Research Paper

Biogeographical patterns of the porcelaneous larger foraminifer *Alveolinella quoyi* through the integration of fossil data ☆

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ABSTRACT

In the present-day Indo-Pacific coral-reef settings two genera of alveolinoidean porcelaneous larger benthic foraminifera (LBF) occur, namely *Alveolinella* and *Borelis*. *Alveolinella* is represented by a single species, *A. quoyi*, whose northernmost record is in Okinawa-jima (central Ryukyu Islands, Japan). Although the Indo-Pacific area, and especially the Coral Triangle, is a biodiversity hotspot since the Early Miocene, in-depth investigation on fossil representatives of present-day LBF is limited to a few taxa. To help bridge this knowledge gap, the palaeobiogeographical dynamics of *A. quoyi* is assessed. Analysis of data from the palaeontological literature shows that its first appearance datum is from the Tortonian (Late Miocene) of East Kalimantan and Papua New Guinea. In the Pliocene–Pleistocene the Indonesian Throughflow constrained the species within the Central Indo-Pacific. Finally, during the Late Pliocene the northward migrants arrived in the shallow-water carbonate settings of Okinawa-jima where the species is still thriving.

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1. Introduction

Porcelaneous larger benthic foraminifera (pLBF) are unicellular prokaryotic organisms with symbiotrophic life housing eukaryotic microalgae. As other LBF, they benefit from the intricate symbiotrophic interplay and build large carbonate tests. Larger benthic foraminifera are essential for the health of reef ecosystems where pLBF thrive since they contribute a significant proportion of the carbonate sediment across reef environments worldwide (Hohenegger, 2006; Langer, 2008). The tests of pLBF can be exposed to sunlight in the shallowest tropical and warm temperate seas because their test wall protects the foraminiferal cell and the symbionts from injurious UV radiation (Hallock, 2000; Hottinger, 2006; Hohenegger, 2011). From these areas, in present-day Indo-Pacific reefal and peri-reefal settings only *Alveolinella* H. Douvillé, 1907 (Early Miocene–Recent) and *Borelis* Montfort, 1808 (late Eocene–Recent) represent the alveolinoid pLBF (Bassi et al., 2021,

2022a). Four present-day species of *Alveolinella* and *Borelis* are currently recognized: *A. quoyi* (d'Orbigny, 1826), *B. pulchra* (d'Orbigny, 1839), *B. schlumbergeri* (Reichel, 1937), and *B. matsudai* Bassi and Iryu, 2023 (in Bassi et al., 2023).

Borelis is widespread from the Western (Red Sea) to the Central Indo-Pacific and the Caribbean Sea coasts, whereas *Alveolinella* occurs in the Central and Eastern Indo-Pacific area. The diversification of *Borelis* species started in the Oligocene of the Neo-Tethys (Bassi et al., 2021). *Alveolinella quoyi*'s ancestor is the extinct *A. borneensis* Tan, 1936, which appeared in the upper Burdigalian of the Central Indo-Pacific Ocean (CIP) area and disappeared in the Serravallian (Bassi et al., 2022a). *Alveolinella quoyi* occurs in the CIP with its northernmost record from the shallow-water settings in Okinawa-jima (Okinawa Island, central Ryukyu Islands, Japan; Hohenegger and Yordanova, 2001).

Despite an extensive body of literature documenting the biogeographical records of LBF (Langer and Hottinger, 2000; Förderer et al., 2018; Prazeres et al., 2020), our understanding of the palaeobiogeographical dynamics of fossil LBF is still in its infancy (Özcan and Less, 2009; Hottinger, 2014; Renema, 2015). Although the Indo-Pacific area has the best fossil record of extant

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taxa, in-depth investigations on palaeobiogeographical dynamics from fossil representatives of present-day LBF have been carried out only on a few taxa (Renema, 2007, 2008, 2015; Bassi et al., 2021, 2022a). Very few benthic organisms have a sufficiently detailed fossil record to permit the examination of these dynamics exhaustively. The lack of scientific research contrasts with the unique LBF biodiversity and ecological services (Hottinger, 1997; Girard et al., 2022; Yasuhara et al., 2022; Bassi et al., 2024) and calls attention for the understanding of key ecological interactions along the depth gradient, including shallow-water warming, eutrophication and substrate changes (Förderer et al., 2018; Kenigsberg et al., 2022). The highest alveolinoidean diversity has been so far identified in the Indo-Australian Archipelago (IAA; Langer and Hottinger, 2000; Bassi et al., 2021, 2022a). 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 (de Bruyn et al., 2014), for example in bivalves, gastropods, corals, and fishes (Hoeksema, 2007; Tittensor et al., 2010; Jablonski et al., 2013).

To help bridge this knowledge gap on palaeobiogeographical dynamics of present-day LBF, we collected literature data of the long known pLBF species of the CIP areas, *Alveolinella quoyi*. Besides assessing the fossil records of this species and its palaeobiogeographical distribution, we consider their extent over the past c. 10 myr and investigate when this species plausibly occurred in the Ryukyu Islands, its northernmost Indo-Pacific record, after appearing first in the western Indo-Pacific Warm Pool (wIPWP). We discuss these observations in the context of palaeogeographical changes, biogeographic connectivity and the importance of oceanic currents.

