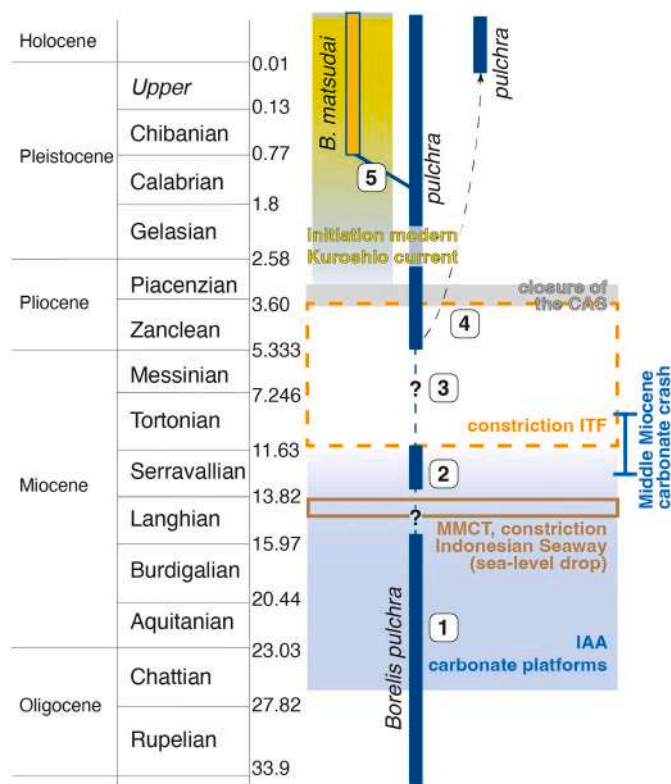
through the seagrass expanded habitats (O’Connell et al., 2012; Fig. 8).

In IAA shallow-water settings the *Borelis pulchra* record shows two gaps in the Langhian and in the Tortonian–Messinian (Bassi et al., 2021a; Fig. 9). This lack of information is probably due to taphonomic bias. In fact this species lives above the fair-weather wave base where the weak porcelaneous spheroidal tests are particularly affected by selective destruction (Yordanova and Hohenegger, 2007). Nonetheless, the shallow-water carbonate platforms well developed during the Early Miocene suffered the Middle Miocene carbonate crash (c. 13.2 and c. 8.7 Ma; Lübberts et al., 2019; Fig. 9), which brought about a significant reduction in shallow-water carbonate settings where alveolinoids (e.g., *Borelis*) thrived.

Following the Middle Miocene Climate Transition (MMCT) the western Pacific Ocean warmed and eastern tropical Indian Ocean

(Sosdian and Lear, 2020) became colder. This was likely caused by the constriction of the Indonesian Seaway (i.e., eustatic sea-level fall) and by the reduced connectivity between the Pacific and Indian Oceans following Antarctic glaciation (Sosdian and Lear, 2020). We hypothesise that the reduced connectivity and the cooler Indian waters hindered the possible westward migration of *B. pulchra* into the Indian Ocean (Figs. 9–10), where *Borelis pulchra* has not been recorded so far in Langhian and Tortonian deposits (Lunt and Allan, 2004; Bassi et al., 2021a, 2021b). Because of the lack of biogeographic connectivity between the Pacific and Indian Ocean due to the Indonesian Throughflow (ITF) restriction (Auer et al., 2019), from the Late Miocene to the Early Pliocene *B. pulchra* was constrained within the Central Indo-Pacific (Bassi et al., 2021a, 2021b).



