Bulletin of the Mizunami Fossil Museum, vol. 50, no. 1, 1–19, 2 figs, 3 plates. ©2023, Mizunami Fossil Museum Manuscript accepted on January 22, 2023; online published on March 17, 2023 https://zoobank.org/urn:lsid:zoobank.org:pub:51224AD1-890F-452F-8025-9C2739C568C3

Fossil whale barnacles (Cirripedia: Thoracica: Coronuloidea) of Japan

Hiroaki Karasawa*

*Mizunami Fossil Museum, 1-47 Yamanouchi, Akeyo, Mizunami, Gifu 509-6132, Japan < gha06103@nifty.com >

Abstract

Fossil whale barnacles (Balanomorpha: Coronulidae) deposited in the Mizunami Fossil Museum, are classified. Seven species in three genera of whale barnacles from the Pliocene–Pleistocene deposits of Japan are recorded and illustrated. *Cetopirus complanatus* (Mörch) from the Middle Pleistocene, *Coronula reginae* Darwin from the Lower Pleistocene (Calabrian), and *Cryptolepas rachianecti* Dall from the Lower Pleistocene (Gelasian) are first reported in the Japanese fossil records. *Coronula* Lamarck comprises five species, *C. barbara* Darwin from the Lower Pleistocene, *C. bifida* Bronn from the Lower Pleistocene (Gelasian), *C. diadema* (Linnaeus) from the Lower Pleistocene (Calabrian)–Middle Pleistocene, *C. reginae* from the Lower Pleistocene (Calabrian), and *C.* sp. from the Middle Pleistocene. A compartment of an undetermined coronulid genus and species from the Lower Pleistocene (Gelasian) compared with that of *Tubicinella major* Lamarck and *Cetolepas hertleini* Zullo is also described.

Key words: Balanomorpha, Coronulidae, Neogene, Quaternary

1. Introduction

The whale barnacle family Coronulidae Leach, 1817, is epibiotic on skins of whales and dolphins (Hayashi, 2013). Hayashi (2013) complied currently known fossil records of Coronulidae of the world. Since Yokoyama (1910) first described *Coronula diadema* (Linnaeus, 1767) as a fossil from the Koshiba Formation of Kanagawa Prefecture, this species has been reported from the Pliocene–Pleistocene deposits from Japan (Hatai, 1938, 1939; Ozaki, 1958; Koizumi and Matsushima, 1992; Tanaka, 1992, 1993; Mimoto, 2001). Thus, whale barnacles have been sparse in the Japanese fossil records.

The purpose of the present paper is to report new and previously recorded whale barnacles from the Pliocene– Pleistocene deposits of Japan, based upon examinations of the paleontological collection in the Mizunami Fossil Museum (MFM). As a result, seven species in three genera, and one undetermined genus and species are recognized, and their occurrences and geologic ranges are provided.

2. Localities

The materials examined herein were obtained from the following localities in Honshu, Shikoku, Okinawa-jima island, and Miyako-jima island, Japan (Fig. 1A).

The present works:

Loc. C01: Ichijiku (=locality of Kimura et al. (2008)), Kimitsu City, Chiba Prefecture; Ichijiku Formation of the Kazusa Group; Middle Pleistocene (ca 0.73– 0.63 Ma) by Ito (1992).

- Loc. C02: Tsukuihama (= locality of Yamaguchi (1971)), Zushi City, Kanagawa Prefecture; Tsukuihama Member of the Miyata Formation; Middle Pleistocene (ca 0.513 Ma) by Toyoda and Okumura (2000).
- Loc. C03: Takamatsu (=locality of Karasawa and Kobayashi (2022)); Tahara City, Aichi Prefecture; Toyohashi Formation of the Atsumi Group; Middle Pleistocene (ca 0.4 Ma) by Nakasima et al. (2008).
- Loc. C04: Ukari (=around loc. U of Nobuhara (1993)), Fukuroi City, Shizuoka Prefecture; Higikata Formation of the Kakegawa Group; Early Pleistocene (ca 1.9–1.6 Ma) by Ibaraki (1986).
- Loc. C05: Hongo (=loc. Hongo-2 of Ozawa et al. (1998)), Kakegawa City, Shizuoka Prefecture; Dainichi Formation of the Kakegawa Group; Early Pleistocene (ca 2.4–1.9 Ma) by Ozawa et al. (1998).
- Loc. C06: Iida (=loc. Iida of Ozawa et al. (1998)), Mori-machi, Shizuoka Prefecture; Dainichi Formation of the Kakegawa Group; Early Pleistocene (ca 2.4–1.9 Ma) by Ozawa et al. (1998).
- Loc. C07: Godaijima (=loc. Godaijima of Ozawa et al. (1998)), Iwata City, Shizuoka Prefecture; Aburayama Formation of the Kakegawa Group; Early Pleistocene (ca 1.9–1.6 Ma) by Ozawa et al. (1998).
- Loc. C08: Ohkuwa (=loc. ONM-1 of Karasawa (1993)), Kanazawa City, Ishikawa Prefecture; the middle part of the Onma Formation; Early Pleistocene (ca 1.5–1.0 Ma) by Kitamura (1994).
- Loc. C09: Zukawa (=loc. ZKW-1 of Karasawa (1993)), Takaoka City, Toyama Prefecture; the upper part of the Zukawa Formation; Late Pliocene (ca 3.5–2.59 Ma) by Amano et al. (2012).
- Loc. C10: Tonohama (=loc. T of Matsubara (2004)), Yasuda-cho, Kochi Prefecture; Ananai Formation of the Tonohama Group; Late Pliocene–Early Pleistocene (ca 2.78 or 2.73–1.97 Ma) by Matsubara (2004).
- Loc. C11: Hane (=loc. N of Matsubara (2004)), Muroto City, Kochi Prefecture; Nobori Formation of the Tonohama Group; Early–Late Pliocene (ca 4.2–3.21 or 3.12 Ma) by Matsubara (2004).
- Loc. C12: Hioki (=loc. F2 of Majima et al. (2003)), Sintomi-cho, Miyazaki Prefecture; Takanabe Formation of the Miyazaki Group; Late Pliocene–

Early Pleistocene (ca 3.4–2.4 Ma) by Sato et al. (2012).

