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Accumulations of Fossils of the Whale Barnacle *Coronula bifida* Bronn, 1831 (Thoracica: Coronulidae) Provides Evidence of a Late Pliocene Cetacean Migration Route through the Straits of Taiwan

John Stewart Buckeridge[1], Benny K.K. Chan[2], and Shih-Wei Lee[3,*]

[1]*Marine & Geological Systems Group, RMIT, Australia. E-mail: john.buckeridge@rmit.edu.au*

[2]*Biodiversity Research Center, Academia Sinica, Taipei 11529, Taiwan. E-mail: chankk@gate.sinica.edu.tw*

[3]*National Museum of Marine Science & Technology, Keelung 202, Taiwan*

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John Stewart Buckeridge, Benny K.K. Chan, and Shih-Wei Lee (2018) This paper describes a remarkably prolific accumulation of the whale barnacle *Coronula bifida* Bronn, 1831 in sediments of late Pliocene to earliest Pleistocene age from central Taiwan. Extant *Coronula* is host-specific to baleen whales; as such, this accumulation of *Coronula* fossils represents a site where cetaceans congregated during the Plio-Pleistocene - perhaps for breeding. Although whale bones are found at the site, they are rare and fragmentary; the relatively robust shells of *Coronula* are thus a useful proxy for establishing ancient cetacean migration routes.

Key words: *Coronula bifida*, Whale barnacles, Plio-Pleistocene, Fossil, Taiwan.

BACKGROUND

The whale barnacle *Coronula* Lamarck, 1802 is a genus of highly specialized, commonly globose-shaped, balanomorph barnacles that are adapted to live partially embedded in the skin of whales. Living specimens of *Coronula diadema* (Linnaeus, 1767), the most often encountered species, are almost always found on the humpback baleen whale (*Megaptera novaeangliae* Borowski, 1781) (Gray 1846) and is widely recorded from *M. novaeangliae* strandings.

A geological horizon with numerous *Coronula* shells suggests that the deposit accumulated in waters where whales congregated to reproduce and give birth. Similar situations occur today, *e.g.* along the Pacific coast of Baja California, where thousands of gray whales migrate to over the December - February period each year (Ross and Emerson 1974: 47; Fertl and Newman 2009).

Coronula is not a common fossil; accumulations of shells are very rare indeed and have been recorded from only a few locations globally (Table 1); however, horizons wherein *Coronula* shells are abundant are useful proxies for whale congregation sites and thus are indicative of ancient cetacean migration routes (see Bianucci et al. 2006a b).

Coronula is relatively unknown, both living and as a fossil in the Taiwan region, with only one previous record, a single empty shell of *Coronula diadema*, noted by Chan et al. (2009: 181), which was collected by benthic trawl, from a depth of 273 metres off the east coast of Taiwan. Even

*Correspondence: E-mail: leesw@mail.nmmst.gov.tw

when the region is extended to include all nearby waters, only one further *Coronula* locality has been recorded, also of *C. diadema* - four specimens removed from a beached whale at Hainan Island (Liu and Ren 2007: 325). This paper describes a remarkably abundant fossil assemblage of the extinct coronulid *Coronula bifida* Bronn, 1831 from Taiwan and of late Pliocene to earliest Pleistocene age. The specimens are from a sandstone and shale escarpment exposed on the Bazhang riverbed near the Chukou Niupu Tourist Center at Niupu, Zhongpu Township, Chaiyi, Western Central Taiwan, where many other fossils of marine invertebrates are also present (Fig. 1).

MATERIALS AND METHODS

Study sites and geological setting

The Liuchungchi Formation and Pan-Chiayi areas are located on the west side of the Central Mountain Range in Taiwan and are formed by convergence of the Eurasian and Philippine crustal plates. This convergence, locally known as the Penglai orogeny, began 6 million years ago in the late Miocene and continues today (*e.g.* Teng 1987 1990).