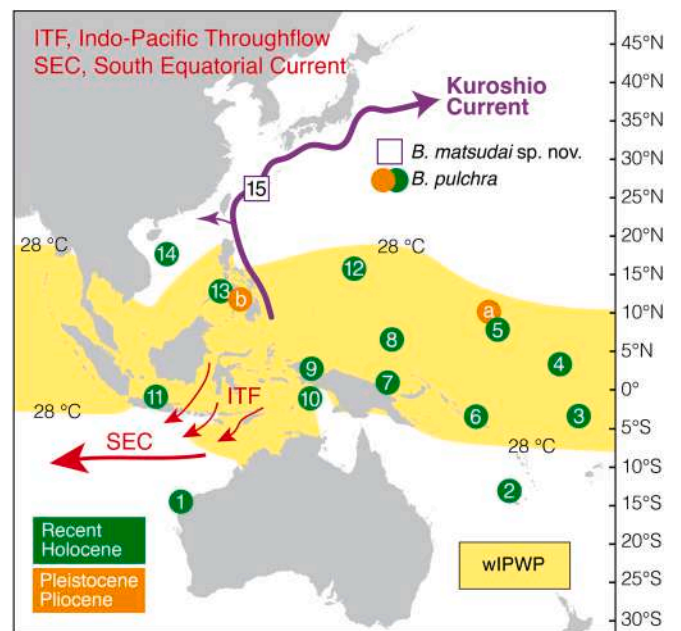


**Fig. 9.** Major events in the palaeobiogeographical history of the Oligocene *Borealis pulchra* and the first appearance datum of *Borealis matsudai* sp. nov. The long lasting species *Borealis pulchra* first occurred in the Rupelian of the Ogasawara Islands (Matsumaru, 2017) and in the Chattian of Eniwetok (Cole, 1954, 1957) (1). The two gaps in the Langhian and in the Tortonian–Messinian are probably related to taphonomic bias (2). However, the Middle Miocene significant reduction in shallow-water carbonate settings along with the constriction of the Indonesian Seaway at the MMCT (i.e., carbonate crash; Lübberts et al., 2019) could have affected the alveolinoid habitats. In the Late Miocene–Early Pliocene the ITF restriction cut off the biogeographic connectivity between the Pacific and the Indian Ocean, constraining the Pliocene–Pleistocene *Borealis pulchra* from Philippines to the Bikini atoll (3). Before the Pliocene closure of the Central America Seaway (CAS; O’Dea et al., 2016) *B. pulchra* migrants arrived in the eastern Pacific and Caribbean, where are still thriving (e.g., Javaux and Scott, 2003) (4). *Borealis matsudai* sp. nov. likely appeared in the central Ryukyu Islands from the Chibanian (5; i.e., Minatogawa Formation, Ryukyu Group). Following the Kuroshio intrusion this new population of its ancestor species represents likely an adaptation of parts of the Pliocene–Pleistocene wIPWP *Borealis pulchra* population to the new northern zone (i.e., southern Ryukyu Islands). See text for details. IAA, Indo-Australian Archipelago; MMCT, Middle Miocene Climatic Transition; ITF, Indonesian Throughflow. Time scale after Cohen et al. (2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

#### 4.2. Pliocene–Recent dispersal pattern

From the Late Miocene to the Early Pliocene a lack of biogeographic connectivity between the Pacific and Indian Ocean due to the Indonesian Throughflow (ITF) restriction (Gallagher et al., 2009; Auer et al., 2019) constrained the Pliocene–Pleistocene *Borealis pulchra* from the Philippines (Matsumaru, 2011) to the Bikini atoll (Todd and Post, 1954; Table 1, Fig. 10). During this time slice the absence of Indo-Pacific pLBF taxa in western Central Indo-Pacific confirms the role of the ITF restriction as a dispersal barrier (Gallagher et al., 2009; Bassi et al., 2021a). In addition, the slowing and cooling of the Leeuwin Current and associated upwelling along the west coast of Australia (Smith et al., 2020) were likely detrimental events for the pLBF dispersal.

During the Oligocene–Miocene *Borealis pulchra* did not migrate



**Fig. 10.** Geographical locations of Pliocene–Pleistocene and present-day *Borealis pulchra* (Orbigny, 1839) in the wIPWP. The Pliocene–Pleistocene *Borealis pulchra* occurs from the Bikini atoll (a) to the Philippines (b). At this time slice the ITF restriction acted as a dispersal barrier for the Indo-Pacific LBF taxa in the western Central Indo-Pacific. From the Late Pleistocene, via the unrestricted stronger ITF (compared to today) and the SEC, westward *B. pulchra* migrants arrived at Mauritius in the Holocene giving rise to the present-day eastern African occurrence. Following the modern Kuroshio current initiated by the latest Pliocene, a marginal part of a *Borealis pulchra* population (e.g., Indonesia, Philippines) gave rise to the studied *Borealis matsudai* sp. nov. recorded in the Sekisei Lagoon (15, southern Ryukyu Islands). Occurrences refer to citations in Table 1 in which detailed information on each record can be found. a, Bikini (Pliocene–Pleistocene; Todd and Post, 1954); b, Philippines (Pliocene–Recent; Matsumaru, 2011). 1, Exmouth, Ningaloo Reef (Betjeman, 1969; Förderer et al., 2018); 2, New Caledonia (Förderer et al., 2018); 3, Funafuti (Chapman, 1901, 1902); 4, Gilbert Islands (Todd, 1961; Förderer et al., 2018); 5, Marshall Islands (Cushman, 1917; Cushman et al., 1954; Förderer et al., 2018); 6, Solomon Islands (Förderer et al., 2018); 7, Madang (Langer and Lipps, 2003); 8, Carolines, Chuuk Lagoon (Förderer et al., 2018); 9, Raja Ampat (Förderer et al., 2018); 10, Irian Jaya (Förderer and Langer, 2018); 11, Jakarta (Förderer et al., 2018); 12, Marianas, Saipan (Todd, 1957; Förderer et al., 2018); 13, Philippines (Graham and Militante, 1959); 14, China Sea (Cheng and Zheng, 1978; Li and Wang, 1985; Zheng and Fu, 2008; Förderer et al., 2018); 15, southern Ryukyu Islands (this study, *Borealis matsudai* sp. nov.). The mean annual isotherm values are from Gallagher et al. (2009). Kuroshio Current system is after Cruz Salmeron et al. (2022).

eastward into Central America as demonstrated by the absence of record in the Caribbean realm (Robinson, 1995). Before the Pliocene closure of the Central America Seaway (O’Dea et al., 2016) *B. pulchra* migrants arrived in the eastern Pacific and Caribbean, where they are still thriving (e.g., Cushman, 1930; Hofker, 1952, 1964; Whittaker and Hodgkinson, 1995; Javaux and Scott, 2003; Fig. 10).

