Zoological Studies **58:** 39 (2019)
doi:10.6620/ZS.2019.58-39

Zoological Studies

Open Access

Paleontological Studies of Whale Barnacles in Taiwan Reveal New Cetacean Migration Routes in the Western Pacific Since the Miocene

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Received 22 May 2019 / Accepted 5 December 2019 / Published 12 December 2019
Communicated by Yoko Nozawa

This paper reports a rediscovery of the first museum specimens of fossil whale barnacles from Taiwan. They are part of the material studied and figured by Ichiro Hayasaka in 1934. After examination of the material, which includes two cut-sections and one slice, the taxonomic assignment is revised to *Coronula bifida* Bronn, 1831. A petrographic study of the surrounding matrix shows that the matrix lacks slate and lithic fragments, indicating that the specimen was deposited in the pre-collision settings during the Miocene to early Pliocene. Figured specimens in Hatai's work in 1939 were examined for comparison. The distribution record of *Coronula* fossils shows that whales passed through the Taiwan Strait to Okinawa and moved northwards via the Pacific coast of Honshu or entered into the Sea of Japan. The fossil record in this region extends back to the upper Miocene in Yamagata prefecture (facing the Sea of Japan) and Boso Peninsula (facing the Pacific Ocean) in Honshu (~11.2 Ma–5.3 Ma). This is one of the oldest cetacean migration routes documented to date.

Key words: *Coronula*, Whale barnacles, Thoracica, Miocene-Pleistocene, Taiwan.

BACKGROUND

The barnacles in the genus *Coronula* are epibiotic, living on the skin of the humpback whale (*Megaptera novaeangliae*) and sometimes on other cetaceans. Because of the obligatory relationship between the *Coronula* barnacles and humpback whales, analysis of their distribution, including that of fossil records, is an indirect method for studying the migration pathways of humpback whales. In addition, the location of *Coronula* fossils can sometimes be used as an indication of the depth at which sedimentation took place, provided that those barnacle fossils are entombed with the whale skeleton and not washed to the shoreline (Hatai 1939). Biannucci et al. (2016) mapped the distribution of *Coronula* fossils worldwide and deduced that there were Pleistocene migratory routes of whales from Vanuatu to New Zealand, and from Ecuador to Antarctica along the west coast of South America. The occurrence of fossils of *Coronula* in the northern Atlantic and Mediterranean Sea revealed a migration of Pleistocene whales from the Atlantic to the Mediterranean migratory path that is not recorded in modern times (Biannucci et al. 2016). *Coronula* shells are made of calcite and thus accumulate oxygen isotope $\delta^{18}O$ as they grow. The profiles of $\delta^{18}O$ vary according to temperature, and are thus useful proxies for ocean temperatures. On this basis, Taylor et. al. (2018) analyzed $\delta^{18}O$ profiles of fossil *Coronula* from base to top of shells collected from Panama (middle to late Pleistocene), and compared these with modern *Coronula* shells collected from California and Alaskan coasts. Results from their study showed that

Citation: Buckeridge JS, Chan BKK, Lin JP. 2019. Paleontological studies of whale barnacles in Taiwan reveal new cetacean migration routes in the western Pacific since the Miocene. Zool Stud **58:**39. doi:10.6620/ZS.2019.58-39.

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the $\delta^{18}O$ profiles are similar from base to top of the shell, revealing that the migratory routes of humpback whales (from west coast of North America to Hawaii in different seasons) have remained much the same from Pleistocene to modern times.

Migration routes of humpback whales in the West Pacific, including from Taiwan to Japan, have received relatively little attention when compared to extensive photo-identification data in Hawaii, west and east coast of America, the Caribbean, Iceland and Greenland (Baker et al. 1990). Proposed migratory information on whales in the West Pacific was based only on the location of historical whaling sites (Baker et al. 1990; Rizzo 2009).

Recently, Buckeridge et al. (2018) reported new evidence of high density of fossil whale barnacles from Taiwan, suggesting that Taiwan was a breeding ground of whales in the Pleistocene. However, there are several older studies on *Coronula* fossils from Taiwan. Professor Ichiro Hayasaka (1891-1977) of Taihoku Imperial University (currently National Taiwan University, Taiwan) first reported two fossil specimens of *Coronula* from southern Taiwan, but unfortunately he did not illustrate these (Hayasaka 1933). Subsequently, he published and illustrated three fossil *Coronula* and cut-sections (Hayasaka 1934), and then reported one additional specimen with stratigraphic information (Hayasaka 1935). Three cut-sections from one individual survived and are housed in the Department of Geosciences, National Taiwan University (NTUG). These specimens have never been photographed in colour and to modern standards. From the records of Hayasaka (1933 1934 1935), Wang and Chen (2007) and Buckeridge et al. (2018), there are at least four localities where fossil whale barnacles have been recovered in Taiwan (Fig. 1). The objective of this study is to redescribe those sections in detail and review all *Coronula* fossil records in Taiwan and the northwestern Pacific region to determine likely Pleistocene migratory routes of humpback whales in the West Pacific.