- Loc. C13: Nakoshi (=loc. NKJ-1 of Karasawa, 1993), Nago City, Okinawa Prefecture; Shinzato Formation; Early Pleistocene (ca 1.65–1.21 Ma) by Yamamoto et al. (2005).
- Loc. C14: Toubaru (=locality of Karasawa, 2020), Uruma City, Okinawa Prefecture; Shinzato Formation of the Shimajiri Group; Early Pleistocene (ca 2.5–1.9 Ma) by Kaneko and Ujiié, 2006).
- Loc. C15: Shikenbaru, Nanjyo City, Okinawa Prefecture; Shinzato Formation of the Shimajiri Group; Early Pleistocene (ca 2.5–1.9 Ma) by Kaneko and Ujiié (2006).
- Loc. C16: Higa (=loc. 5 of Sato et al. (2004)), Miyakojima City, Okinawa Prefecture; Yonahama Formation of the Shimajiri Group; Early Pliocene– Late Pliocene (ca 4.3–3.4 Ma) by Sato et al. (2002).
- Loc. C17: Awasegai (=loc. 21 of Amano et al. (2000)), Daisen City, Akita Prefecture; Tentokuji Formation; Late Pliocene (ca 3.5 Ma) by Amano et al. (2000).

Previous records referred to the present work:

- Loc. A: Koshiba, Yokohama City, Kanagawa Prefecture; Koshiba Formation; Early Pleistocene (ca 1.7–1.4 Ma) by Fujioka et al. (2003); *Coronula diadema* by Yokoyama (1910).
- Loc. B: South of Kakegawa City (=around Locs. C04 and C05), Ogasa-gun, Totomi Province and near Dainiti, Ogasa-gun, Totomi Province (=around Kakegawa City, Shizuoka Prefecture); Dainichi and Higikata formations of the Kakegawa Group; Early Pleistocene (ca 2.4–1.6 Ma); *Coronula barbara* as *C. diadema* by Hatai (1939).
- Loc. C: Byoubugaura, Choshi City, Chiba Prefecture; Obama Formation of the Inubou Group; Early Pleistocene (ca 1.71–0.95 Ma) by Fujioka and Kameo (2004); *Coronula diadema* by Ozaki (1958).
- Loc. D: Iwase, Kamakura City, Kanagawa Prefecture;
 Ofuna Formation; Early Pleistocene (ca 1.76–1.7
 Ma) by Fujioka et al. (2003); *Coronula barbara* as *C. diadema* by Koizumi and Matsushima (1992).
- Loc. E: Hongo (=Loc. C05), Kakegawa City, Shizuoka Prefecture; Dainichi Formation of the Kakegawa Group; Early Pleistocene (ca 2.4–1.9 Ma); *Coronula bifida* as *C. diadema* by Tanaka (1992).

- Loc. F: Ukari, Fukuroi City and Ieshiro, Hongo, and Ketuenji, Kakegawa City (=around Locs. C04 and C05), Shizuoka Prefecture; Dainichi and Higikata formations of the Kakegawa Group; Early Pleistocene (ca 2.4–1.6 Ma); *Coronula barbara* as *C. diadema* by Tanaka (1993).
- Loc. G: Hane (=Loc. C11), Muroto City, Kochi Prefecture; Nobori Formation of the Tonohama Group; Early–Late Pliocene (ca 4.2–3.21 or 3.12 Ma); *Coronula bifida* as *C. diadema* by Mimoto (2001).

3. Taxonomy

Order Balanomorpha Pilsbry, 1916 Superfamily Coronuloidea Leach, 1817 Family Coronulidae Leach, 1817

Genus Cetopirus Ranzani, 1817

Type species: Lepas balaenaris Gmelin, 1791 (*non Lepas balaenaris* Müller, 1776) (*=Lepas complanata* Mörch, 1853), by subsequent designation of Ranzani (1818).

Diagnosis: Body within a depressed, often domeshaped shell, consisting of six subequal compartments; circumference subcircular in apical view; orifice of the body chamber rounded-hexagonal, not larger than the basal opening; opercular valves present, much smaller than the orifice; sheath short, smooth to somewhat grooved, whose basal edge does not project freely; ala square and thin; compound radius moderately to very thick, whose closely spaced, copiously branching sutural septa originate from a main septum running along the outer edge of the radius; external radius rather narrow and transversely striated; paries thin, provided with broad longitudinal ribs having Tshaped terminations (primary T-shaped flanges) that form a secondary outer lamina; primary T-shaped flanges perforated by longitudinally elongated tubes or tubules; secondary T-shaped flanges present in the form of minute projections that abut from the primary T-shaped flanges; core of the ribs solidly calcified; ribs externally flattened, ornamented by weak transverse growth folds and fine longitudinal striae, lacking transverse interlocking crenulations; apex of the shell presenting four ribs forming three cavities in-between; secondary branching very symmetrical and

frequent, occurring near the apex of the shell and resulting in the basal edge of each compartment presenting a tree-like aspect (adapted from Collareta et al., 2022, p. 2).

Cetopirus complanatus (Mörch, 1853)

(Pl. 1, figs. 1a-3d)

- Lepas balaenaris Gmelin, 1791, p. 3208 (non Lepas balaenaris Müller, 1776).
- Lepas complanata Mörch, 1853, p. 67 (non Lepas complanata polythalamia Chemnitz, 1785).
- Ceteopirus [sic] complanatus: Mörch, 1853, p. 67.
- *Coronula complanata*: Pilsbry, 1916, p. 276, pl. 63, figs. 1–3a (synonymy).
- Cetopirus complanatus: Hayashi, 2013, p. 164 (synonymy).

Diagnosis: Shell very shortly barrel-shaped or cylindric, basal opening at least as large as orifice; sheath shorter than the inner wall, its basal edge not overhanging; ribs along sutures, in the base, having several symmetrically arranged branches in adult individuals; radii almost as thick as the compartments; opposed edges of terminal flanges of ribs roughened but not crenulate; form depressed (modified from Pilsbry, 1916, p. 273).

Remarks: All specimens have erosional external surfaces. The present species recognized as a fossil is recorded for the first time from Japan. Although *C. complanatus* is the obligate epibiont on skins of the right whales, *Eubalaena australis* and *E. glacialis*, from the Arctic, Atlantic, North Pacific, and Antarctica (Ten et al., 2022), the extant record has not yet been known from Japan.

Material examined: MFM143050–143053 (laterals/carinolaterals) from Loc. C01; MFM143054 (lateral/carinolateral) from Loc. C02.

Fossil occurrences of Japan: Loc. C01, Ichijiku Formation, Middle Pleistocene; Loc. C02, Miyata Formation; Middle Pleistocene.

Geologic range of Japan: Middle Pleistocene (ca 0.73–0.513 Ma).