From the Late Pleistocene (Gallagher et al., 2009), following the unrestricted stronger ITF (compared to today) and the South Equatorial Current (Tomczak and Godfrey, 2003), connecting the wIPWP (c. 28 °C) with the Indian Ocean and the Western Australian shelf (Potemra, 2005), westward *B. pulchra* migrants arrived at Mauritius in the Holocene (BouDagher-Fadel, 2018) giving rise to the present-day Eastern African occurrence (Thissen and Langer, 2017; Förderer et al., 2018). During the early Holocene the westernmost part of the wIPWP became warmer than the threshold 28 °C suggesting its westward extension (Saraswat et al., 2019). This westward warmer dispersal route was likely followed by *B. pulchra* migrants.

With the intensification of the North Pacific Gyre and Northern Hemisphere ice sheet expansion the modern Kuroshio current initiated by the latest Pliocene, allowing the wIPWP marine species to migrate northward to the Ryukyu Islands (Gallagher et al., 2009). The Kuroshio migration route is supported by the first occurrence of the larger alveolinoid foraminifer *Alveolinella quoyi* in the Pleistocene (Matsumaru, 1977; Bassi et al., 2022a). Following the northward Kuroshio intrusion *Borelis matsudai* sp. nov. likely appeared in the southern Ryukyu Islands from the Chibanian (Fig. 9). *Borelis matsudai* sp. nov. was in fact identified in Chibanian Ryukyu sedimentary successions and no fossil record has been so far identified from older deposits from more southern areas (Fig. 9). The fossil record of *Borelis matsudai* sp. nov. in the upper part of the Ryukyu Group along with *A. quoyi* confirms the enhanced richness in shallow-water marine taxa from the Pliocene–Pleistocene (Yasuhara et al., 2016).

Laboratory studies performed on only *Alveolinella quoyi* showed that reduced shell growth and photosynthetic efficiency are in the water temperature threshold of below 26 °C and above 32 °C (Doo et al., 2014). *Borelis matsudai* sp. nov. thrives likely within this range of sea-surface temperature that was reached by the wIPWP first at c. 14 ka and then remained above 28 °C since c. 12 ka (Zhang et al., 2022).

Since poleward coral mass migrations have been tracked in this region and can occur relatively easily (Takeda et al., 2021), considering the near warming future we cannot rule out the northward migration of *Borelis matsudai* sp. nov. toward the northern Ryukyu Islands. The southern Ryukyu Islands (i.e., Sekisei Lagoon) represented, therefore, a biogeographical stepping stone relay station in northward migration of the shallow-water benthic organisms along the Kuroshio dispersal route (Fig. 9).

We speculated about the adaptation of parts of the wIPWP *Borelis pulchra* population to the new zone (i.e., southern and central Ryukyu Islands) where they could rapidly transform into a population with the preferred genotype composition (Hohenegger, 2014). This *Borelis matsudai* sp. nov. population represented a marginal part in significant contact with its ancestor (i.e., *B. pulchra*), which was widespread southward since the Miocene (e.g., Indonesia, Philippines; Bassi et al., 2021a). From the Chibanian in southern and central Ryukyu Islands the adaptive zone occurred over a time and developed contemporaneously with the first larger zone of the ancestor species (i.e., Indonesia, Philippines), representing an example of peripatric cladogenesis (e.g., Renema, 2015).

With global warming, since the Kuroshio current moved northward at c. 34.5 °N over the last century (Gallagher et al., 2015; Shen et al., 2022), we expect in future to record more common occurrences of *B. matsudai* sp. nov. northward. Nonetheless, this species may be much more widely and commonly distributed southward of its type locality than is currently known.

## 5. Concluding remarks

According to the larger proloculus and a higher index of elongation, which combined differ from the other *Borelis* species, *Borelis matsudai* sp. nov. is distinguished from *Borelis pulchra*. The absence of Y-shaped septula in the studied new species ascribes it to the group of *B. inflata* (only fossil), *B. pulchra* (fossil and Recent) and *B. pygmaea* (only fossil).

Our comprehensive literature survey showed that the Late Miocene–Early Pliocene ITF pattern constrained *Borelis pulchra* from the Philippines to the Bikini atoll. The Late Pliocene unrestricted stronger ITF and South Equatorial Current allowed *B. pulchra* migrants to reach Mauritius in the Holocene. The northward expansion of the modern Kuroshio current acted as dispersal route for *Borelis matsudai* sp. nov. which likely appeared in the southern and central Ryukyu Islands from the Chibanian (Middle Pleistocene).

## New species registration

The following information was supplied regarding the registration of the new larger porcelaneous foraminiferal species:

Publication LSI: urn:lsid:zoobank.org:pub:3D6F73F2-E5AA-4B42-BA4C-11178F7E4382.

## Declaration of Competing Interest

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

## Data availability

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

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