The Department of Geosciences, National Taiwan University (NTUG) houses an important historical collection of fossil and mineral specimens dating from the 1930s. The core collection consists of two parts.

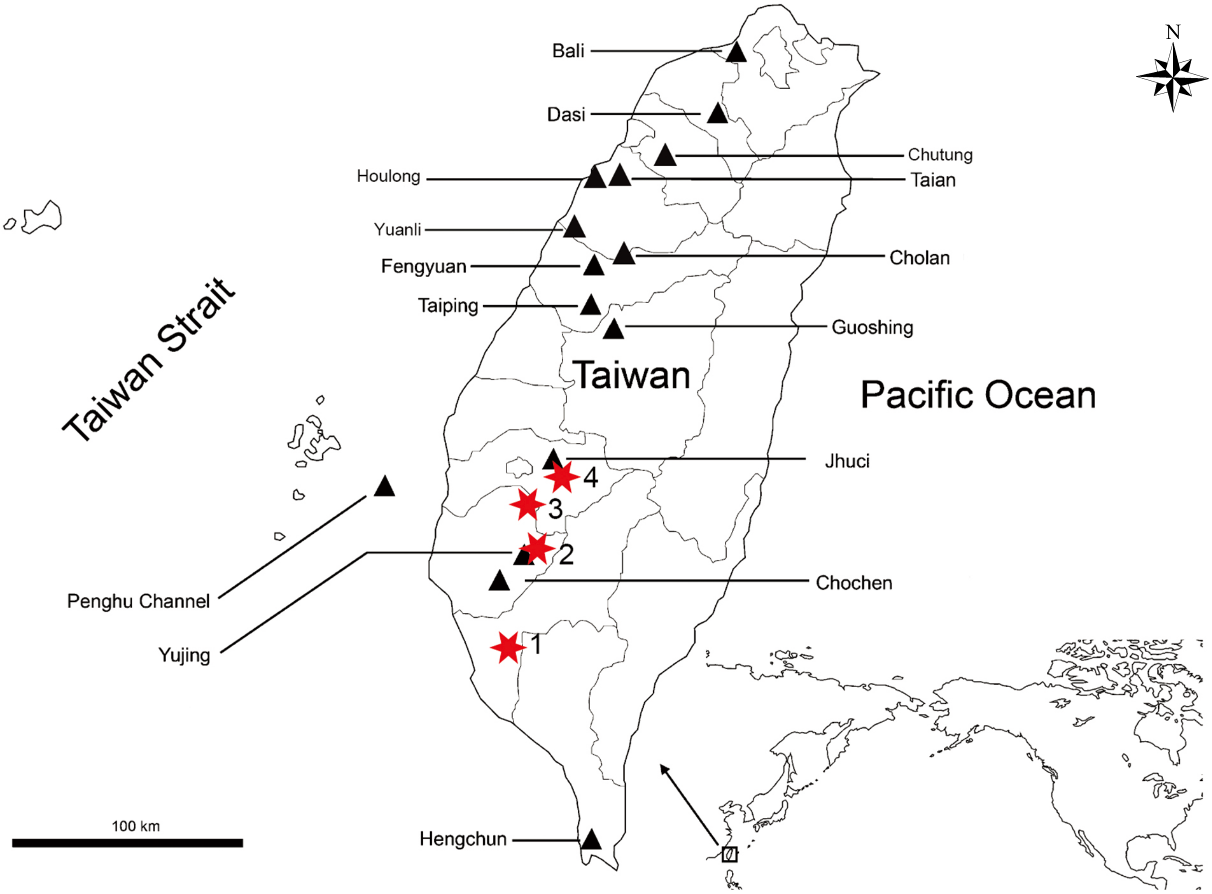

Fig. 1. Occurrences of fossil cetaceans (solid triangles) (modified from Tsai et al. 2013) and whale barnacles (stars) (Hayasaka 1933 1934 1935; Wang and Chen 2007; Buckeridge et al. 2018; this study) in Taiwan.