Other fossil occurrences: Middle Pleistocene of South Africa (Collareta et al., 2017); Holocene of Spain (Álvarez-Fernández et al., 2014; Bosselaers et al., 2017), The Netherlands (Holthuis et al., 1997), and Argentina (Pastorino and Griffin, 1996).



Fig. 1. A, Map showing the whale barnacle-bearing localities of Japan; the map is derived from the Geospatial Information Authority of Japan (http://geolib.gsi.go.jp/). **B**, Geologic range and occurrence of each species.

Type species: Lepas diadema Linnaeus, 1767, by subsequent designation of Pilsbry (1916).

Diagnosis: Shell composed of 6 equal-sized compartmental plates; parietes with similar structure throughout, without internal midribs; radiating accordion-like folds of parietes (ribs) ending in T-shaped flanges forming exterior of wall; ribs on either side of sutures unbranched or asymmetrically branched; opposed sides of terminal flanges crenulate; radii well developed, less than half thickness of compartmental plates, leaving cavity between radii and adjacent alae; sheath smooth, as long as inner wall. Orifice of body chamber larger than basal openings (modified from Newman et al., 1969, p. 289).

Coronula barbara Darwin, 1854

(Pl. 1, figs. 4a–7b; Pl. 2, figs. 1a–2b)

- Coronula barbara Darwin, 1854, p. 421, pl. 15, fig.
 6; De Alessandri, 1895, p. 303, pl. 3, figs. 8a–b;
 De Alessandri, 1906, p. 317, pl. 18, figs. 12a–12b; Zullo, 1969, p. 21, figs. 73–77; Hayashi, 2013, p. 163 (synonymy); Collins et al., 2014, p. 223, figs. 6O, 9A–9B.
- *Coronula bifida barbara*: Menesini, 1968: 395, pl. 3, figs. 3a–5c, pl. 4, figs. 2, 4, 6.
- *Coronula diadema*: Hatai, 1939, p. 227, figs. 1–2; Koizumi and Matsushima, 1992, figs. 7.3–7.4; Tanaka, 1993, p. 2, pls. 1–2.

Diagnosis: Shell crown-shaped; longitudinal parietal ribs on compartments convex, prominent, crossed by widely spaced prominent, transverse growth ridges; radii moderately thick; spaces between radii and alae solidly filled up (modified from Darwin, 1854, p. 421, and Collins et al., 2014, p. 233).

Remarks: Menesini (1968) regarded *Coronula barbara* as the subspecies of *Coronula bifida*. Subsequently, Dominici et al. (2011) suggested that *C. barbara* was synonymized with *C. bifida* and several subsequent workers (i.e., Collareta et al., 2018; Buckeridge et al., 2019) followed their opinion. However, Hayashi (2013) and Collins et al. (2014) treated *C. barbara* as a distinct species. I concur. The convex parietal ribs with widely spaced growth ridges readily distinguish *C. barbara* from *C. bifida*.

Hatai (1939) described complete shells of *Coronula* diadema from the Pliocene–Pleistocene Kakegawa Group of Shizuoka Prefecture. Most recently, Buckeridge et al. (2019) assigned them to shells of *Coronula bifida*; however, these specimens are identified with *C. barbara* by having parietal ribs with widely spaced prominent growth ridges. *Coronula di*adema from the Lower Pleistocene Ofuna Formation (Koizumi and Matsushima, 1992) and Lower Pleistocene Kakegawa Group (Tanaka, 1992) are also identical with *C. barbara* of the presence of widely spaced prominent growth ridges on parietal ribs.

Material examined: MFM143055–143056 (laterals) from Loc. C04; MFM143057 (lateral/carinolateral) from Loc. C05; MFM143058 (articulated compartments with rostrum, lateral, and carinolateral) from Loc. C06; MFM143059–143060 (rostrum) from Loc. C07; MFM143061 (rostrum), MFM143062 (articulated compartments with lateral, carinolateral, and carina), and MFM143063 (articulated compartments with lateral, carinolateral, and carina) from Loc. C08; MFM143064 (articulated compartments with lateral. carinolateral, and carina) from Loc. C13.

Fossil occurrences of Japan: Locs. C04, B, and F; Higikata Formation, Early Pleistocene; Locs. C05, C06, B, and F, Dainichi Formation, Early Pleistocene; Loc. C07, Aburayama Formation, Early Pleistocene; Loc. C08, Onma Formation, Early Pleistocene; Loc. C13, Shinzato Formation, Early Pleistocene; Loc. D, Ofuna Formation, Early Pleistocene.

Geologic range of Japan: Early Pleistocene (ca 2.4–1.0 Ma).

Other fossil occurrences: Pliocene of England (Darwin, 1854; Collins et al., 2014), Italy (De Alessandri, 1906; Menesini, 1968), and California, USA (Zullo, 1969).

Coronula bifida Bronn, 1831

(Pl. 2, figs. 3a–9b)

- *Coronula bifida* Bronn, 1831, p. 126; De Alessandri, 1895, p. 302, pl. 3, figs. 7a–7b; De Alessandri, 1906, p. 315, pl. 18, figs. 8–1b; Hayashi, 2013, p. 163 (synonymy).
- *Coronula dormitor* Pilsbry and Olsson, 1951, p. 202, pl. 11, figs. 1–5 (junior synonym by Bianucci et al., 2006a, p. 118).

- *Coronula bifida bifida*: Menesini, 1968, p. 387, pls. 1–3, pl. 4, figs. 1, 3, 5.
- *Coronula diadema*: Tanaka, 1992, p. 34, figs. 2–6; Mimoto, 2001, figs. 1–2b.

Diagnosis: Shell globose; longitudinal parietal ribs on compartments gently convex, usually bifurcated, furrowed by densely crenated fold; buttresses irregularly branched (modified from De Alessandri, 1895, p. 302).

Remarks: Kim et al. (2020) assigned all Japanese fossils to *Coronula bifida* and mapped their occurrences, based upon Buckeridge et al. (2019). However, examination of MFM collections suggests the existence of five species belonging to *Coronula* in the Pliocene–Pleistocene deposits of Japan. Furthermore, the specimens listed in Hatai (1938, 1939) have never been illustrated and should be revisited. For the time being, it is more correct to think that there are multiple species for Japanese fossils, as in Buckeridge et al. (2019).

Material examined: MFM143065–143068 (rostra, laterals, carina) from Loc. C05; MFM143069–143073 (rostrum, laterals) from Loc. C06; MFM143074 (articulated compartments with rostrum and laterals) from Loc. C09; MFM143075 (lateral) from Loc. C10; MFM143076–143077 (laterals) from Loc. C11; MFM143078 (rostrum) from Loc. C12; MFM143080 (disarticulated compartments) from Loc. C14; MFM143081–143084 (rostrum, carinolaterals/laterals) from Loc. C16; MFM143099 (carinolateral/lateral) from Loc. C17.

