

A forgotten cirripedological gem: a new species of whale barnacle of the genus *Cetopirus* from the Pleistocene of the United States West Coast

Alberto COLLARETA^{1,2*} , Mark BOSSELAERS^{3,4}, Patricia A. HOLROYD⁵ and Ashley DINEEN⁵

¹ Dipartimento di Scienze della Terra, Università di Pisa, via S. Maria 53, 56126 Pisa, Italy.

² Museo di Storia Naturale, Università di Pisa, via Roma 79, 56011 Calci, Italy.

³ Koninklijk Belgisch Instituut voor Natuurwetenschappen, Operationele Directie Aarde en Geschiedenis van het Leven, Vautierstraat 29, 1000 Brussel, Belgium.

⁴ Koninklijk Zeeuwsch Genootschap der Wetenschappen, Kousteensedijk 7, 4331 JE, PO Box 378, 4330 AJ Middelburg, the Netherlands.

⁵ University of California Museum of Paleontology, 1101 Valley Life Sciences Building, Berkeley, CA 94720-4780, USA.

*Corresponding author. Email: alberto.collareta@unipi.it

ABSTRACT: A small lot of fossil whale barnacles from the Upper Pleistocene of California and the Middle Pleistocene (Chibanian) of Oregon (United States West Coast), described in a 1972 unpublished MA thesis, are formally described and illustrated herein. In that thesis, a new genus and species name were proposed; however, according to the International Code of Zoological Nomenclature, they have no taxonomic standing and are thus unavailable. Based on our reappraisal, two specimens in this lot belong to a new, extinct species that can be assigned to the purportedly extant genus *Cetopirus*. *Cetopirus polysyrinx* sp. nov. differs from congeners in that its secondary T-shaped flanges are multitubiferous internally, that is, they are perforated by a high number of irregularly-sized and irregularly-spaced tubules that result in a spongy aspect in transverse section. Whether or not this peculiar condition had any adaptive significance is difficult to determine. Considering that *Cetopirus* is currently known as an obligate epibiont of right whales (including the North Pacific form *Eubalaena japonica* (Lacépède 1818)), the host of *C. polysyrinx* sp. nov. was *E. japonica* or some other species of *Eubalaena*. The Plio-Pleistocene deposits of the Pacific coast of North America have yielded a rather idiosyncratic fossil whale barnacle fauna, inclusive of the genera *Cetolepas*, *Cryptolepas* and now *Cetopirus*, which seemingly contrasts with all other coeval assemblages worldwide, the latter being in turn dominated by *Coronula* spp.



KEY WORDS: California, *Cetopirus polysyrinx* sp. nov., Chibanian, Cirripedia, Coronulidae, epibiosis, Oregon, taxonomy, Upper Pleistocene.

1. Introduction

Fifty years ago, Clark William Davis, a graduate student at San Francisco State University, USA, authored one of the most relevant contributions to the modern understanding of the skeletal anatomy and functional morphology of the extant and extinct whale barnacles (Cirripedia: Coronulidae) in the form of a MA thesis (Davis 1972) that is currently available online (Collareta *et al.* 2022a). In that thesis, entitled ‘Studies on the barnacles epizoic on marine vertebrates’, Davis (1972) informally described a new genus and species of whale barnacle, ‘*Polysyrinx zulloi*’, on the basis of a handful of fossils from the United States West Coast. However, both the names ‘*Polysyrinx*’ and ‘*P. zulloi*’ have not been formally published and are thus unavailable in light of the International Code of Zoological Nomenclature (1999: articles 8 and 9; see also Dubois *et al.* 2013), whereas they are published herein as *nomina nuda*

(International Code of Zoological Nomenclature 1999: articles 11 and 13, and glossary). While we were unable to track down the author of this particular MA thesis, we did succeed in tracing three out of four specimens referred by Davis (1972) to ‘*Polysyrinx zulloi*’. Below we describe Davis’ new coronulid taxon on solid nomenclatural grounds and discuss its palaeontological significance.