2. Diagnostic shell characters, stratigraphical distribution and environmental settings

Alveolinella and *Borelis* are members of the family Borelidae Schmarda, 1871 (superfamily Alveolinoidea Ehrenberg, 1839) which are characterized by floors separating superposed regular layers of chamberlets within a chamber (Hottinger, 1960; Fleury and Fourcade, 1990). Although randomly oriented crystal matrix typical of the porcelaneous foraminiferal shell constitutes the bulk of the test wall of these two taxa, their outermost test wall is characterized by aligned needle-shaped crystals oriented parallel to the test surface (Parker, 2017). *Alveolinella* and *Borelis* develop a strategy of constructing a glasshouse when living in high energy environments by elongating their chambers along the coiling axis yielding spindle-shaped fusiform tests (Hohenegger, 2009).

Alveolinella quoyi is characterized by a fusiform (prolate) shell with a ratio of the coiling axis length and the diameter of the equator ranging from 3.31 to 5.40 (Bassi et al., 2022a). This species differs from *A. borneensis* in having (*i*) the first whorl with one basal layer of main chamberlets (f1, f2, f3) with one layer of attic per chamberlet (Fig. 1), and (*ii*) in the later whorls up to three layers of main chamberlets with one layer of attic per chamberlet. Twisted/convoluted polar torsion is particularly evident in the larger specimens.

The stratigraphical distribution of the two species does not overlap, and specimens with intermediate characters range from the late Serravallian to the Tortonian (Bassi et al., 2022a). *Alveolinella quoyi* has been considered a fossil taxon in the Letter-classification for the late Tf–Th corresponding to the late Middle Miocene–Pleistocene (Lunt and Allan, 2004; Renema, 2007; Lunt and Luan, 2022). Neogene pLBF-bearing deposits, in which *Alveolinella* also occurs, have been interpreted as formed in shallow-water carbonate settings above the fair-weather wave base

(Buxton and Pedley, 1989; Hottinger, 1997; Beavington-Penney and Racey, 2004; Haig et al., 2020; Simmons, 2020).

In modern shallow-water coral-reef related settings, although found at 3–12 m water depth (Papua New Guinea; Lipps and Severin, 1984), *Alveolinella quoyi* shows its highest abundance at 20–40 m water depth, and occurs up to 65 m (Queensland: Scoffin and Tudhope, 1985; Sesoko-jima: Hohenegger, 1994, 2000). The strong dependence of *A. quoyi* on hard substrates has been found from coarse-grained sand, boulders, and coral gravels (Hohenegger, 1994; Hohenegger and Yordanova, 2001). This pLBF inhabits the shallower slope avoiding the enormous hydrodynamic forces near the reef edge (Hohenegger, 1994; Hohenegger et al., 1999). Individuals live in tiny grooves or holes and are normally fixed to the substrate by pseudopods extruding from one pole (Hohenegger et al., 1999; Bassi et al., 2022b). These settings with high current intensities lead to downslope (fore reef) transport of *A. quoyi*, whose tests are highly buoyant (Yordanova and Hohenegger, 2007). The large size and the low settling velocity tend to concentrate the tests during subsequent resuspension near the sediment-water interface (Severin and Lipps, 1989; Yordanova and Hohenegger, 2007). The tests of *A. quoyi* are, therefore, transported further than thick-lenticular amphisteginids (Yordanova and Hohenegger, 2002, 2007).

3. Material and methods

The Ryukyu Islands extend from Tanegashima Island to Taiwan, for a distance of c. 1200 km. Most of the islands are rimmed by fringing reefs characterized by the development of reef flats and reef slopes. The initiation (1.7–1.4 Ma) and development of coral reefs in the Ryukyu Islands are related to the formation of a back-arc basin, the Okinawa Trough, behind the Ryukyu Island Arc during the Miocene to Early Pleistocene (Letouzey and Kimura, 1985; Iryu et al., 2006; Watanabe et al., 2023). The island shelf around the Ryukyu Islands is mostly flat and slopes gently seaward. Its width varies from place to place, ranging from 0 to 25 km, with its shelf edge at 90 to 170 m water depth (Matsuda and Iryu, 2011). The studied fossil and present-day *Alveolinella quoyi* specimens were collected from the Ryukyu Islands. Fossil specimens were identified in the Calabrian–Chibanian (Pleistocene) Kourijima Formation of the Ryukyu Group cropping out on the Motobu Peninsula (Yamamoto et al., 2006; Iryu et al., 2006). The present-day specimens were collected from coral rubble on a forereef slope (15 m water depth) at Kushibaru, Aka-jima (Aka-jima Island; 26°12′46.7′′N, 127°16′28.8′′E).

The biostratigraphical assessment of *Alveolinella quoyi* shows that it ranges from the Late Miocene to the Recent in the Indo-Pacific areas. This assessment is based on 38 (15 fossil and 23 present-day) published reports ranging from monographs on LBF to marine sedimentology articles. A search of the available literature on the fossil and modern records and their locations was conducted using sedimentological, biostratigraphical, stratigraphical and systematic papers also using Scopus (Elsevier, accessed on 30 April 2024). Table 1 lists at which geographical and, if available, age the record was identified and, if available, the related illustrations. Diagnostic characters for genus and species are discussed in Bassi et al. (2022a), which helped to assess taxonomic identification and the reliability of the record independently of the reported names.