All specimens were collected from the Liuchungchi Formation, which is comprised of a series of medium to fine sandstones and shales, and has been dated as late Pliocene to earliest Pleistocene (Piacenzian to Gelasian) by Shao and Kao (2009). The primary collector was the local naturalist Mr Wen-Ji Xue, who made his collections between 1980 and 2000 (Xue 2004). The remains include many complete barnacle shells, although no opercula have yet been recovered. This place is famous for its fossil Lagerstätte. The associated fauna includes abundant molluscs, decapods, echinoderms and corals, along with teleosts, ungulates and cetaceans (Xue 2004: Fig. 2) and the balanomorph cirripedes described herein, *Amphibalanus* sp. cf. *A. reticulatus* (Utinomi, 1967) and *Striatobalanus*? sp. Importantly, *A. reticulatus* is still found living in Taiwanese waters (0-10 m) at the present time (Chan et al. 2009: 234).

Taphonomy and Palaeoecology

The record from Niupu, Chaiyi is such that there is little deformation of complex shells, which are often preserved in concretions (see Hu and Tao 1996; Xue 2004). There are numerous decapod remains associated with the barnacles, and most of these retain their appendages intact and appear *in situ*. Associated ichnofossils (*e.g.* specimen numbers 2263, 2264, 2265, 2267 of Chia-Yi Municipal Museum, see Fig. 2) indicate that the sedimentary environment in the area was shallow and had relatively low energy. None of the *Coronula* shells have opercula preserved with them. This is almost certainly due to the opercula of *Coronula* being both small and embedded within an opercular cuticle in the living animal; this cuticle, with the opercula, is easily detached from the rest of the barnacle shell shortly post-mortem. Further, the terga in *C. diadema* are either absent or vestigial; the scuta are very small, and as such, they are prone to dissolution. The presence of

Table 1. Accumulations of *Coronula* shells. This table only includes fossil localities where two or more specimens have been recovered. As such, they can likely be assessed as whale congregation sites. (For a list of all localities from which fossil *Coronula* has been recorded, see Bianucci et al. 2006a)

Species	Age	Location	Reference
†*Coronula bifida* Bronn, 1831	Late Pliocene	Taiwan	New data
†*Coronula bifida* Bronn, 1831	Early Pleistocene	Italy	Collareta et al. 2016 2018a
†*Coronula bifida* Bronn, 1831	Early Pleistocene	Italy	Collareta et al. 2016 2018a
†*Coronula bifida* Bronn, 1831*	Pleistocene	Ecuador	Bianucci et al. 2006a b
†*Coronula bifida* Bronn, 1831	Late Pliocene	England	Darwin 1854a
Coronula diadema (Linnaeus, 1767)	Plio-Pleistocene	Ecuador	Bianucci et al. 2006b
†*Coronula intermedia* Buckeridge 1983	Early Pleistocene	New Zealand	Buckeridge 2015

*This record for *Coronula bifida* Bronn, 1831 was named *Coronula dormitor* Pilsbry and Olsson 1951 who distinguished it from *Coronula bifida* Bronn, 1831 primarily on the absence of branching ribs in the compartments (*loc. cit.* p. 203). This variation is considered to be ontogenetic - Pilsbry and Olsson's largest specimen, which they selected as holotype, is only 25 mm in height and does possess a bifurcating rib (*loc. cit.* Pl. 11, fig. 2). As such, we concur with the suggestion made in Bianucci et al. 2006a that *C. dormitor* Pilsbry and Olsson, 1951 is a junior synonym of *C. bifida*. †indicate extinct species. † = extinct taxon.

Fig. 1. Location of the *Coronula bifida* Lagerstätte site near Niupu, Zhongpu Township, Chiayi, Western Central Taiwan. Insert showing the site on the Bazhang riverbed near the Chukou Niupu in Chaiyi City.