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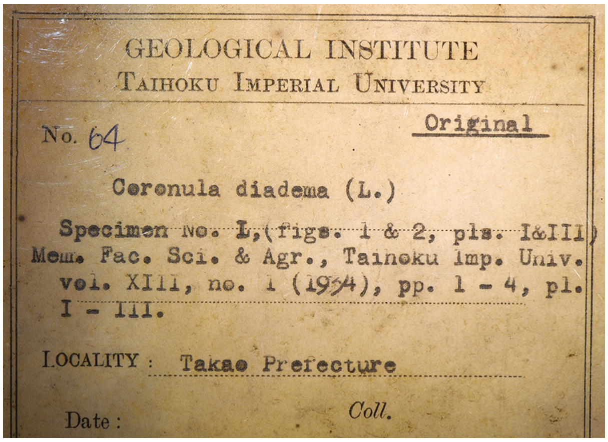
The first comprises older specimens that were inherited from the predecessor of the department (Geological Institute of Taihoku Imperial University). The second part of the collection was accumulated gradually by faculty members and students after the establishment of National Taiwan University in 1947. The fossil barnacles described herein belong to the former collection. Fossil barnacles deposited at the Tohoku University Museum of Natural History, which is also known as Institute of Geology and Paleontology, Sendai (IGPS), have been examined also for comparison.

MATERIALS AND METHODS

Taiwan

The specimens come with a typewritten label: "*Coronula diadema* (L.) Specimen No. 1. (figs. 1 & 2, pls. I & III) Mem. Fac. Sci. & Agr., Taihoku Imp. Univ. vol. XIII, no. 1 (1934), pp. 1-4, pl. I-III. Locality: Takao Prefecture" (note Takao refers to present day Kaoshiung) (Fig. 2)

There are several issues that must be clarified. First, this label (Fig. 2) does not belong to the surviving specimen, although it is part of the original material described in Hayasaka (1934). The surviving cut sections and slice belong to specimen no. 2 (figs. 3 and 4, pls. II & III) (Fig. 3A–H) in Hayasaka (1934). Secondly, the published figures only show the cross-sectional view in grey scale. These samples are re-illustrated here in colour with three additional views (Fig. 3A–K). In addition, one unpublished slice is illustrated here for the first time (Fig. 3I–K). Thirdly, Taihoku Imperial University was founded during the Japanese occupation of Taiwan (1895–1945). Thus, this label is pre-1945.



GEOLOGICAL INSTITUTE
TAIHOKU IMPERIAL UNIVERSITY

No. 64 Original

Coronula diadema (L.)

Specimen No. 1, (figs. 1 & 2, pls. I&III)
Mem. Fac. Sci. & Agr., Taihoku Imp. Univ.
vol. XIII, no. 1 (1934), pp. 1 - 4, pl.
I - III.

LOCALITY : Takao Prefecture

Date : Coll.

Fig. 2. The original museum label associated with fossil barnacle specimens (NTUG110-F000023).

Takao Prefecture was one of the old administrative divisions. It consisted of modern-day Kaohsiung City and Pingtung County.

Japan

The two specimens (IGPS63173 and IGPS63172) labelled as "*Coronula diadema*" are from the original description in Hatai (1939) housed in Tohoku University Museum of Natural History. Localities: South of Kakegawa, Ogasa-gun, Tôtômi province (Hizikata beds?) for specimen IGPS63172); Near Dainiti, Ogasa-gun, Tôtômi province for specimen IGPS63173 (Fig. 4).

Delete Tôtômi province is equivalent to western Shizuoka Prefecture in Honshu today.

RESULTS

SYSTEMATICS

Superfamily Coronuloidea Leach, 1817
Family Coronulidae Leach, 1817

Coronula Lamarck, 1802

Diagnosis: Shell with six equal-sized compartments; opercular valves present; parietes with similar structure throughout, without internal mid ribs; parietal ribs radiate accordion-like to end as T-shaped flanges forming exterior of wall; radii less than half thickness of parietes; orifice of body chamber larger than basal opening; sheath smooth, extending entire length of inner wall; radiating ribs on either side of sutures unbranched or asymmetrically branched; opposed sides of terminal flanges crenulate.

Distribution: Upper Miocene-Recent (Cosmopolitan) (Buckeridge, 1983; Buckeridge et al. 2018).

Coronula bifida Bronn, 1831
(Figs. 2, 3A–K)

Coronula bifida Bronn, 1831: 126.
Coronula barbara Darwin, 1854: 421.
Coronula diadema Hayasaka, 1933: 50, 1934: 3, pl. 2, figs 1–3, pl. 3, figs 3–5, 1935: 1, figs 1–2.-Hatai, 1939: 262, figs 1–5.
Coronula dormitor Pilsbry and Olsson, 1951: 202.
Coronula bifda bifda Menesini, 1968: 387.
Coronula bifda barbara Menesini, 1968: 395.
Coronula bifida Collareta et al., 2018: 15.-Buckeridge et al., 2018: 4.