2. Material and methods

2.1. Institutional abbreviations

CAS: California Academy of Sciences (San Francisco, California, USA); LACM: Natural History Museum of Los Angeles (Los Angeles, California, USA), in the Invertebrate Paleontology (=LACMIP) department; UCMP: University of California Museum of Paleontology (Berkeley, California, USA).

2.2. Digital imaging

Two of the specimens studied herein were scanned by one of us (PAH) on a Phoenix Nanotom-M nanofocus X-ray computed tomography (CT) system in the Functional Anatomy and Vertebrate Evolution Laboratory at the University of California-Berkeley at a resolution of 10 microns per pixel. Reconstructed slices were cropped in Fiji 1.53q (Schindelin *et al.* 2012), rendered in three dimensions using Slicer 4.11 (Fedorov *et al.* 2012) using the SlicerMorph extension (Rolfe *et al.* 2021), segmented and the segmentation exported as an STL file. The resultant STL file was imported into Meshlab (Cignoni *et al.* 2008) and decimated to approximately one-third the number of original faces to produce a smaller, web-viewable PLY file using their variant of quadric edge-collapse decimation (Garland & Heckbert 1997). Both the cropped CT-stack and decimated PLY files were uploaded to MorphoSource.org.

3. Geological framework

The whale barnacle fossils dealt with in the present paper are represented by three specimens, including the holotype and a single paratype of a new species of *Cetopirus*, plus a third specimen that is left herein in open nomenclature.

As reported by Davis (1972), one of these originated from LACM locality 1210, San Pedro, Los Angeles County, California, USA (Fig. 1). Also referred to as LACMIP 1210, this locality is described in the museum records as a 'bed of fossil shells in unconsolidated sand thickening from 2 feet at west end to 6 feet at east end; where it is underlain by single layer of cobble conglomerate and has some cross bedding in layers with fossils above.' This bed no longer appears to be accessible, but did occur on the small bluff formed by the Gaffey Syncline, between modern-day N. Gaffey Street and the West Basin in the north-western part of the town of San Pedro, approximately where Westmont Drive and industrial buildings sit today. The locality was mapped in Wehmiller *et al.* (1977; fig. 2h) and Muhs *et al.* (1992; fig. 3). Woodring *et al.* (1946) recognised the deposits cropping out in this area as being entirely part of their 'first terrace' of the Palos Verdes Sand Formation. Wehmiller *et al.* (1977) recorded amino acid stereochemistry values from the bivalve genus *Saxidoma* from LACM 1210 and assigned the locality to the early part of the Marine Isotope Stage (MIS) 5. Muhs *et al.* (1992) showed that faunas from Woodring *et al.*'s (1946) 'first terrace' represented two temporally different highstands, with LACM 1210 being assigned to the 125 ka highstand (i.e., MIS 5e). Based on the most recent synthesis of data bearing on the age of MIS 5e sites along the west coast of North America (Muhs *et al.* 2021; Muhs 2022), the age of locality LACM 1210 is estimated to be 130 to 115 ka.

According to Davis (1972), two additional specimens were recovered from UCMP localities B7376 and B7380, near Cape Blanco, Curry County, Oregon, USA (Fig. 1). With regard to the former locality, it was described as in the 'same horizon as B7375 and about 100 feet south'. Both UCMP B7375 and B7376 were collected by Jack A. Wolfe and Victor A. Zullo during the same field trip, but data on geology and location were recorded only on the locality card for B7375. UCMP B7375 occurs in a well-sampled stretch of uplifted terraces exposed on cliffs north of the mouth of the Elk River, Curry County, Oregon, USA, that have produced diverse invertebrate assemblages and rarer marine mammals. The invertebrate assemblages were the topic of an unpublished PhD thesis by Roth (1979) and the vertebrate faunas were most recently reviewed by both Boessenecker (2013a) and Welton (2015). Locality UCMP B7375 was collected by Wolfe and Zullo in March 1960 from a unit described in the UCMP records as '25 feet below the conglomerate in the lower buff sandstone' approximately 100