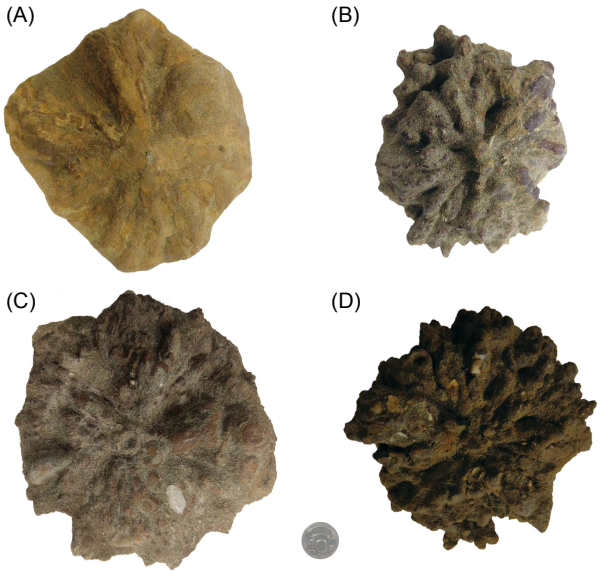

Fig. 2. Trace fossils from the Liuchungchi Formation,Chukou Niupu at Chaiyi City, Taiwan. (A) *Asterosoma i*sp. (#2267); (B) *Bifasiculus*? *i*sp. (#2265); (C) *Asterosoma i*sp. (#2263); (D) *Asterosoma i*sp. (#2264). These ichnofossils were likely formed by annelids, and give evidence for low-energy sea bottom conditions. Specimens held in the Chia-Yi Municipal Museum, Chaiyi City. (The diameter of the coin is 26 mm).

calcareous concretions in this horizon suggests that small calcareous remains would likely be dissolved.

Repositories

Specimen accession numbers contain the prefix CIMFO (*e.g.* CIMFO0047-0058) and have no prefix (*e.g.* 0860-0869); they are held in the palaeontological collection of the Chia-Yi Municipal Museum, Chaiyi City, Taiwan. Those with the prefix ASIZCR (*e.g.* ASIZCR000400-000409) are held in the Biodiversity Research Museum, Academia Sinica, Taipei, Taiwan; those with the prefix NMMST (*e.g.* NMMSTM000125) are held in the National Museum of Marine Science & Technology, Keelung, Taiwan; and those with the prefix G (*e.g.* G.324) are held in the Marine & Geological Systems collection at RMIT, Melbourne, Australia.

RESULTS

SYSTEMATICS

Superfamily Coronuloidea Leach, 1817
Family Coronulidae Leach, 1817
Coronula Lamarck, 1802

Diagnosis: Shell comprising six compartments of equal size, walls thin, deeply folded, with folds forming cavities, open basally; radii wide; body chamber relatively small, cup-shaped; opercular valves, paired terga and scuta, diminished in size, not articulated, together much smaller than the orifice; orifice of body chamber wider than basal opening; basis membranous. Attached to whales.

Remarks: The number of species in *Coronula* is now somewhat reduced from the seven listed in Newman and Ross (1976). Of the three in Darwin's 1854a monographs, only *Coronula diadema* (Linnaeus, 1767) and *Coronula reginae* Darwin, 1854a remain. *Coronula balaenaris* (Gmelin, 1791) has been assigned to *Cetopirus complanatus* (Mörch, 1853), and *Coronula barbara* Darwin, 1854a, is now regarded as *Coronula bifida* - a possibility that was contemplated by Darwin himself - see Darwin 1854a: 40 (Menesini 1968). Species proposed since Darwin include *Coronula ficarazzensis* De Gregorio, 1895 - now likely to be *Cetopirus* (Collareta et al. 2018a: 13), *Coronula dormitor* Pilsbry & Olsson, 1951, is *Coronula bifida*, and *Coronula macsotayi* Weisbord, 1971, is now considered *Coronula diadema* (Bianucci et al. 2006a b). This leaves two taxa from the antipodes, both fossil, and both defined by isolated plates: *Coronula aotea* Fleming, 1959 and *Coronula intermedia* Buckeridge, 1983. Both of these species are likely to have had a lower profile shell than *Coronula bifida* or *Coronula diadema*, to lie somewhat intermediate between these and *C. reginae*, or perhaps *Cetopirus*. Even with these later additions, only five species (*i.e.* †*C. aotea*, †*C. bifida, C. diadema*, †*C. intermedia*, and *C. reginae*) are currently assigned to *Coronula*. Those with † are known only as fossil, *C. diadema* has a record from Pliocene to Recent.