Fossil occurrences of Japan: Locs. C05, C6, and E, Dainichi Formation, Early Pleistocene; Loc. C07, Aburayama Formation, Early Pleistocene; Loc. C09, Zukawa Formation, Late Pliocene; Loc. C10, Ananai Formation, Late Pliocene–Early Pleistocene; Locs. C11 and G, Nobori Formation, Early–Late Pliocene; Loc. C12, Takanabe Formation, Late Pliocene–Early Pleistocene; Loc. C14 and C15, Shinzato Formation, Early Pleistocene; Loc. C16, Yonahama Formation, Early Pliocene–Late Pliocene; Loc. C17, Tentokuji Formation, Early Pleistocene.

Geologic range of Japan: Early Pliocene–Early Pleistocene (ca 4.3–1.9 Ma).

Other fossil occurrences: Pliocene of Ecuador (Pilsbry and Olsson, 1951; Bianucci et al., 2006b); Pliocene–Pleistocene of Italy (De Alessandri, 1906; Menesini, 1968) and Taiwan (Buckeridge et al., 2018; 2019).

Coronula diadema (Linnaeus, 1767) (Pls. 3–4)

Lepas diadema Linnaeus, 1767, p. 1109.

Coronula diadema: Lamarck, 1818, p. 387; Hayashi, 2013, p. 163 (synonymy).

Coronula macsotayi Weisbord, 1971, p. 91, pl. 20, figs. 1–4 (junior synonym by Bianucci et al., 2006b, p. 329).

Diagnosis: Shell crown-shaped with convex ribs and crenated edges, crossed by narrow, beaded growth ridges; basal edges of ribs crenated; radii as wide in upper part as parietes in lower part, about 1/2 thickness of whole plate; orifice larger than basal opening; terga vestigial or absent; scuta small and embedded in thick opercular cuticle; sheath descends almost to basal inner edge of wall; outer edge of wall much deeper in host's skin than inner edge (after Foster, 1978, p. 116).

Remarks: This species is the common epibiont on the humpback whale, *Megaptera novaeangliae*, from the Atlantic, Pacific, and Indian oceans (Hayashi, 2013; Ten et al., 2022). The oldest record of Japan is known from the Early Pleistocene Koshiba Formation (Yokoyama, 1910) and Obama Formation (Ozaki, 1958).

Material examined: MFM143086–143090 (complete shells), MFM143091 (articulated compartments with lateral, carinolateral, and carina), and MFM143092 (lateral) from Loc. C01; MFM143093–143094 (laterals) from Loc. C02; MFM143095 (complete shell) from Loc. C08.

Fossil occurrences of Japan: Loc. C01, Ichijiku Formation, Middle Pleistocene; Loc. C02, Miyata Formation, Middle Pleistocene; Loc. C08, Onma Formation, Early Pleistocene; Loc. A, Koshiba Formation, Early Pleistocene; Loc. C, Obama Formation, Early Pleistocene.

Geologic range of Japan: Early Pleistocene (ca 1.71 Ma)–Recent.

Other fossil occurrences: Pliocene of Ecuador (Bianucci et al., 2006b); Pleistocene of Italy (Dominici et al., 2011), Cyprus (De Alessandri, 1906), Venezuela (Weisbord, 1971), Galápagos Islands (Zullo, 1986), New Zealand (Beu, 1971; Buckeridge, 1983), Vanuatu (Bianucci et al., 2006a), and Rodrigues Ridge (Gale, 2020).

Coronula reginae Darwin, 1854

(Figs. 2.5a–2.5c)

Coronula reginae Darwin, 1854, p. 419, pl. 15, fig. 5, pl. 16, fig. 4.

Coronula reginae: Hayashi, 2013, p. 163 (synonymy).

Diagnosis: Shell low, conical with flattened ribs which have crenate lateral edges and crossed by delicate, beaded growth-ridges; basal edges of ribs crenulated; radii considerably narrower in upper part than lower part of parietes, and not more than 1/4 thickness of the whole plate; orifice larger than basal opening, basal edge of sheath free. Terga absent; scuta small and embedded in opercular cuticle; 1/4 to 1/2 whole diameter embedded in skin of whale (after Foster, 1978, p. 116).

Remarks: The present specimens from the Lower Pleistocene Onma Formation represent the first fossil and oldest record of *C. reginae*. This species is known as the obligate epibiont of baleen whales from Arctic, Atlantic, North Pacific, Indian, and Antarctic oceans (Ten et al., 2022).

Material examined: MFM143096 (complete shell) from Loc. C08.

Fossil occurrences of Japan: Loc. C08, Onma Formation, Early Pleistocene.

Geologic range of Japan: Early Pleistocene (ca 1.5–1.0 Ma)–Recent.

Coronula sp.

(Figs. 2.2a–2.3c)

Remarks: Karasawa and Kobayashi (2022) reported the carinolateral/lateral and rostral compartments of an unnamed species of *Coronula* from the Middle Pleistocene Atsumi Group. After that, Collareta et al. (2022) suggested that these specimens had great affinities with the species of *Cetopirus*. However, compartments from the Atsumi Group have transverse interlocking crenulations of ribs, not seen in *Cetopirus*. Therefore, the taxonomic status of these specimens is retained.

Material examined: MFM142475 (lateral/carinolateral) and MFM142999 (carina) from Loc. C03. *Fossil occurrences of Japan*: Loc. C03, Toyohashi Formation, Middle Pleistocene.

Geologic range of Japan: Middle Pleistocene (ca 0.4 Ma).

Genus Cryptolepas Dall, 1872

Type species: *Cryptolepas rachianecti* Dall, 1872, by original designation.

Diagnosis: Shell depressed with body-chamber shortly cylindric; parietes bearing radial lamellar folds which are irregularly branched in adults, not forming outer wall; sheath grooved transversely; radii moderately developed; basis membranous; opercular valves present (modified from Pilsbry, 1916, p. 279).

Cryptolepas rachianecti Dall, 1872

(Figs. 2.1a–2.1d)

Cryptolepas rachianecti Dall, 1872, p. 300. Cryptolepas rachianecti: Pilsbry, 1916, p. 279, pl. 66, figs. 1–5a (synonymy).