feet along the cliff. Topographically, the site corresponds to the area where Welton (2015) measured his Section 1 at Gold-washer's Gully, the northernmost of four sections, and containing the vertebrate localities UCMP V74042 and NMMNH 9241. The locality description suggests that the site is in the Lower Brown Sandstone Member, an interpretation also indicated in Roth (1979). This unit falls within all modern interpretations of the Port Orford Formation (e.g., Boessenecker 2013a; Wiley *et al.* 2014; Welton 2015), although older literature and records (e.g., museum locality registers; Leffler 1964; Davis 1972; Roth 1979) refer to this unit as part of the Elk River Formation.

UCMP B7380 occurs in the same stretch of uplifted terraces as UCMP B7375 and B7376, between Welton's (2015) sections 3 and 4, where the lower part of the Port Orford Formation is covered (see also Boessenecker, 2013a; fig. 1.4 for an outcrop photograph). Fossils were collected *in situ* from the Upper Brown Sandstone Member by Wolfe and Zullo in March 1960 and again in 1961 by a class field trip from the University of California, Department of Paleontology. UCMP B7380 is stratigraphically higher than B7375 and B7376, being separated from the Lower Brown Sandstone Member by approximately 14 m of the Blue Argillaceous Sandstone Member. Welton (2015) followed Baldwin (1945, 1959) in including the Upper Brown Sandstone Member in the Elk River Beds, whereas Boessenecker (2013a) and Wiley *et al.* (2014) considered it to be part of the Port Orford Formation. Whichever stratigraphic nomenclature is used, molluscs from the Upper Brown Sandstone Member (from LACM locality 3960) were dated to 500,000 ± 100,000 years via amino acid racemisation, and the rocks are reported to have normal palaeomagnetic polarity (Wehmiller *et al.* 1978). Kennedy *et al.* (1982) also reported a potentially younger age interpretation (early MIS 3) of a terrace at Cape Blanco on the basis of amino acid racemisation, but also noted that the fauna was otherwise indistinguishable from the cool-water fauna associated with late stage 5 localities. Both studies indicate that these rocks and their associated faunas are Chibanian (Middle Pleistocene) in age, although currently available data do not permit greater refinement.

In addition to the specimens described here, Roth (1979) noted the presence of a single plate from this same area at UCMP locality B7371, in the Upper Brown Sandstone Member. He referred it to *Cetopirus complanatus* (Mörch 1853), but the specimen was not formally catalogued and could not be located at the UCMP. Roth (1979) also noted that the record of *Coronula* (*Cetopirus*) in the Pleistocene of Oregon listed by Newman *et al.* (1969) was likely based on his specimen, although we cannot exclude the possibility that they were referring to the specimens described here, especially as Zullo, being co-author of the paper by Newman *et al.* (1969), was also one of the collectors. Interestingly, the occurrence of *Coronula complanata* (= *Cetopirus complanatus*) in Late Pliocene [*sic*] deposits at Cape Blanco, Oregon was also reported by Zullo (1969).

4. Systematics

Family Coronulidae Leach, 1817

Genus *Cetopirus* Ranzani, 1817

Type species: *Lepas complanata* Mörch, 1853, Late Pleistocene to Recent (possibly extinct; see Bosselaers *et al.* 2017).

Distribution: Early Pleistocene to Recent. Currently known as an obligate epibiont of *Eubalaena* spp., living in temperate seas.

Diagnosis (emended after Collareta *et al.* 2016): Body within a depressed, often dome-shaped 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



Figure 1. Location of the finds of *Cetopirus polysyrinx* sp. nov. along the Pacific coast of the USA. Geographical base map after wikimedia.org.