Diagnosis: *Coronula* with globose shell; compartments with convex longitudinal parietal ribs that often bifurcate; ribs with strong, transverse, beaded

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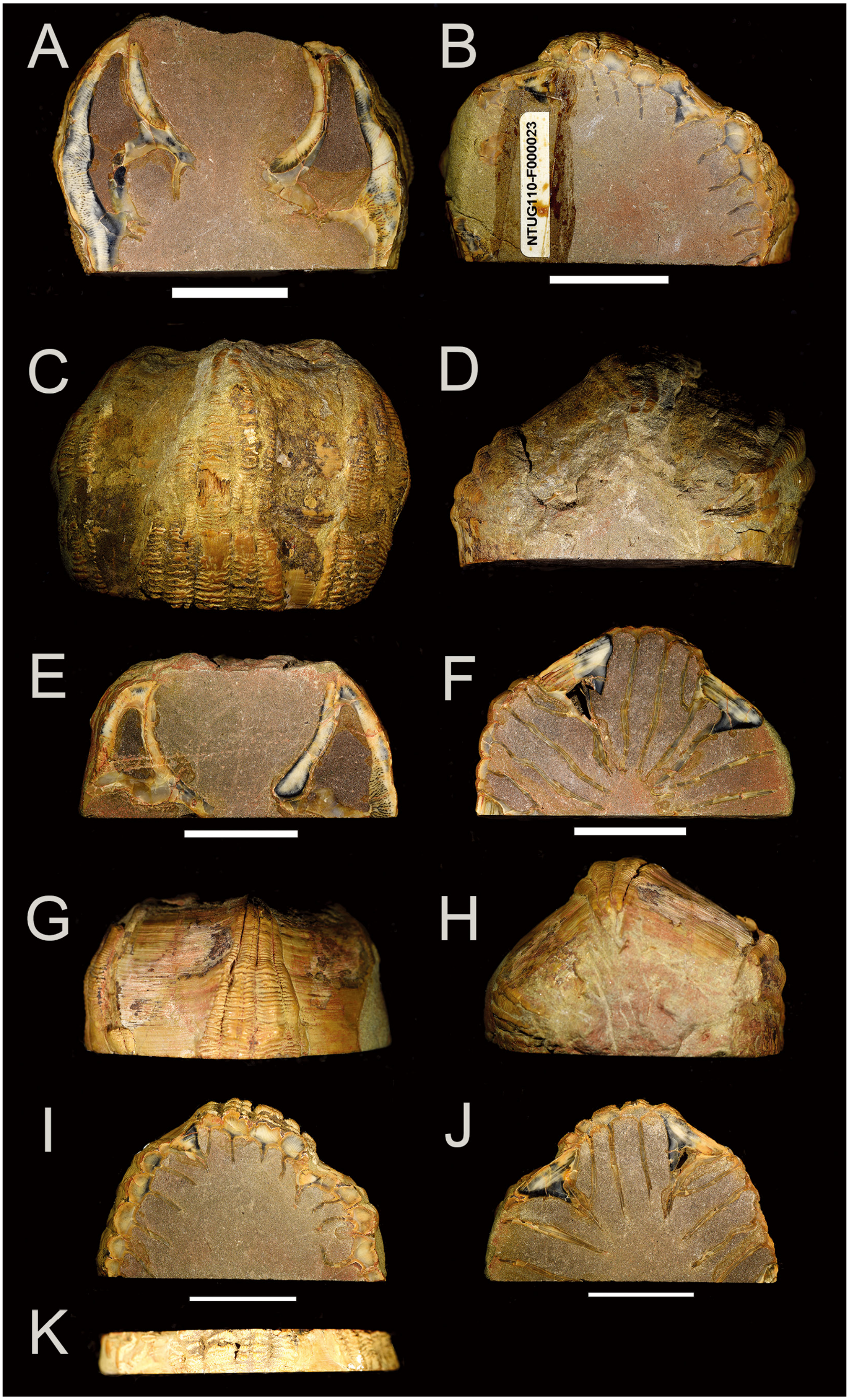

Fig. 3 Cut and polished sections (NTUG110-F000023) of *Coronula bifida* Bronn, 1831 from Plio-Pleistocene strata in southern Taiwan; (A–D) Studied and figured specimen in Hayasaka (1934: pl. 3, fig. 3); (E–F) Studied and figure specimen in Hayasaka (1934: pl. 3, fig. 4); (I–K) Unpublished slice in the same collection, used for making a thin-section (see Fig. 5A, B). Scale bars = 2 cm.

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growth ridges; radii broad, flat, becoming narrower in the lowermost third; body chamber relatively shallow, sub-cylindrical; sheath equal to or less than half that of total shell height.

Distribution: Miocene-Pleistocene (Taiwan; Japan; Calabrian; Western Europe; California; Ecuador) (Hatai 1938 1938; Buckeridge et al. 2018).