4. Results

The stratigraphical ranges of the two known species of *Alveolinella*, namely *A. borneensis* and *A. quoyi*, do not overlap each other (Fig. 2). The first appearance of *Alveolinella borneensis* is in the
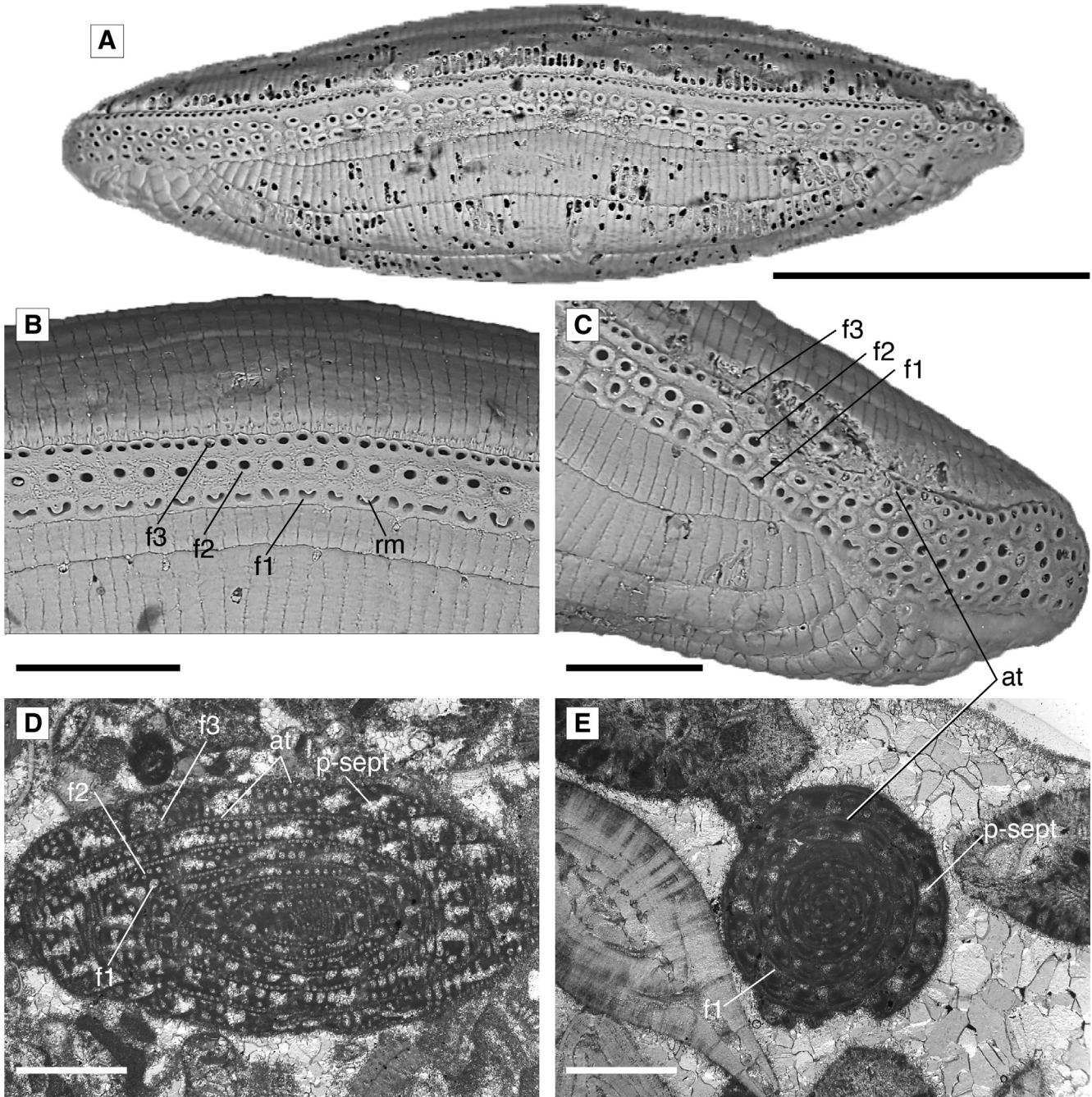
Fig. 1. *Alveolinella quoyi* (d'Orbigny, 1826). **A–C.** Recent material from Kushibaru, Aka-jima, Japan. Scanning Electron Microscope photos showing the entire shell (A) and details of the apertural face (B, C) illustrating the foramina in the basal and second layers of chamberlets (f1, f2) and in the attics (f3). **D, E.** Calabrian–Chibanian Kourijima Formation, Ryukyu Group (Yamamoto et al., 2006), Okinawa-jima. Oblique sub-axial section (D; Nakijin) and sub-equatorial section near the proloculus (E; Tobaru, Motobu peninsula) (Bassi et al., 2022a). Abbreviations: at, attic; f1, foramina in the basal layer of chamberlets; f2, foramina in the second layer of chamberlets; f3, supplementary foramina in the attic; p-sept, preseptal passage; rm, reverse masks; sept, septula. Scale bars: 500 μm (A, D, E), 200 μm (B, C).