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 T-shaped 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.

Cetopirus polysyrinx sp. nov.

(Figs 2–4)

?1961 *Coronula complanata* – Zullo, p. 14

?1969 *Coronula (Cetopirus)* – Newman *et al.*, p. R289

1972 '*Polysyrinx zulloi*' [unavailable name, published herein as a *nomen nudum*] – Davis, p. 36 (*partim*); figs 35–37, 39, 40

Diagnosis: A *Cetopirus* species in which the secondary T-shaped flanges that comprise the primary outer lamina are internally multitubiferous, being perforated by a high number of irregularly-sized and irregularly-spaced tubules that provide them with a spongy aspect in transverse section.

Holotype: LACMIP 1210.158 (=LACMIP Type 14915), isolated right carinolatus.

Etymology: The new species name derives from the Greek and means 'many tubes', which appears very appropriate in light of the multitubiferous condition of its primary T-shaped flanges. The same combination of Greek words was selected by Davis (1972) as the (unavailable) genus name of his (unpublished) new taxon. Thus, our choice also pays a due tribute to Davis' remarkable contribution to cirripedology.

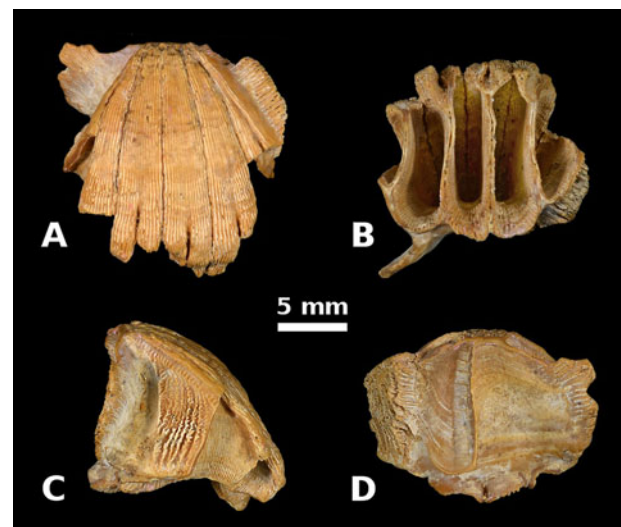


Figure 2. *Cetopirus polysyrinx* sp. nov. (holotype), LACMIP 1210.158, isolated right compartment (carinolatus) collected at San Pedro (Los Angeles County, California, USA) from Upper Pleistocene deposits. (a) external view; (b) basal view; (c) alar view; and (d) central view. Photographs by Lindsay Walker.

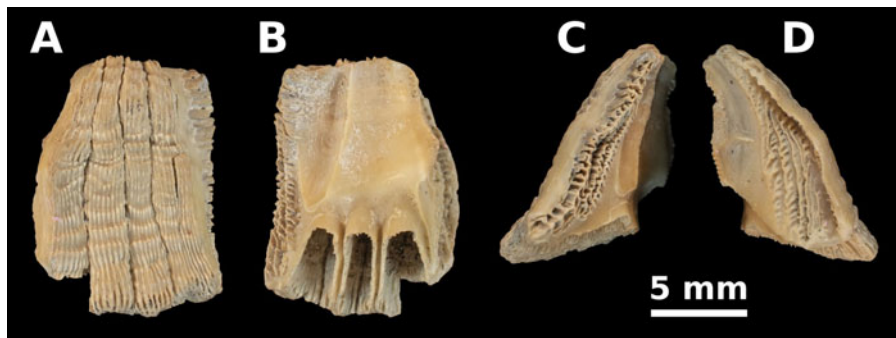


Figure 3. *Cetopirus polysyrinx* sp. nov. (paratype), UCMP 131833, isolated right compartment (carinolatus) collected near Cape Blanco (Los Angeles County, California, USA) in Middle Pleistocene (Chibanian) deposits. (a) external view; (b) internal view; (c) radial view; and (d) alar view. Photographs by Bob Day.