Material: Three cut sections from one individual (NTUG110-F000023), from an upper Miocene-Pliocene stratum in SW Taiwan. Two complete specimens from Japan, including IGPS63173 (Hatai, 1939: 395 pl. 10, figs. 1-3) and IGPS63172 (Hatai, 1939: pl. 10, figs. 4, 5), housed at Tohoku University Museum of Natural History.

Description: Shell globose (crown-shaped), externally with prominent, convex, occasionally bifurcated longitudinal ribs; ribs crossed by narrow, beaded growth ridges, edges crenulated; basal edges of ribs crenulated; radii slightly wider at orifice than parietes at their widest, tapering to become narrow towards the base. Orifice large, hexagonal; body chamber cup-shaped, subcylindrical, extending basally to approximately half the height of the shell; basal opening less than half the diameter of the orifice; sheath less than half the total shell height.

DISCUSSION

This specimen conforms to the morphological envelope of *Coronula bifida* as described in Buckeridge et al. (2018). The key differences between this and

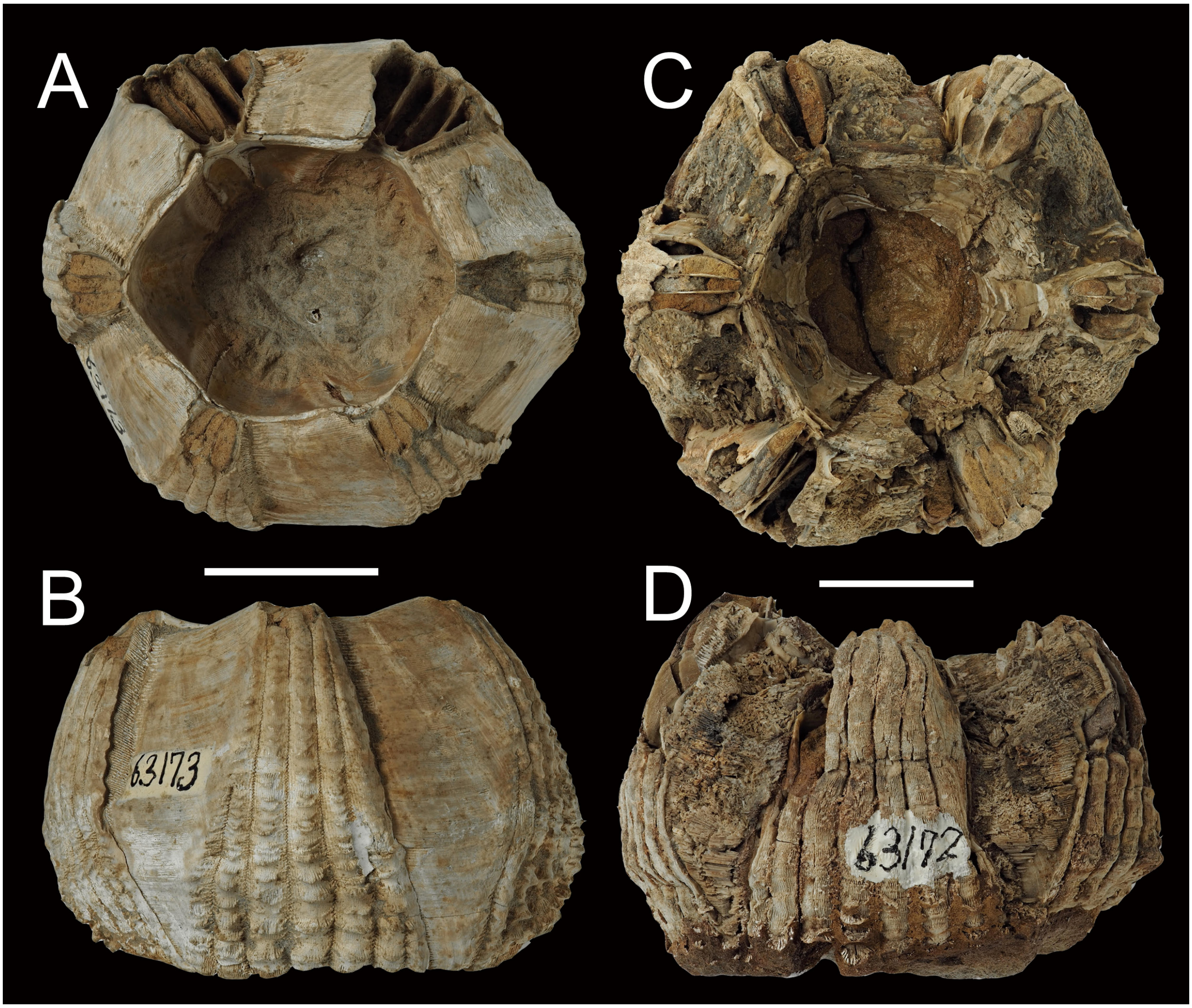

Fig. 4 New photographs of two specimens *Coronula bifida* Bronn, 1831 illustrated in Hatai (1939) and housed at the Tohoku University Museum of Natural History; (A, B) IGPS63173 (Hatai, 1939: pl. 10, figs. 1-3); (C, D) IGPS63172 (Hatai, 1939: pl. 10, figs. 4,5). Scale bars = 2 cm.