Lower Miocene Coral Triangle area corresponding to the present-day CIP (Renema et al., 2008; Förderer et al., 2018; Reuter et al., 2019; Bassi et al., 2022a). During the late Oligocene–Early Miocene, the IAA area was characterized by a number of shallow-water carbonate platforms (de Bruyn et al., 2014) representing the largest suitable habitats for LBF in the region at that time (Yasuhara et al., 2016). Thriving in shallow-water carbonate settings above the fair-weather wave base (Buxton and Pedley, 1989; Hottinger, 1997; Haig et al., 2020; Simmons, 2020), *A. borneensis* and *Alveolinella* ex. interc. *borneensis* et *quoyi* reached Indonesia, Bikini and Eniwetok in the Middle Miocene (Bassi et al., 2022a) following

the eastward expansion of the seagrass settings (Wilson and Rosen, 1998). In Sangatta (East Kalimantan) the last appearance datum of *A. borneensis* is from the lowermost Tortonian (Bassi et al., 2022a), whereas the first appearance datum of *A. quoyi* is in the Tortonian of Indonesia (Renema et al., 2015; Bassi et al., 2022a; Figs. 2, 3). *Alveolinella quoyi* is reported from the late Langhian–Tortonian of Java with no illustration (BouDagher-Fadel and Lokier, 2005: Fig. 3). The studied species has been identified in the Pliocene of seven areas, from Malaysia to New Caledonia and Eniwetok (Table 1; Fig. 3). In the Philippines, *A. quoyi* occurs in the Pliocene (Matsumaru, 2011, 2017) and in the Pleistocene

Table 1
Stratigraphical and geographical distribution of *Alveolinella quoyi* (d'Orbigny, 1826). Ryukyu Isls, Ryukyu Islands.

References	Referred to as	Age	Locality	Illustrations
Matsumaru (2011)	*A. quoyii*	Burdigalian–Pliocene–Holocene	Philippines	no
Renema (2007)	*A. quoyii*	Tortonian–Recent	SE Asia	no
Renema et al. (2015)	*A. quoyi*	Tortonian–Messinian	East Kalimantan	fig. 5B
Wonder and Adams (1991)	*A. quoyi*	early Tf3	Papua New Guinea	fig. 12
Whittaker and Hodgkinson (1979)	*A. quoyi*	Pliocene	Malaysia	pl. 8, fig. 11
Bassi et al. (2022a)	*A. quoyi*	Piacenzian	Togopi, Malaysia	no
Coleman (1963)	*A. quoii*	Pliocene	Solomon Islands	pl. 1, fig. 1
Wonders and Adams (1991)	*A. quoyi*	Pliocene–Pleistocene	Togopi, Borneo	figs. 8–9
Cole (1957)	*A. quoyi*	post-Miocene	Eniwetok	pl. 240, figs. 16, 19
Matsumaru (2017)	*A. quoyii*	Pliocene	Philippines	pl. 41, fig. 10; pl. 43, figs. 11–15
Hanzawa (1957)	*A. quoii*	Pliocene–Pleistocene	Palau	pl. 23, fig. 2a–b
Bassi et al. (2022a)	*A. quoyi*	Calabrian, Pleistocene	Cebu, Philippines	no
Matsumaru (1977)	*A. quoyii*	middle Pleistocene	Ryukyu Isls	pl. 5, figs. 1, 10–15
Bassi et al. (2022a)	*A. quoyi*	Calabrian, Pleistocene	Ryukyu Isls	fig. 7
Webster et al. (2022)	*A. quoyi*	Pleistocene, MIS 3	NW Australia	fig. 5H
BouDagher-Fadel (2018)	*A. quoyi*	Recent Holocene	Papua New Guinea	fig. 7.2 pl. 7.2, figs. 2–4
Cushman (1921)	*Alveolina boscii*	Recent	Philippines	pl. 17, figs. 2–5
Hofker (1930)	*A. Quoyi*	Recent	Kei Islands, Rotti Island, Indonesia	pl. 41, figs. 6–8; pl. 61, figs. 8–10, 12–13; pl. 64, figs. 1–4, 6
Cushman (1933)	*A. quoyi*	Recent	Pacific	pl. 19, fig. 10
Hofker (1952)	*A. Quoyi*	Recent	Pacific	figs. 61–62
Graham and Militante (1959)	*A. quoyi*	Recent	Philippines	pl. 10, fig. 12
Adams (1973)	*A. quoyi*	Recent	Pacific	pl. 2, fig. 6
Hottinger (1974)	*A. quoyi*	Recent	Torres Strait, Australia	pl. 105, fig. 5; pl. 106, figs. 1–4
Zheng (1979)	*A. quoyi*	Recent	Xisha Island	text-fig. 12; pl. 9, fig. 11; pl. 27, figs. 1–3, 5
Boichard et al. (1985)	*A. quoyi*	Recent	East Kalimantan	pl. 15, fig. 18
Scoffin and Tudhope (1985)	*A. quoyi*	Recent	Great Barrier Reef	fig. 16
Severin and Lipps (1989)	*A. quoyi*	Recent	Papua New Guinea	fig. 9
Wonders and Adams (1991)	*A. quoyi*	Recent	New Caledonia, Maldives	figs. 10–11
Hatta and Ujiié (1992)	*Borelis pulchra*	Recent	Ryukyu Isls	pl. 14, figs. 11–12; pl. 15, fig. 1
Loeblich and Tappan (1994)	*A. quoii*	Recent	Sahul shelf	pl. 107, figs. 1–4
Hohenegger et al. (1999)	*A. quoyi*	Recent	Sesoko-jima	fig. 13
Renema et al. (2001)	*A. quoyii*	Recent	Sulawasi	fig. 10e
Lạc (2002)	*A. quoyi*	Recent	Vietnam	pl. 1 figs. 1–3
Yordanova and Hohenegger (2002)	*A. quoyi*	Recent	Sesoko-jima	pl. 30, figs. 5–7
Förderer et al. (2018)	*A. quoyi*	Recent	geographic list	no
BouDagher-Fadel and Price (2021)	*A. quoyi*	Recent	Port Moresby, New Guinea	pl. 7, figs. e–g; fig. 9
Bassi et al. (2022a)	*A. quoyi*	Pleistocene	Ryukyu Isls	fig. 7
		Recent	Ryukyu Isls	fig. 8
		Recent	Vanuatu	fig. 9
Bassi et al. (2023)	*A. quoyi*	Recent	Ryukyu Isls	fig. 1