Diagnosis: Almost wholly embedded in host's skin, mostly on head and back, only opercular membrane and parts of radii or sometimes more prominent ribs exposed; compartments normally having 30 ribs and 30 lobes; having four ribs on each of parietes; radial ornamentation denticulated with alaeal ornamentation of adjacent compartment; ribs on compartments finely striae vertically and crenulated at edge; sheath very long, not quite reaching to base, transversely grooved, and not overhanging or prominent on its basal margin; radii usually as thick as compartments, their edges intricately sculptured with crimped sutural laminae; terga absent or rudimentary; scuta piled up by caustic layers (adapted from Hayashi, 2012, p. 112).

Remarks: The specimen corresponds to the carinolateral or lateral compartment of a cylindric form described by Pilsbry (1916, p. 280, pl. 66, figs. 2–2a). The present specimen from the Upper Pleistocene Shinzato Formation represents the first fossil record for *Cryptolepas rachianecti* from Japan. This species is typically attached to skins of the gray whale, *Eschrichtius robustus*, from the North Pacific (Hayashi, 2013; Ten et al., 2022).

Material examined: MFM143097 (carinolateral/lateral) from Loc. C14. *Fossil occurrences of Japan*: Loc. C14, Shinzato Formation, Early Pleistocene.

Geologic range of Japan: Early Pleistocene (ca 2.5–1.9 Ma)–Recent.

Other fossil occurrences: Upper Pliocene–Lower Pleistocene of Ecuador (Taylor et al., 2022); Holocene of The Netherlands (Bosselaers and Collareta, 2016).

Coronulidae, genus and species indeterminate (Figs. 2.4a–2.4b)

Remarks: The specimen is only represented by an incomplete, isolated carinolateral/lateral compartment. The compartment is thin, the flattened paries is longitudinally striated with seven transverse ridges, the sheath is long, a narrow radius has a dentate

margin, and the ala is also narrow. It is somewhat similar to the compartment of *Tubicinella major* Lamarck, 1802, from the Atlantic and South oceans, but differs by the absence of rounded transverse ridges of the paries. Although the specimen is compared with an oldtype compartment of *Cetolepas hertleini* Zullo, 1969, from the Upper Pliocene San Diego Formation of California, it lacks the longitudinally elevated ribs on the paries. A further identification of it awaits the discovery of more well-preserved material.

Material examined: MFM143098 (carinola-teral/lateral) from Loc. C14.

Fossil occurrences of Japan: Loc. C14, Shinzato Formation, Early Pleistocene.

Geologic range of Japan: Early Pleistocene (ca 2.5–1.9 Ma).



Fig. 2. *1a–d*, *Cryptolepas rachianecti* Dall, 1872, MFM143097 (carinolateral/lateral) from Loc. C14. *2a–3c*, *Coronula* sp. from Loc. C03; 2a–c, MFM142475 (lateral/carinolateral); 3a–c, MFM142999 (carina). *4a–b*, Coronulidae, genus and species indeterminate, MFM143098 (carinolateral/lateral) from Loc. C14. *5a–c*, *Coronula reginae* Darwin, 1854, MFM143096 (complete shell) from Loc. C08. Scale bars = 5 mm. 1a, 2a, 3a, 4a, 5b, 5c, external; 1b, 2b, 4b, 3b, internal; 1c, 2c, 3c, lateral; 5a, dorsal; 1d, basal view.

4. Acknowledgements

This paper is dedicated to the late senior researcher, A. Koizumi (formerly, Curator of the Iida City Museum). I am very grateful to T. Goda (Konan, Aichi), T. Kaede (Mizunami, Gifu), N. Kobayashi (Gamagori, Aichi), and Y. Kurihara (Faculty of Education, Mie University) for offering their specimens, H. Kato (Natural History Museum and Institute, Chiba) and T. Haga (Department of Geology and Paleontology, National Museum of Nature and Science) for providing access to their collections, and A. Collareta (Dipartimento di Scienze della Terra, Università di Pisa) for providing useful comments. The manuscript benefited greatly from the critical review of S. K. Donovan (Swinton, Manchester, UK).

5. References

Álvarez-Fernández, E., R. P. Carriol, J. F. Jordá, J. E. Aura, B. Avezuela, E. Badal, Y. Carrión, J. García-Guinea, A. Maestro, J. V. Morales, G. Perez, M. Perez-Ripoll, M. J. Rodrigo, J. E. Scarff, M. P. Villalba, and R. Wood. 2014. Occurrence of whale barnacles in Nerja Cave (Málaga, southern Spain): indirect evidence of whale consumption by humans in the Upper Magdalenian. Quaternary International 337: 163–169.

DOI: 10.1016/j.quaint.2013.01.014

Amano, K., M. Hamuro, T. Hamuro, T. Sato, and R. Ogihara. 2012. Influence of the latest Pliocene cooling to the benthic fauna from the central part of the Japan Sea borderland: Molluscan fauna from the Zukawa Formation in Toyama Prefecture. The Journal of the Geological Society of Japan 118: 810–822.

DOI: 10.5575/geosoc.2012.0058

- Amano, K., M. Suzuki, and T. Sato. 2000. Warm-water influx into Japan Sea in the middle Pliocene—Molluscan fauna from the Tentokuji Formation around Mt. Taihei in Akita Prefecture—. The Journal of the Geological Society of Japan 106: 299–306. DOI: 10.5575/geosoc.106.299
- Beu, A. G. 1971. Further fossil whale barnacles from New Zealand. New Zealand Journal of Geology and Geophysics 14: 898–904.

Bianucci, G., W. Landini, and J. S. Buckeridge. 2006a. Whale barnacles and Neogene cetacean migration routes. New Zealand Journal of Geology and Geophysics 49: 115–120.

DOI: 10.1080/00288306.2006.9515152

Bianucci, G., C. Di Celma, W. Landini, and J. S. Buckeridge. 2006b. Palaeoecology and taphonomy of an extraordinary whale barnacle accumulation from the Plio-Pleistocene of Ecuador. Palaeogeography, Palaeoclimatology, Palaeoecology 242: 326–342.

DOI: 10.1016/j.palaeo.2006.07.004

Bosselaers, M., and A. Collareta. 2016. The whale barnacle *Cryptolepas rhachianecti* (Cirripedia: Coronulidae), a phoront of the grey whale *Eschrichtius robustus* (Cetacea: Eschrichtiidae), from a sandy beach in The Netherlands. Zootaxa 4154: 331–338.