Distribution: Cosmopolitan, on whales. Pliocene to Recent.

Coronula bifida Bronn, 1831
(Fig. 3)

Coronula bifida Bronn, 1831: 126.
Coronula barbara Darwin, 1854a: 421.
Coronula dormitor Pilsbry and Olsson, 1951: 202.
Coronula bifida bifida Menesini, 1968: 387.
Coronula bifida barbara Menesini, 1968: 395.
Coronula bifida Collareta et al., 2018a: 15.
Coronula bifida Collareta et al., 2018b: 147

Distribution: Late Pliocene to early Pleistocene (Piacenzian to Gelasian, Taiwan - this work); Middle Pliocene to mid-lower Pleistocene (Calabrian, Western Europe; California; Ecuador). As *C. barbara*: Marquet et al. 2009; Zullo 1969; Beu 1971 Pilsbry and Olsson 1951; Darwin 1854b; De Alessandri 1960 Bianucci et al. 2006b; Collareta et al. 2016 2018a b (see full references in Collareta et al. 2018a).

Material Examined: Taiwan. 0860-0869: 10 complete shells (without opercula), 17.4-37.0 mm C-R diameter, 13.6-31.2 height; CIMFO0047-CIMFO0058 and NMMSTM000125: 13 complete shells (without opercula), 41.2-78.5 mm C-R diameter, 25.0-54.8 mm height; ASIZCR000400-ASIZCR000409: 10 complete shells (without opercula) 21.0-56.5 mm C-R diameter, 18.3-44.7 mm height; G.340: one specimen (without opercula), C-R diameter 47 mm, height 38 mm (Table S1). All specimens were collected by Mr Wen-Ji Xue between 1980 and 2000 and from an actively eroding escarpment at Chaiyi Niupu - 23°25'40.8"N, 120°33'25.7"E.

Diagnosis: *Coronula* with globose shell; compartments with convex longitudinal parietal ribs that often bifurcate, and with strong transverse ridges; radii broad, flat, becoming narrower in their lowermost third; body chamber relatively shallow,

Fig. 3. *Coronula bifida* Bronn, 1831 from Niupu, Chiayi, Western Central Taiwan, Liuchungchi Formation (Plio-Pleistocene). Specimens (#0860-0869) held by the Chia-Yi Municipal Museum, Chaiyi City, Taiwan.

sub-cylindrical; sheath less than half that of the total shell height.

Description: Shell globose; in adults, lower half of compartments developing five to six convex longitudinal parietal ribs; parietal ribs with strong transverse ridges in which bifurcation is rare; ridges spaced by at least their own height; basal edges of ribs crenated; orifice narrower than basal opening; compartments (*i.e.* ribs) noticeably worn in upper third of shell; radii broad, flat, summits horizontal; centrally radii are slightly wider than paries, becoming narrower in their lowermost third; body chamber relatively shallow, sub-cylindrical; sheath less than half of the total height of the shell. Opercula unknown.

Remarks: *Coronula bifida* is close to *Coronula diadema*; a phyletic lineage from *C. bifida* to *C. diadema* has been proposed by Dominici et al. (2011: 99), and as the ranges of these species are not known to overlap, this seems a reasonable conclusion. It differs from *C. diadema* in its more widely spaced transverse ridges on the parietal ribs and a shallower body chamber. In general *C. bifida* has more parietal ribs on each compartment than observed in *C. diadema* (*i.e.* the ribs branch less frequently in the latter species). The worn (= exposed) portion of the compartments suggests that the shell was embedded into the cetacean skin by slightly more than half of its height. Specimens of *C. diadema* in the collection at RMIT tend to show a proportionately greater worn zone, permitting us to conclude that *C. bifida* was buried deeper into the whale's skin. These observations are consistent with specimens of *C. bifida* recovered from the Mediterranean (Collareta et al. 2018a).