(W.R., pers. obs.). The first northernmost occurrence of *A. quoyi* is in the Calabrian–Chibanian shallow-water carbonate deposits of the Ryukyu Islands (Matsumaru, 1977; Iryu et al., 2006; Bassi et al., 2022a; Fig. 2), where the species is still thriving in coral-reef related settings (Hohenegger, 2000; Bassi et al., 2022a).

5. Discussion

The extensive shallow-water carbonate platforms of the Early–Middle Miocene suffered a prolonged episode of carbonate impoverishment in the equatorial Indian Ocean from c. 13.2 to c. 8.7 Ma, related to the carbonate crash (Lübbers et al., 2019; Gallagher et al., 2024; Fig. 2), which brought about a conspicuous reduction in shallow-water carbonate settings where alveolinoids (e.g., *Alveolinella*) thrived. Although the Langhian peak in pLBF richness occurred in shallow-water reef-related areas and expanded latitudinally during the Miocene Climatic Optimum (Steinthorsdottir et al., 2021), the temperature asymmetry of c. 4 °C across the Pacific Ocean throughout the Middle Miocene limited the eastward dispersion of pLBF species (Bassi et al., 2024). The first appearance of *Alveolinella quoyi* in the Tortonian of the CIP (Fig. 3) was likely promoted by an El Niño-like mean state identified at c. 9.6–6.5 Ma in a more open Indonesian Gateway (Gallagher et al., 2024). This interval of increased productivity records El Niño-like conditions across the tropical Pacific and the initial phase of a widespread biogenic bloom (Nathan and Leckie, 2009). In the Late Miocene CIP only three still extant pLBF species occur (*Borelis pulchra*, *B. schlumbergeri*, and *Alveolinella quoyi*; Bassi et al., 2024), at SST lower than 28 °C (Lu et al., 2021). 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, 2024; Auer et al., 2019) constrained the Pliocene *A. quoyi* within the CIP (Bassi et al., 2022a; Table 1; Figs. 2, 3). An additional ITF restriction event may have occurred in the Pleistocene (Smith et al., 2020). During this time slice the absence of Indo-Pacific pLBF taxa in westernmost CIP confirms the role of ITF restriction as a dispersal barrier (Gallagher et al., 2009, 2024; Bassi et al., 2021).