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the living *Coronula diadema* (Linnaeus 1767) are the shallower body chamber and the slightly more common bifurcation of external ribbing of this species. The other two species of *Coronula* described from the late Cenozoic of the Western Pacific are *Coronula aotea* Fleming 1959 (upper Pliocene, New Zealand) and *Coronula intermedia* Buckeridge 1983 (lower Pleistocene, New Zealand). These two species are distinguished from this material by the lower profile that their shells would have had. As noted in Buckeridge et al. (2018), *C. aotea* and *C. intermedia* are likely to have been progenitors of *Coronula reginae* Darwin, 1854. In turn, as *C. bifida* was the likely progenitor of *C. diadema*, any differences between *C. bifida* and *C. diadema* can be expected to reduce during the early Pleistocene (Bianucci et al. 2006; Dominici et al. 2011; Buckeridge et al. 2018).

Hatai (1939) did not formally describe the *Coronula* specimen that he had, although he did photograph it (Hatai, 1939: figs 1-5) (Fig. 4A–D) and labelled it as *Coronula diadema* in the figure's caption. These images show that the parietes have well developed and well-spaced transverse growth ridges. Examination of the two specimens (IGPS63173, Fig. 4A, B; and IGPS63172, Fig. 4C, D) described in Hatai (1939) shows that the number of parietal ribs on each plate can be as many as eight (Fig 4D); furthermore, the upper zone of weathering indicates that the shell was embedded for at least half its length in the whale's tissue. These features conform to those of *C. bifida* (see Buckeridge et al., 2018: p6). In addition, the widely accepted range of *C. diadema* is from late Pliocene to Recent (Bianucci et al., 2006). Hatai (1939) did not discuss *C. bifida*, perhaps because it was not a well-known taxon at that time, being recorded only from the Tertiary of Italy (Newman and Ross, 1976: 45). On the basis of the forgoing, a re-assignment of Hatai's Miocene Japanese material (Fig. 4) to *C. bifida* is proposed here.

When considering the age determination of the cut and polished specimens from Taiwan, there are two approaches. Hatai (1939) interpreted the Taiwan *Coronula* materials as being from the Byôritsu Beds of Pliocene (now as Pleistocene in age; Sato et al. 2016). The systematics and stratigraphic information of Cenozoic bivalves from Taiwan were reviewed and revised recently. Based on Hayasaka (1934), the co-occurring fossil bivalves include *Dosinia gruneri*, *Arca* sp., *Crassatelites* sp., *Paphia* sp., and *Anadara* sp. They range from Miocene to Pleistocene (Sato et al. 2016). In addition, a petrographic study of a thin section of the matrix shows that it is dominated by quartz grains (Fig. 5). Based upon the complex orogenic and active tectonic history of Taiwan in the late Cenozoic, the absence of distinctive slate or lithic fragments is indicative of a pre-collision setting, and was thus re-evaluated as Miocene to early Pliocene (Chen et al. 2019).

Bianucci et al. (2006) hypothesized ancient cetacean migration routes on the basis of fossil specimens of *Coronula* spp. as *Coronula*, and sister taxa are host-specific. A literature review of fossil occurrences in Taiwan (Hayasaka 1933 1934 1935; Wang and Chen 2007; Hayashi 2012; Buckeridge et al. 2018) and Japan (Nomura and Hatai 1936; Hatai 1938 1939; Mimoto 1991) reveals an ancient cetacean route in the western Pacific (Fig. 6) and a breeding area of whales that can reach to Taiwan's waters (see fossil whale evidence in Tsai et al. 2014). Based on whaling records (1920–1950), humpback whales once wintered at Okinawa and Taiwan (Iwashi and Kubo 2001). Based on the distribution of *Coronula* fossils, it appears that whales passing through the Taiwan Strait to Okinawa