Type locality: LACM locality 1210, San Pedro, Los Angeles County, California, USA (Fig. 1). Davis (1972; 37) further detailed the site as follows: ‘North end of Los Angeles Harbor District Yard, Torrance, Calif. Bed begins 2/5 miles due east of intersection of Westmont Drive and Gaffey Street and runs east for 3/5 mile.’

Type horizon: Palos Verdes Sand Formation, Upper Pleistocene.

Paratype: UCMP 131833, isolated right carinolatus.

Locality and horizon of the paratype: UCMP locality B7380, near Cape Blanco, Curry County, USA (Fig. 1). Port Orford Formation, Chibanian. Davis (1972) further detailed the site of the find as follows: ‘Fossils from bluff sandstone about 75 ft. above beach in the northwest quarter of Sec. 18 (Cape Blanco quad., USGS 1954 ed. map).’

Description, comparisons and remarks: Both LACMIP 1210.158 and UCMP 131833 conform to the typical outline of *Cetopirus* compartments as detailed in the diagnosis above (Figs 2, 3).

The holotype (note that the same specimen was proposed as the holotype of ‘*Polysyrinx zulloi*’ by Davis 1972) consists of a partly damaged right carinolatus lacking part of the radius as well as the lowermost portion of the paries (although the periphery is locally preserved) (Fig. 2). The sheath is distinctly grooved in its radial portion (corresponding to the alar depression *sensu* Collareta *et al.* 2019), less prominently so in its alar portion (Fig. 2d). The thin, small ala displays a serrated distal margin (Fig. 2c). Both the sutural edges of the compartment are as thick as the compartment itself (Figs 2c, d). Judging from its overall morphology, LACMIP 1210.158 was part of a dome-shaped shell.

The paratype (note that the same specimen was proposed as one of the paratypes of ‘*Polysyrinx zulloi*’ by Davis 1972) consists of a right carinolatus that is broken transversely to the ribs some 6–7 mm below the basis of the sheath. The sheath is smooth throughout (Fig. 3b) (Fig. 3). The distal margin of the ala is regularly serrated (Fig. 3D). The sutural edges of the wall plate are almost as thick as the wall plate itself (Figs 3c, d). In profile view (Figs 3c, d), UCMP 131833 features a slightly sigmoidal outer wall that hints at a truncated-conical, irregularly depressed shell shape. This feature may be interpreted as an unusual growth form due to substrate anomalies or clustering with other nearby whale barnacle individuals. A cropped CT-stack and a three-dimensional (3D)-model of UCMP 131833 are available via MorphoSource at <https://doi.org/10.17602/M2/M432082> and <https://doi.org/10.17602/M2/M432154>, respectively.

In both the holotype and the paratype, the primary T-shaped flanges (*sensu* Collareta *et al.* 2022b) are internally perforated by a high number of irregularly-sized and irregularly-spaced tubules that lend them a spongy aspect in transverse section (Fig. 4). In the Recent species *Cetopirus complanatus*, each of these flanges is mostly hollow and its ‘opposite [i.e., inner and outer] sides are seen to be connected by shelly longitudinal plates’ (Darwin 1854), the resulting tubules being large and arranged in a single row (Collareta *et al.* 2016; fig. 4a). In turn, in the extinct species *Cetopirus fragilis* Collareta *et al.* 2016, the core of each flange is calcified, and a few tubules occur apart from the main axis of the flange, being aligned parallel to the outer wall and separated from each other by relatively thick septa (Collareta *et al.* 2016; fig. 4b). The peculiar condition observed in *C. polysyrinx* sp. nov. was described by Davis (1972; 40) as follows: ‘[t]he outermost laminar complex of the flange possesses one to three longitudinal tubes per septal pair, the majority being two. [...] In paratype UCMP XXXXXb [= 131833], a [...] carinolateral plate, [...] the number of tubes varies from one to three, the majority being two.’