With the intensification of the North Pacific Gyre and Northern Hemisphere ice sheet expansion, the modern Kuroshio current
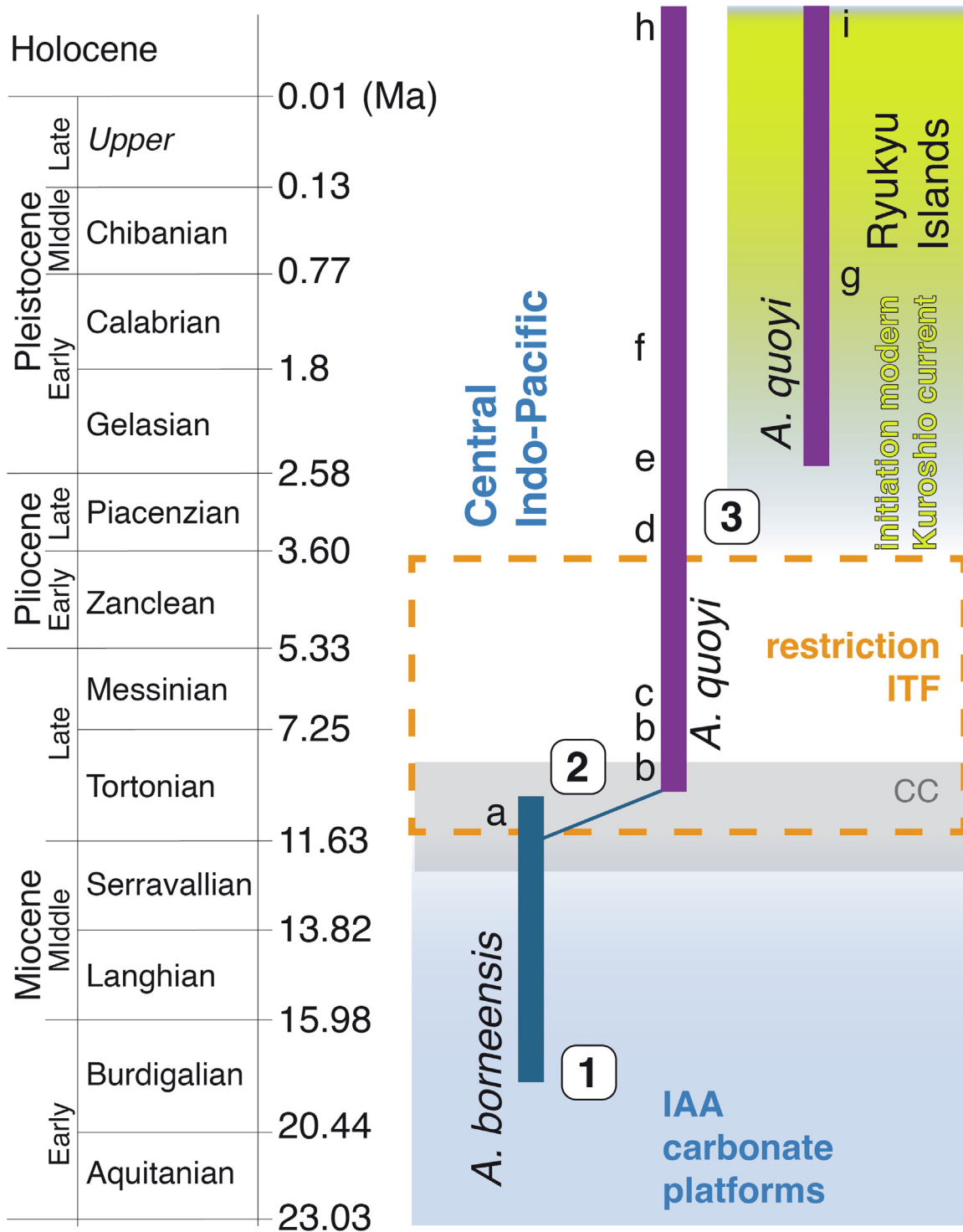
Fig. 2. Major events in the palaeobiogeographical history of the Late Miocene–Recent *Alveolinella quoyi* (d'Orbigny, 1826). *Alveolinella* presumably appeared in the latest Burdigalian as *A. borneensis* (1), which disappears in the early Tortonian of Sangatta, East Kalimantan (a; Bassi et al., 2022a). The first appearance datum (FAD) of *A. quoyi* is in the late Tortonian of East Kalimantan and Papua New Guinea (2, b, c). The Upper Miocene–Lower Pliocene Indonesian Throughflow (ITF) restriction constrained *A. quoyi* within the CIP areas. From the uppermost Pliocene (3) the Indo-Pacific LFB species migrated northward to the Ryukyu Islands, where the occurrence of *A. quoyi* is Calabrian–Chibanian (g). See text for details. Occurrences: a: early Tortonian, East Kalimantan (Bassi et al., 2022a); b: early Tortonian, Papua New Guinea (Wonders and Adams, 1991), late Tortonian, Kalimantan (Bassi et al., 2022a); c: Tortonian–Messinian, East Kalimantan (Renema et al., 2015; Bassi et al., 2022a); d: Pliocene–Pleistocene, Borneo (Wonders and Adams, 1991); Pliocene, Malaysia (Whittaker and Hodgkinson, 1979); Piacenzian, Togopi, Malaysia (Bassi et al., 2022a); Pliocene, Solomon Islands (Coleman, 1963), Philippines (Matsumaru, 2017); e: Pliocene–Pleistocene, Palau (Hanzawa, 1957); f: Calabrian, Pleistocene, Cebu, Philippines (Bassi et al., 2022a); g: Calabrian, Pleistocene, Ryukyu Islands (Matsumaru, 1977; Bassi et al., 2022a); h: Holocene, Papua New Guinea (BouDagher-Fadel, 2018); Vanuatu (Bassi et al., 2022a); i: Holocene, Ryukyu Islands (Hatta and Ujiié, 1992; Hohenegger, 1994; Bassi et al., 2022a, 2023; this study). Abbreviations: CC, Indo-Pacific carbonate crash; IAA, Indo-Australian Archipelago. Time scale after Cohen et al. (2013).
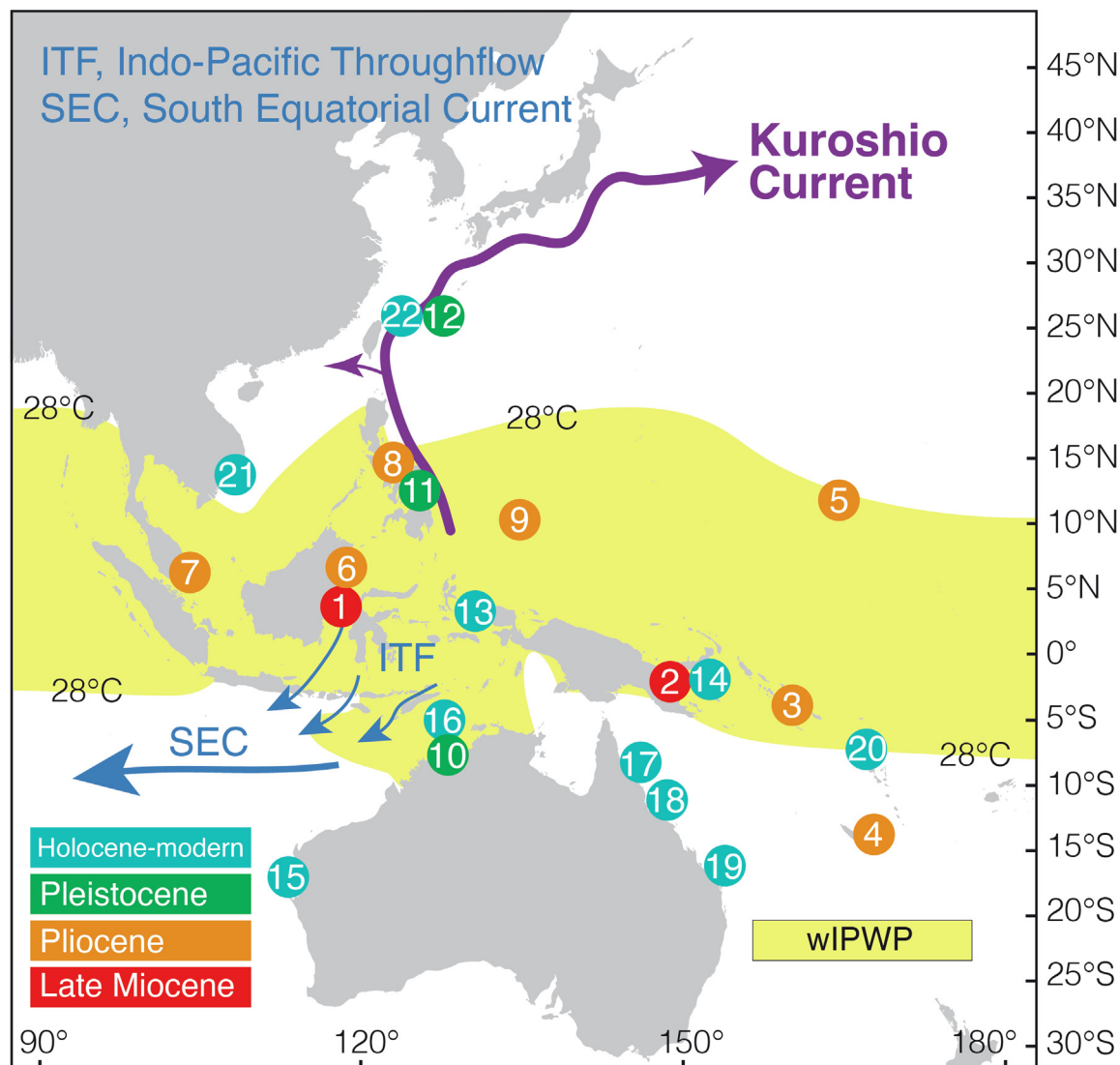
Fig. 3. Geographical location of Upper Miocene–modern *Alveolinella quoyi* (d'Orbigny, 1826) in the CIP. The Pliocene–Pleistocene *Alveolinella quoyi* occurs from Borneo (Wonders and Adams, 1991), the Philippines (Matsumaru, 2017) and Malaysia (Whittaker and Hodgkinson, 1979; Bassi et al., 2022a) to the Solomon Islands (Coleman, 1963). At this time slice, the ITF restriction acted