DOI: 10.11646/zootaxa.4154.3.8

- Bosselaers, M., F. Van Nieulande, and A. Collareta. 2017. A new record of *Cetopirus complanatus* (Cirripedia: Coronulidae), an epibiont of right whales (Cetacea: Balaenidae: *Eubalaena* spp.), from a beach deposit of Mediterranean Spain. Atti della Società Toscana di Scienze Naturali, Memorie, Serie A 124: 43–48.
- Bronn, H. 1831. Italiens Tertiär-Gebilde und deren organische Einschlüsse: vier Abhandlungen. Groos. Heidelberg. 176 p.
- Buckeridge, J. S. 1983. The fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia.New Zealand Geological Survey, Paleontological Bulletin 50: 1–151, 14 pls.
- Buckeridge, J. S., B. K. K. Chan, and S.-W. Lee. 2018. 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. Zoological Studies 57: 54.

DOI: 10.6620/ZS.2018.57-54

Buckeridge, J. S., B. K. K. Chan, and J. P. Lin. 2019. Paleontological studies of whale barnacles in Taiwan reveal new cetacean migration routes in the western Pacific since the Miocene. Zoological Studies 58: e39.

DOI: 10.6620/ZS.2019.58-39

- Chemnitz, J. H. 1785. Neues systematisches Conchylien-Cabinet. Tom. 8. Bey Gabriel Nicholaus Raspe. Nurnberg. ixviii + 372 p., 102 pls.
- Collareta, A., M. Bosselaers, P., Holroyd, and A. Dineen. 2022. A forgotten cirripedological gem: A new species of whale barnacle of the genus *Cetopirus* from the Pleistocene of the United States West Coast. Earth and Environmental Science Transactions of the Royal Society of Edinburgh: 1–8.

DOI: 10.1017/S1755691022000214

- Collareta, A., G. Insacco, A. Reitano, R. Catanzariti, M. Bosselaers, M. Montes, and G. Bianucci. 2018.
 Fossil whale barnacles from the early Pleistocene of Sicily shed light on the coeval Mediterranean cetacean fauna. Carnets de Géologie 18: 9–22.
- Collareta, A., C. W. Marean, A. Jerardino, and M. Bosselaers. 2017. *Cetopirus complanatus* (Cirripedia: Coronulidae) from the late Middle Pleistocene human settlement of Pinnacle Point 13B (Mossel Bay, South Africa). Zootaxa 4237: 393–400.

DOI: 10.11646/zootaxa.4237.2.12

Collins, J. S. H., S. K. Donovan, and C. Mellish. 2014. An illustrated guide to the fossil barnacles (Cirripedia) from the Crags (Plio-Pleistocene) of East Anglia, Proceedings of the Geologists' Association 125: 215–226.

DOI: 10.1016/j.pgeola.2014.01.004.

- Dall, W. H. 1872. On the parasites of the cetaceans of the N.W. coast of America, with descriptions of new forms. Proceedings of the California Academy of Sciences 4: 299–301.
- Darwin, C. 1854. A Monograph on the Subclass Cirripedia with Figures of all the Species. The Balanidae, the Verrucidae, etc. Ray Society. London. 684 p. 30 pls.
- De Alessandri, G. 1895. Contribuzione allo studio dei Cirripedi fossili d'Italia. Bollettino della Società Geologica Italiana, Roma 13: 234–314, 5 pls.
- De Alessandri, G. 1906. Studi monografici sui cirripedi fossili d'Italia. Palaeontographia Italica 12: 207–324, 18 pls.
- Dominici, S., M. Bartalini, M. Benvenuti, and B. Balestra. 2011. Large kings with small crowns: a Mediterranean Pleistocene whale barnacle. Bollettino della Società Paleontologica Italiana 50: 95–101. DOI: 10.4435/BSPI.2011.10

- Foster, B. A. 1978. The marine fauna of New Zealand: barnacles (Cirripedia: Thoracica). New Zealand Oceanographic Institute Memoir 69: 1–143.
- Fujioka, M., and K. Kameo. 2004. Correlation between the Obama Formation of the Inubou Group in the Choshi district and the Kiwada, Otadai and Umegase Formations of the Kazusa Group in the Boso Peninsula, central Japan, based on key tephra layers. The Journal of the Geological Society of Japan 110: 480–496.

DOI: 10.5575/geosoc.110.480

Fujioka, M., K. Kameo, and N. Kotake. 2003. Correlation based on key tephra layers between the Ofuna-Koshiba Formations in the Yokohama district and the Kiwada Formation in the Boso Peninsula, control Japan. The Journal of the Geological Society of Japan 109: 166–178.

DOI: 10.5575/geosoc.109.166

- Gale, A. S. 2020. Bathyal Pliocene–early Pleistocene cirripedes (Crustacea, Thoracica) from the Rodrigues Ridge, Mascarene Plateau, Indian Ocean. Part 2. Cainozoic Research 20: 189–207.
- Gmelin, J. F. 1791. Caroli a Linné systema naturae per regna tria naturae. Editio decima tertia aucta reformata, cura J. F. Gmelin. Tom 1, Pars. 6, Vermes Testacea. Impensis Georg. Emanuel. Beer. Leipzig. p. 3021–3910.
- Hatai, K. M. 1938. A review of the fossil Cirripedia and shark's teeth from the region of the northeast Honsyu, Japan. Bulletin of the Biogeographical Society of Japan 8: 95–102.
- Hatai, K. M. 1939. On the occurrence of *Coronula* from the Kakegawa series in Totomi, Japan. Bulletin of the Biogeographical Society of Japan 9: 261– 265.
- Hayashi, R. 2012. Atlas of the barnacles on marine vertebrates in Japanese waters including taxonomic review of superfamily Coronuloidea (Cirripedia: Thoracica). Journal of the Marine Biological Association of the United Kingdom 92: 107–127. DOI: 10.1017/S0025315411000737
- Hayashi, R. 2013. A checklist of turtle and whale barnacles (Cirripedia: Thoracica: Coronuloidea). Journal of the Marine Biological Association of the United Kingdom 93: 143–182.
 DOI: 10.1017/S0025315412000847

- Holthuis, L. B., C. Smeenk, and F. J. Laarman. 1998.
 The find of a whale barnacle, *Cetopirus complanatus* (Mörch, 1853), in 10th century deposits in the Netherlands. Zoologische Verhandelingen 323: 349–363.
- Ibaraki, M. 1986. Neogene planktonic foraminiferal biostratigraphy of the Kakegawa area on the Pacific coast of central Japan. Reports of Faculty of Science, Shizuoka University 20: 39–173.
- Ito, M. 1992. High-frequency depositional sequences of the upper part of the Kazusa Group, a middle Pleistocene forearc basin fill in Boso Peninsula, Japan. Sedimentary Geology 76: 155–175. DOI: 10.1016/0037-0738(92)90081-2
- Kaneko, N., and H. Ujiié. 2006. Geology of the Itoman and Kudakajima District. Quadrangle Series, 1:50,000.Geological Survey of Japan, AIST. Tsukuba. 47 p.
- Karasawa, H. 1993. Cenozoic decapod Crustacea from southwest Japan. Bulletin of the Mizunami Fossil Museum 20: 1–92.
- Karasawa, H. 2020. Cenozoic pedunculate barnacles (Cirripedia: Thoracica) deposited in the Mizunami Fossil Museum, Japan. Bulletin of the Mizunami Fossil Museum 47: 21–40.