It is noteworthy that both Darwin (1854a: 420) and later Dominici et al. (2011: 97) commented that the differences between *C. diadema* and *Coronula reginae* are minimal. Darwin considered *C. reginae* more closely related to *C. balaenaris* than *C. diadema*, which is interesting, as *C. balaenaris* is now recognized as *Cetopirus* (see above). What this does is demonstrate the significant variation in whale barnacle morphology due to crowding and location on the whale. This variation is also demonstrated by the rather broad spectrum of shell morphologies in this collection of *C. bifida*.

Superfamily Balanoidea Leach, 1817

Family Archaeobalanidae
***Striatobalanus* Hoek, 1913**

Diagnosis: Shell comprising six solid compartments; radii solid, narrow with smooth sutural edges; scutum with well-formed adductor ridge; tergum with deep tergal furrow; paries generally strongly interlocked with calcareous base.

Distribution: Miocene to Recent: Indo-West Pacific (Recent taxa are often fouling).

***Striatobalanus*? sp.**
(Fig. 4)

Distribution: Late Pliocene to early Pleistocene (Piacenzian - Gelasian); Taiwan, (this record).

Material Examined: Taiwan. CIMFO0059-0062: from an actively eroding escarpment at Chaiyi Niupu - 23°25'40.8"N, 120°33'25.7"E

Description: Shell smooth, high-conic, with six solid compartments, radii solid, narrow with smooth, rounded sutural edges, summits steeply dipping; paries strongly interlocked with a solid, calcareous base (Fig. 4); opercula unknown. Exterior with alternating dark and light transverse banding.

Remarks: A lack of opercula prevents an accurate taxonomic placement for this material. *Striatobalanus* is represented in the modern Taiwan fauna by four species - *S. amaryllis*, *S. krugeri*, *S. taiwanenis* and *S. tenuis* - all of which possess very pale shells (Chan et al. 2009).

Family Balanidae Leach, 1817
***Amphibalanus* Pitombo, 2004**

Diagnosis: Shell comprising six compartments, exterior smooth; paries with single row of longitudinal pores; radii solid, transverse teeth on sutural edge with denticles on lower region; basis calcareous with a single layer of radially oriented pores; scutum with conspicuous adductor ridge.

Distribution: Cosmopolitan, Miocene to Recent (Newman and Ross 1976: 62).

Amphibalanus* sp. cf. *A. reticulatus
(Utinomi, 1967)
(Fig. 5)

Distribution: Late Pliocene to early Pleistocene (Piacenzian - Gelasian); Taiwan- (this work).

Material Examined: Taiwan. CIMFO0059-0062: four complete shells (without opercula). All specimens were collected by Wen-Ji Xue between