as a dispersal barrier for the species into the CIP (compare with Fig. 2). From the Pleistocene, the westward *A. quoyi* migrants moved into the western CIP to the Maldives (Wonders and Adams, 1991). From the Pliocene, *A. quoyi* followed the Kuroshio current arriving in the Ryukyu Islands in the Calabrian (Matsumaru, 1977; Bassi et al., 2022a). From the Tortonian, *Alveolinella quoyi* persisted in the CIP, but there are also modern records from the Sahul shelf, Western Australia, Queensland and Lizard Island. Occurrences refer to citations in Table 1 in which detailed information on each record can be found. The mean annual isotherm values are from Gallagher et al. (2009). Kuroshio current system is after Cruz Salmeron et al. (2022). Abbreviations: ITF, Indo-Pacific Throughflow; SEC, South Equatorial Current. Localities: 1, late Tortonian–Messinian, East Kalimantan (Renema et al., 2015; Bassi et al., 2022a); 2, Tortonian, Papua (Wonders and Adams, 1991); 3, Pliocene, Solomon Islands (Coleman, 1963); 4,?Late Pliocene, New Caledonia (Wonders and Adams, 1991); 5, post-Miocene, Eniwetok (Cole, 1957; Bassi et al. 2022a: table 5); 6, Late Pliocene, Borneo (Wonders and Adams, 1991); 7, Pliocene, Malaysia (Whittaker and Hodgkinson, 1979), Togopi (Piacenzian; Bassi et al., 2022a); 8, Pliocene, Philippines (Matsumaru, 2017); 9, Pliocene–Pleistocene, Palau (Hanzawa, 1957); 10, Pleistocene, NW Australia (Webster et al., 2022); 11, Calabrian, Pleistocene, Cebu, Philippines (Bassi et al., 2022a); 12, Calabrian, Pleistocene, Ryukyu Islands (Matsumaru, 1977; Bassi et al., 2022a); 13, Modern, Rawack, Raja Ampat Islands (type locality; d'Orbigny, 1826); 14, Holocene, Papua New Guinea (BouDagher-Fadel, 2018), Vanuatu (Bassi et al., 2022a); 15, Modern, Ningaloo Reef, Western Australia (Hottinger, 1974; Förderer et al., 2018); 16, Modern, Sahul shelf (Loeblich and Tappan, 1994); 17, Modern, Lizard Island, Australia (Förderer et al., 2018); 18, Modern, Queensland; Palm and Magnetic Passages (Scoffin and Tudhope, 1985); 19, Modern, Queensland, Moreton Bay (Förderer et al., 2018); 20, Modern, Vanuatu (Bassi et al., 2022a); 21, Modern, southern-central Vietnam, Cà Ná (Lạc, 2002); 22, Modern, southern and central Ryukyu Islands (Hatta and Ujiié, 1992; Hohenegger and Yordanova, 2001; Bassi et al., 2022a, 2022b; Bassi et al., 2023).