DOI: 10.50897/bmfm.47.0_21

Karasawa, H., and N. Kobayashi. 2022. Cirripedes from the middle Pleistocene Atsumi Group, Japan, with a reevaluation of the genus *Adna* Sowerby, 1823 (Balanoidea: Pyrgomatidae). Bulletin of the Mizunami Fossil Museum 49: 67–93.

DOI: 10.50897/bmfm.49.0_67

Kim. H. K., B. K. K. Chan, C.-B. Kang, H. W. Kim, and W. Kim. 2020. How do whale barnacles live on their hosts? Functional morphology and matinggroup sizes of *Coronula diadema* (Linnaeus, 1767) and *Conchoderma auritum* (Linnaeus, 1767) (Cirripedia: Thoracicalcarea). Journal of Crustacean Biology 40: 808–824.

DOI: 10.1093/jcbiol/ruaa075

- Kimura, T., S. Isaji, and T. Yanagisawa. 2008. A Pleistocene delphinid from the Ichijiku Formation, Chiba Prefecture, Japan. Bulletin of Gunma Museum of Natural History 12: 35–45.
- Kitamura, A. 1994. Depositional sequences caused by glacio-eustatic sea-level changes in the upper part of the early Pleistocene Omma Formation, The

Journal of the Geological Society of Japan 100: 463–476.

DOI: 10.5575/geosoc.100.463

- Koizumi, K., and Y. Matsushima. 1992. Upper bathyal molluscan fossils, Crustacea and fishes from the Lower Pleistocene Ofuna Formation in Kamakura, Southern Kanto. Natural History Report of Kanagawa 13: 119–128.
- Lamarck, J. B. P. A. 1802. Mémoire sur la Tubicinelle. Annales du Muséum National d'Histoire Naturelle 1: 461–464.
- Lamarck, J. B. P. A. 1818. Histoire naturelle des animaux sans vertébrés, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, en n, l'exposition des principes fondamentaux de la zoologie, vol. 5. Verdière. Paris. p. 1–612.
- Leach, W. E. 1817. Distribution, systematique de la class Cirripedes. Journal de Physique de Chimie et d'Histoire Naturelle, Paris 85: 67–69.
- Linnaeus, C. von. 1767. Systema Naturae. ed. 12, vol. 1 (2). Laurentii Salvii. Holmiae [= Stockholm]. p. 533–1372.
- Majima, R., K. Ikeda, H. Wada, and K. Kato. 2003. An outer-shelf cold-seep assemblage in forearc basin fill, Pliocene Takanabe Formation, Kyushu Island, Japan. Paleontological Research 7: 297–311. DOI: 10.2517/prpsj.7.297
- Matsubara, T. 2004. Catalogue of the Pliocene Mollusca from the Tônohama Group in Kôchi Prefecture, Shikoku, Japan, in the Museum of Nature and Human Activities, Hyogo (Takao Sendô Collection). Nature and Human Activities 8: 49–95.
- Menesini, E. 1968. Osservazioni su *Coronula bifida* Bronn. Atti della Società Toscana di Scienze Naturali Memorie, serie A 75: 387–398.
- Mimoto, K. 2001. Macrocheira sp. (Decapoda) and other crustacean fossils from the Pliocene Nobori Formation, Shikoku, Japan. Chigakukenkyu 50: 131–135.
- Mörch, O. A. L. 1853. Catalogus conchyliorum quae reliquit D. Alphonso d'Aguirra & Gadea Comes de

Yoldi, Regis Daniae Cubiculariorum Princeps, Ordinis Dannebrogici in Prima Classe & Ordinis Caroli Tertii Eques. Fasc. 2, Acephala, Annulata, Cirripedia, Echinodermata. Ludovici Kleine. Hafniae. 74 p.

- Müller, O. F. 1776. Zoologica Danicae Prodromus seu Animalium Daniae et Norvegiae indigenarum characters, nomine, et synonyma imprimis popularium. Typis Hallageriis. Copenhagen. 1–282.
- Nakashima, R., K. Mizuno, and A. Furusawa. 2008. Depositional age of the Middle Pleistocene Atsumi Group in Atsumi Peninsula, central Japan, based on tephra correlation. The Journal of the Geological Society of Japan 114: 70–79.

DOI: 10.5575/geosoc.114.70

- Newman, W. A., V. A. Zullo, and T. H. Withers. 1969. Cirripedia. In R. C. Moore, ed., Treatise on Invertebrate Paleontology, part R, Arthropoda 4,1. The Geological Society of America, Inc. and The University of Kansas Press. Boulder, Colorado and Lawrence, Kansas. p. R206–R295.
- Nobuhara, T. 1993. The relationship between bathymetric depth and climate change and its effect on molluscan faunas of the Kakegawa Group, central Japan. Transactions and proceedings of the Paleontological Society of Japan. New series 170: 159– 185.

DOI: 10.14825/prpsj1951.1993.170_159

- Ozaki, H. 1958. Stratigraphical and Paleontological Studies on the Neogene and Pleistocene Formations of the Tyosi District. Bulletin of the National Science Museum 4: 1–182.
- Ozawa, T., Tanaka, T., and S. Tomida. 1998. Pliocene to Early Pleistocene warm water molluscan fauna from the Kakegawa Group, central Japan. Nagoya University Furukawa Museum Special Report 7: 1– 141, 31 pls.
- Pastorino, G., and M. Griffin. 1996. An extant whale barnacle (Cirripedia, Coronulidae) from Holocene deposits of Buenos Aires (Argentina). Crustaceana 69: 769–772.
- Pilsbry, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. Bulletin of the United States National Museum 93: 1–366.

DOI: 10.5479/si.03629236.93.1

- Pilsbry, H. A., and A. A. Olsson. 1951. Tertiary and Cretaceous Cirripedia from northwestern South America. Proceedings of the Academy of Natural Sciences of Philadelphia 103: 197–210.
- Ranzani, C. A. 1817. Osservazioni su I Balanidi -Parte II. Opuscoli scientifici 1: 269–276.
- Ranzani, C. A. 1818. Osservazioni su I Balanidi -Parte III. Opuscoli scientifici 2: 63–93.
- Sato, T., S. Chiyonobu, and M. Farida. 2012. Terminal Neogene events and beginning of the Quaternary climate system based on calcareous nannofossils. The Journal of the Geological Society of Japan 118: 87–96.