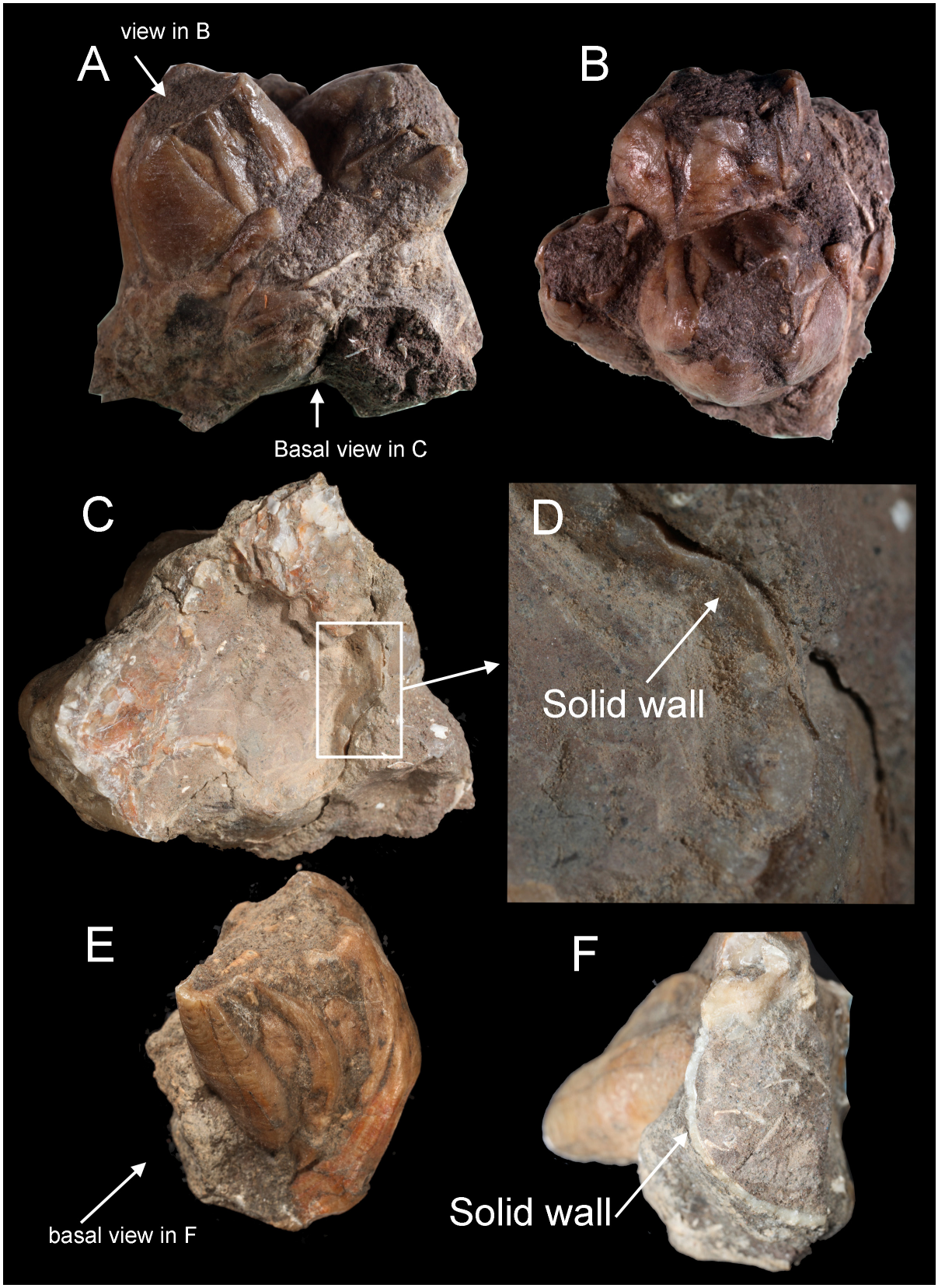

Fig. 4. (A-F) *Striatobalanus* sp. collected from the Liuchungchi Formation, Niupu, Chiayi, Western Central Taiwan, during the Plio-Pleistocene. Note that the shell walls, radii and bases are solid (*i.e.* non-tubiferous).