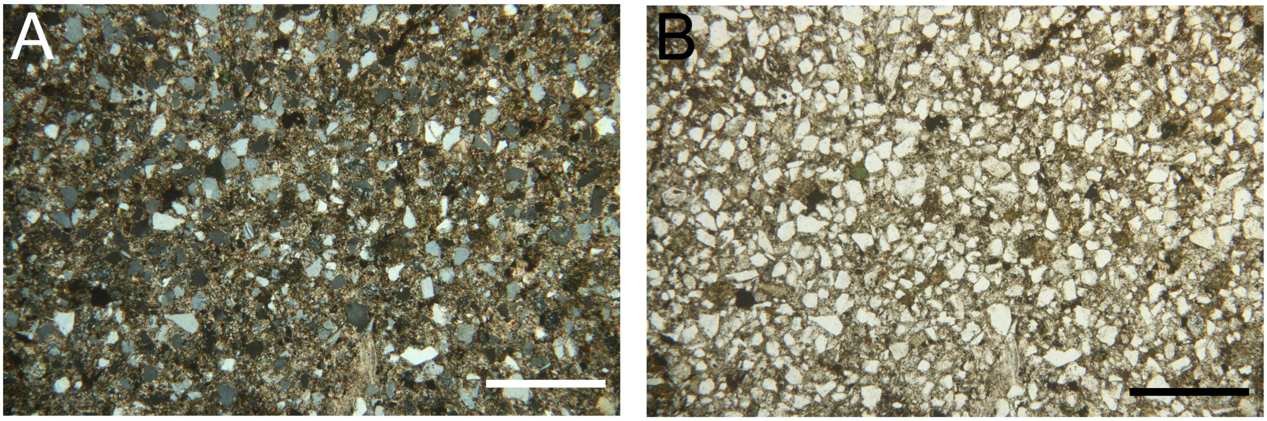

Fig. 5. Thin-section photomicrographs of the matrix of fossil barnacle (NTUG110-F000023) (Fig. 3I); (A) specimen with plane-polarized light (PPL); (B) specimen with crossed polars (XPL). It consists of mainly quartz grains and lacks of lithic or slate fragments (see Type I sandstone in Chen et al., 2019). Scales = 0.5 mm.

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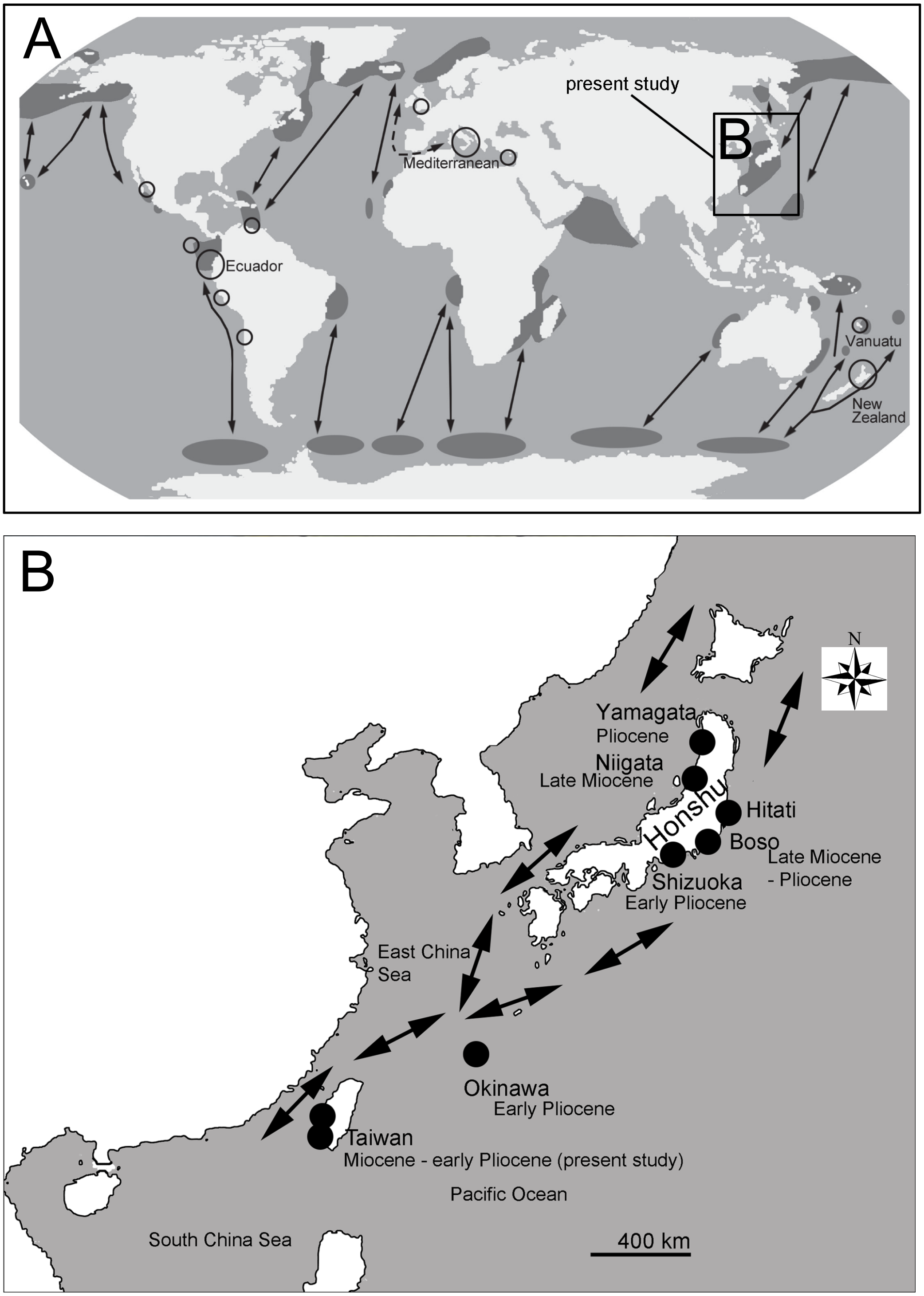