DOI: 10.5575/geosoc.2011.0005

Sato, T., H. Nakagawa, J. Komatsubara, R. Matsumoto, Y. Iryu, H. Matsuda, A. Omura, K. Odawara, and R. Takeuchi. 2004. Geological age of the Chinen Formation in southern Okinawa-jima based on calcareous microfossils. The Journal of the Geological Society of Japan 110: 38–50. DOI: 10.5575/geogge.110.28

DOI: 10.5575/geosoc.110.38

- Sato, T., T. Saito, and S. Yuguchi. 2002. Late Pliocene calcareous nannofossil paleobiogeography of the Pacific Ocean: Evidence for glaciation at 2.75 Ma. Revista Mexicana de Ciencias Geológicas 19: 175–189.
- Tanaka, T. 1992. Fossil *Coronula* from the Pliocene in Kakegawa City. Kasekinotomo 39: 34–36.
- Tanaka, T. 1993. Pliocene fossil *Coronula* from in Kakegawa City and its environs. Kasekinotomo 40: 2–7.
- Taylor, L., J. Abella, and J. M. Morales-Saldaña. 2022.
 New fossil remains of the commensal barnacle *Cryptolepas rhachianecti* provide evidence of gray whales in the prehistoric South Pacific. Journal of Paleontology 96: 583–590.
 DOI: 10.1017/jpa.2021.113
- Ten, S., J. A. Raga, and F. J. Aznar. 2022. Epibiotic Fauna on Cetaceans Worldwide: A Systematic Review of Records and Indicator Potential. Frontiers in Marine Science 9: 846558.

DOI: 10.3389/fmars.2022.846558

Toyota, H., and K. Okumura. 2009. ESR Ages of the Pleistocene Miyada Formation in the Miura Peninsula, Central Japan. The Quaternary Research 39: 559–568.

DOI: 10.4116/jaqua.39.559

- Weisbord, N. E. 1971. A new species of *Coronula* (Cirripedia) from the Lower Pliocene of Venezuela. Bulletin of American Paleontology 60(265): 87–96.
- Yamaguchi, T. 1971. Fossil barnacles from the Pleistocene Miyata Formation. Science Report of the Yokosuka City Museum 18: 122–129, 1 pl.
- Yamamoto, K., Y. Iryu, T. Sato, and E. Abe. 2005. Stratigraphy of the Ryukyu Group on northern Motobu Peninsula, Okinawa-jima, Ryukyu Islands, Japan., The Journal of the Geological Society of Japan 111: 527–546.
 - DOI: 10.5575/geosoc.111.527

- Yokoyama, M. 1910. On the Occurrence of *Coronula diadema* L., in the Tertiary of koshiba. The Journal of the Geological Society of Japan 17: 227–229.
- Zullo, V. A. 1969. Thoracic Cirripedia of the San Diego Foration, San Diego County, California. Contributions in Science of the Los Angeles County Museum of Natural History 159: 1–25.
- Zullo, V. A. 1986. Quaternary barnacles from the Galápagos Islands. Proceedings of the California Academy Sciences 44: 55–66.

Explanation of Plates

Plate 1

Figs. 1a-3d. Cetopirus complanatus (Mörch, 1853)

- 1a-e, MFM143050 (lateral/carinolateral) from Loc. C01.
- 2a-d, MFM143051 (lateral/carinolateral) from Loc. C01.
- 3a-d, MFM143053 (lateral/carinolateral) from Loc. C01.
- 1a, 2a, 3a, external; 1b, 2b, 2c, 3b, internal; 1c, 1d, 3c, 3d, lateral view;
- 1e, 2d, close-up images of terminal transverse loops of ribs.

Figs. 4a-7b. Coronula barbara Darwin, 1854

4a-4c. MFM143061 (rostrum) from Loc. C08.

- 5. MFM143062 (articulated compartments with lateral, carinolateral, and carina) from Loc. C08.
- 6a-c. MFM143063 (articulated compartments with lateral, carinolateral, and carina) from Loc. C08.
- 7a-b. MFM143064 (articulated compartments with lateral. carinolateral, and carina) from Loc. C13.

4a, 5, 6b, 7b, external; 4b, 6c, internal; 6a, 7a, dorsal; 4c, 6c, lateral view.

Scale bars = 5 mm except for figs. 1e and 2d.





Plate 2

Figs. 1a-2b. Coronula barbara Darwin, 1854

1a-c. MFM143060 (rostrum) from Loc. C07.

2a-b. MFM143058 (articulated compartments with rostrum, lateral, and carinolateral) from Loc. C06.

1a, 2b, external; 1b, internal; 2a, dorsal; 1c, lateral view.

Figs. 3a-9b. Coronula bifida Bronn, 1831

3a-c. MFM143065 (lateral) from Loc. C05.

4a-c. MFM143066 (rostrum) from Loc. C05.

5a-c. MFM143067 (carina) from Loc. C05.

6a-b. MFM143068 (lateral) from Loc. C05.

7a-c. MFM143081 (rostrum) from Loc. C15.

8. MFM143080 (disarticulated compartments) from Loc. C14.

9a-b. MFM143074 (articulated compartments with rostrum and laterals) from Loc. C09.

3a, 4a, 5a, 6a, 7a, 8, 9a, external; 3b, 4b, 5b, 6b, 7b, 9b, internal; 3c, 7c, 5c, lateral view.

Scale bars = 5 mm.





Plate 3

1a-7c. Coronula diadema (Linnaeus, 1767)

1a-b. MFM143095 (complete shell) from Loc. C08.

2a-c. MFM143092 (lateral) from Loc. C01.

3a-c. MFM143086 (complete shell) from Loc. C01.

4a-c. MFM143087 (complete shell) from Loc. C01.

5a-b. MFM143091 (articulated compartments with lateral, carinolateral, and carina) from Loc. C01.

6a-c. MFM143088 (complete shell) from Loc. C01.

7a-c. MFM143089 (complete shell) from Loc. C01.

1a, 3a, 4a, 6a, 7a, dorsal; 1b, 2a, 3b, 4b, 5a, 6b, 7b, external; 2b, 5b, inter-

nal; 2c, lateral; 2c, 3c, 4c, 6c, 7c, basal view.

Scale bars = 5 mm.