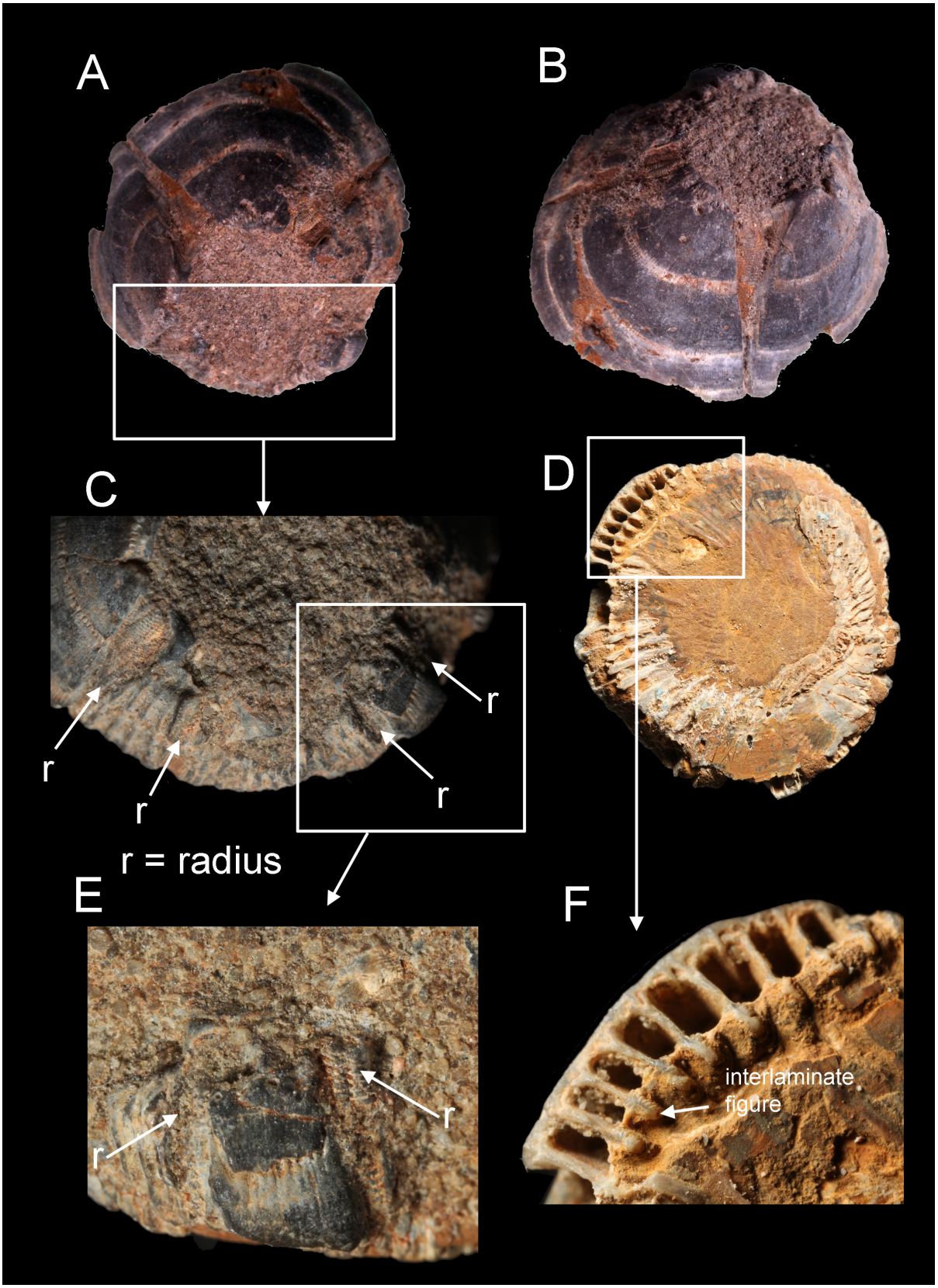

Fig. 5. (A-F) *Amphibalanus*? sp. collected from the Liuchungchi Formation, Niupu, Chiayi, Western Central Taiwan, (Plio-Pleistocene age). Note that the shell compartment are tubiferous and possess interlaminate figures.

1980 and 2000 and are from an actively eroding escarpment at Chaiyi Niupu - 23°25'40.8"N, 120°33'25.7"E; Specimens are held by the Chia-Yi Municipal Museum, Chaiyi City, Taiwan.

Description: Shell high-conic with six compartments, each with a single row of longitudinal pores; orifice rhomboid, toothed; radii solid, narrow, summits sub-vertical; exterior smooth, with cross-hatched pattern of thin, reddish-brown longitudinal bands crossed by similar transverse bands on a cream background; base calcareous with single row of radiating pores (Fig. 5). Opercula unknown.

Remarks: The absence of any opercula prevents a firm taxonomic placement of this material. The porous paries; the solid, narrow radii; and a base with single row of pores - and perhaps the coloration, places this within *Amphibalanus*. These specimens are closest to *Amphibalanus reticulatus* (Utinomi 1967), a common fouling species and which is known from the Recent of Taiwan (Chan et al. 2009). This occurrence supports a shallow water depositional environment.