Fig. 6. (A) A map reproduced after Bianucci et al. (2006), showing the review data of world-wide fossil records (empty circles) and the distribution of humpback whales (gray patches). The broken arrow indicates a prehistorical migration route from North Atlantic to Mediterranean, as reported in Bianucci et al. (2006). Note that the rectangular insert (which is the study region in the present study) in the northwest Pacific contains no fossil records in the review in Bianucci et al. (2006). (B) Magnified region in the northwest Pacific based on A, showing a further migration path of humpback whales in the north western Pacific based on updated fossil occurrences of *Coronula* spp. (black circles). Fossil records in Taiwan are based on Buckeridge et al. (2018) and the present study. Okinawa is based in Neomura and Hatai, 1936. Fossils in Honshu, Japan are based on review data in Hatai (1938 1939). The names of locations in Honshu in the present figure are modern names, whereas those names were old names in Hatai (1938 1939): Yamagata is equivalent to Uzen Province, Boso is equivalent to Kazusa Province, Shizuoka is equivalent to Musasi Province, Niigata is equivalent to Etigo Province.

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moved northwards via the Pacific coast of Honshu or passed through the Sea of Japan in the Neogene (Fig. 6). The fossil record in this region extends back to the upper Miocene in Yamagata prefecture (facing the Sea of Japan) and Boso Peninsula (facing the Pacific Ocean) in Honshu (~11.2 Ma–5.3 Ma) (Hatai 1938); thus, the cetacean migration route between the feeding area in the Arctic Ocean and the breeding area in Taiwan waters has been established for more than 5Ma (Fig. 6). This is one of the oldest cetacean migration routes documented to date. However, the modern migration routes of humpback whales, based on photographic records (Iwashi and Kubo 2001), shows that they move northward along the Pacific coast of Japan Honshu; interestingly, there are no photo-ID records of humpback whales in the Taiwan Strait or Sea of Japan in recent literature.

CONCLUSIONS

This study confirms the observation in Buckeridge et al. (2018) that Taiwan contains important *Coronula*-bearing fossil sites in the northwestern Pacific. Re-examination of key historical specimens extends the study of fossil whale barnacles in Taiwan back to the early 1930s. In turn, this permits a better understanding of both local and global fossil records of *Coronula* and thus the timing of barnacle-whale co-evolution in the past. According to the distribution record of *Coronula* fossils, whales passed through the Taiwan Strait to Okinawa and moved northwards via the Pacific coast of Honshu or entered into the Sea of Japan. The fossil record in this region extends back to the upper Miocene in Yamagata prefecture (facing the Sea of Japan) in Honshu (~11.2 Ma–5.3 Ma). This is one of the oldest cetacean migration routes documented to date.

Acknowledgments: We would like to thank the anonymous reviewers for their constructive criticism on the previous drafts. Research was supported by Taiwan-ROC grants (MOST 106-2116-M-002-018, 107-2116-M-002-007, 108-2116-M-002-014) to JPL. Thanks to Professor Wen-Shan Chen, Yoko Nozawa and one anonymous reviewer for commenting on the earlier drafts; W.-S. Chen for interpreting the thin section; J. Nemoto at IGPS for the access to photograph the figured specimens and stacking images. Thanks also to Professor Tsung-Kwei Liu for curating and cataloguing the NTUG collection; the NTU librarian Pi-Fang Tsai for locating key references.

Authors' contributions: JSB, BKKC and JPL wrote the manuscript. We confirm that our manuscript is not under consideration for publication in any other journals.

Competing interests: The authors declare that they have no conflict of interest.

Availability of data and materials: Fossil samples have been deposited in the Department of Geosciences, National Taiwan University, Taipei, Taiwan.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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