initiated by the latest Pliocene, allowing the Indo-Pacific species to migrate northward to the Ryukyu Islands (Gallagher et al., 2009; Fig. 2). Because *Alveolinella quoyi* is known in the Calabrian–Chibanian shallow-water carbonates of the Ryukyu Group (Iryu et al., 2006; Bassi et al., 2022a; Watanabe et al., 2023), the northernmost occurrence of this species, and no fossil record has been so far reported from the southern Ryukyu Islands, the northward migrants moved from the Philippines to the Ryukyu Islands following the Kuroshio current no earlier than the Pleistocene. From the Late Pleistocene, the unrestricted stronger (compared to today) ITF

and the South Equatorial Current (Tomczak and Godfrey, 2003) connected the wIPWP with the Indian Ocean and the Western Australian shelf (Potemra, 2005; Gallagher et al., 2009). The wIPWP is characterized by sea-surface temperatures greater than 28 °C (Sosdian and Lear, 2020; Fig. 3). Considering that *Alveolinella quoyi* thrives within a wide depth range with no detrimental effects of temperature (Hohenegger, 2000; Narayan et al., 2022), it is likely that during this time the westward *A. quoyi* migrants moved into the western CIP, thus giving rise to the present-day Maldivian occurrence (Hottinger, 1980, p. 11; Parker and Gischler, 2011, pl.

3, figs. 16–17). The Kuroshio current varied according to the El Niño–Southern Oscillation (ENSO; Shen et al., 2022). The oligotrophic Kuroshio intrusion from the Luzon Strait was enhanced during the Middle to Late Holocene under the influence of increased El Niño frequency (Shen et al., 2022; Zhang et al., 2022). This Kuroshio intrusion favoured the oligotrophic coral-reef settings in the Ryukyu areas where abundant *A. quoyi* population thrive (Yordanova and Hohenegger, 2007).

In the present-day wIPWP several other benthic taxa followed the northern expansion of the tropical high diversity zone into mid-latitudes (Renema et al., 2008; Jablonski et al., 2013). The assessed dispersal pattern of *A. quoyi* can be explained by a high dispersal capacity of the species. This capacity is consistent with that reported for other LBF (Faichney et al., 2011; Renema, 2015; Prazeres et al., 2020). *Alveolinella quoyi* was able to migrate northward from the IAA to mid-latitudes and distantly isolated islands in the Pacific (Fig. 3). Because during the Last Glacial Maximum the Kuroshio current remained relatively unchanged, the IAA reef front was only limitedly contracted, allowing *Alveolinella quoyi* likely to benefit from the strong surface currents which improved long-distance coral larval dispersal along the Ryukyu Arc (Vogt-Vincent and Mitarai, 2020). Yasuhara et al. (2022) showed that earlier 'Centre-of' theories about the Miocene–Modern IAA were based on the analysis of recent biotas with no palaeontological foundation. Our study supports the 'Hopping Hotspots' model (Renema et al., 2008; Yasuhara et al., 2022) according to which the locations of biodiversity peaks are related to wIPW faunal elements.

6. Conclusion

The analysis of literature data of the pLBF *Alveolinella quoyi* of the CIP areas is pivotal in indicating a palaeobiogeographical scenario of the dispersal route of coral-reef related taxa. Assessing the fossil record of *A. quoyi* and its palaeobiogeographical distribution, we found that during the Late Pliocene *A. quoyi* was constrained within the CIP. After the initiation of the Kuroshio current in the latest Pliocene, the northward migrants arrived in the central Ryukyu Islands (Calabrian–Chibanian). Probably during the Late Pleistocene, following the unrestricted stronger ITF, the westward *A. quoyi* migrants moved into the western CIP, giving rise to the present-day Maldivian occurrence. These results support the role of Hopping Hotspots in generating species diversity. The northward dispersal route of *A. quoyi* was characterized by complex coastlines and numerous islands among which unrestricted stronger ITF and the Kuroshio current favoured the migrants.

8. Data availability

Data analyzed in this study are based on references listed in Table 1.

CRediT authorship contribution statement

Davide Bassi: Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Yasufumi Iryu:** Writing – original draft, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Johannes Pignatti:** Writing – original draft, Formal analysis, Data curation, Conceptualization. **Kazuhiko Fujita:** Data curation, Methodology, Writing – review & editing. **Willem Renema:** Writing – original draft, Formal analysis, Data curation, Conceptualization.

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.

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