DISCUSSION

Palaeoecology

The use of cirripede fossils to determine ancient cetacean migration routes is not new (Bianucci et al. 2006a b; Dominici et al. 2011; Collareta et al. 2016 2018a b). The idea utilizes fossils that are generally more robust and potentially more plentiful than fossilized whale bones. As *Coronula* Lamarck, 1802 and its sister taxa are generally host-specific, their presence in horizons, especially places where it is as abundant as at Chaiyi Zhongpu, are useful proxies for cetacean palaeo-migration paths. Whale fossil records in the Taiwan Strait have been studied (Tsai et al. 2014). The Chia-Yi Municipal Museum, Chaiyi City has a large baleen whale mandible on display. This mandible was thought to have been from the blue whale, *Balaenoptera musculus*, on the basis of size (Linnaeus 1758). However, a re-appraisal by museum staff changed the conclusion to the humpback whale (*Megaptera novaeangliae*) (Fig. 6). If this is so, this whale would have been larger than any known specimen of *M. novaeangliae*.

Fig. 6. A large fossil baleen whale mandible, currently attributed to the humpback whale, *Megaptera novaeangliae* Gray, 1846. Recovered from the Liuchungchi Formation, Zhongpu Township, Chiayi, Western Central Taiwan. On display in the Chia-Yi Municipal Museum, Chaiyi City, Taiwan.

Living *Coronula diadema* is restricted to a small number of cetaceans - primarily the humpback (*M. novaeangliae*) and gray whales (*Eschrichtius robustus* Liljeborg, 1861), both of which are smaller than *B. musculus*. *Balaenoptera musculus* is not known to become infested with *Coronula*, leading to the possibility that in the Pliocene, *M. novaeangliae* (the larger of the two species) grew to a greater length than it does in the present day.

In addition to intertidal and shallow water cirripedes, the Liuchungchi Formation contains a diverse faunal assemblage, characterized by abundant molluscs, decapods and echinoderms corals, along with teleosts, ungulates and cetaceans (Xue 2004). A shallow marine depositional environment, perhaps less than 30 metres deep, is supported by the presence of land vertebrates (ungulates) and shallow water species such as the intertidal barnacle *Amphibalanus* and the upper subtidal barnacle *Striatobalanus*.

CONCLUSIONS

These deposits are the most prolific *Coronula*-bearing sediments in the western Pacific, and globally are only rivalled by the *Coronula diadema*-rich horizons of Ecuador (Bianucci et al. 2006a). This is without question the most complete known location of *Coronula bifida*. The abundance of the barnacle remains suggests that this was a site where whales grouped, perhaps for breeding and calving purposes. They also indicate that this area of Central Taiwan was, during the late Pliocene or earliest Pleistocene, part of an important whale migration route.

Acknowledgments: The authors thank the late Wen-Ji Xue, an enthusiastic and careful observer of nature, who first noticed these specimens in the outcrop at Chaiyi Niupu, and was astute enough to recognize them as having special significance. We thank Jia-Feng Chen and Shih-Chuan Chen for their assistance in the field work. Ewan Fordyce (Otago University, Dunedin) provided useful advice about the maximum size of living humpback whales. Thanks to Pei-Chen Tsai (Academia Sinica, Taiwan) for taking the photograph of the fossil whale bone in the Chai-Yi Municipal Museum. The authors also thank an anonymous reviewer and Tomáš Kočí (Natural History Museum, Prague, Czech Republic), for helpful comments on the manuscript.

Author contributions: JSB, BKKC and SWL wrote the manuscript. JSB, BKKC and SWL performed morphological examinations. All authors confirmation that our manuscript has not been sent to other journals for consideration at the same time.

Competing interests: JSB, BKKC and SWL declare that they have no conflict of interest.

Availability of data and materials: Fossil samples have been deposited in the Chia-Yi Municipal Museum, Chaiyi City, Taiwan; Biodiversity Research Museum, Academia Sinica, Taipei, Taiwan; National Museum of Marine Science & Technology, Keelung, Taiwan; and in the Marine & Geological Systems collection at RMIT, Melbourne, Australia.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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Supplementary Material

Table S1. Shell size range of *Coronula bifida* Bronn, 1831 from Taiwan. C-R diameter is the maximum width of the shell along the carinal-rostral axis. (download)