Davis (1972) regarded LACMIP 1210.158 and UCMP 131833 as representative of a new coronuloid genus and species, which he informally named as ‘*Polysyrinx zulloi*’. However, both these

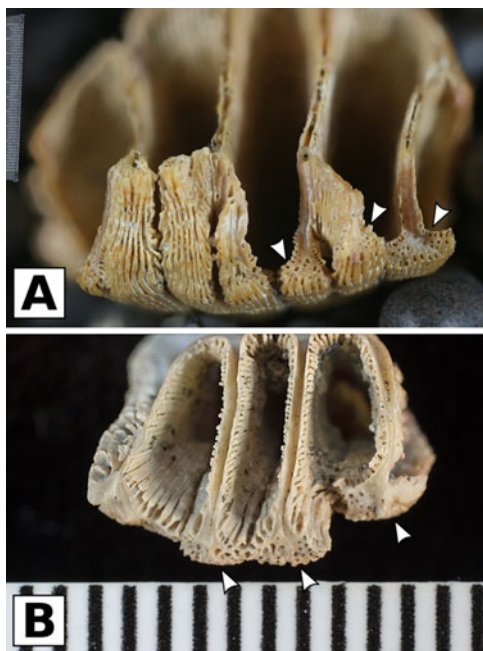


Figure 4. *Cetopirus polysyrinx* sp. nov., close-up of the inner structure of the primary T-shaped flanges, indicated by arrowheads, as observable in transverse cross-section of the shell (broken surfaces). (a) LACMIP 1210.158 (holotype), photograph by Lindsay Walker; and (b) UCMP 131833 (paratype), photograph by Bob Day. Divisions of the scale bars equal 0.1 mm in panel (a) and 1 mm in panel (b).

specimens display characters that are regarded as diagnostic of *Cetopirus*, namely: flat and broad parietal ribs, which tend to bifurcate symmetrically and lack transverse interlocking crenulations (Darwin 1854); thin and square alae (Darwin 1854); a basal edge of the sheath that does not project freely (Darwin 1854); a rather depressed outline (Pastorino & Griffin 1996); a narrow radius (Pastorino & Griffin 1996) that is strongly striated transversely (Collareta *et al.* 2016); and primary T-shaped flanges that are internally perforated by longitudinal tubules (Darwin 1854). At the same time, these specimens differ from the other congeners known to date by displaying secondary T-shaped flanges that are internally multitubiferous, and as such, somewhat spongy; furthermore, they differ from *C. fragilis* by virtue of their thicker sutural edges. All things considered, LACMIP 1210.158 and UCMP 131833 are best interpreted as representing a new, extinct species – *Cetopirus polysyrinx* sp. nov. – within the Recent genus *Cetopirus*.

Davis (1972) included two additional specimens in the hypodigm of ‘*Polysyrinx zullo*’, namely, an uncatalogued compartment kept in the palaeontological collections of the CAS and UCMP 131832. Whereas the former specimen – originating from UCMP locality B7375 – seems to be lost (Christine Garcia, pers. comm., December 2021), the latter is an isolated carina that seemingly differs from *Cetopirus* based on at least one character, and as such, is provisionally identified herein as belonging to cf. *Cetopirus polysyrinx* (see below).

cf. *Cetopirus polysyrinx*
(Fig. 5)

Referred material: UCMP 131832, isolated carina.

Occurrence: UCMP locality B7376, near Cape Blanco, Curry County, USA. Port Orford Formation, Middle Pleistocene (Chibanian). Davis (1972; 37) described the site of the find as ‘100 ft. south of UCMP locality B7375. UCMP Loc. B7375: 100–200 ft. south of large gully in Sec. 12 (Cape Blanco quad., USGS 1954 ed. map).’

Remarks: While resembling *Cetopirus polysyrinx* sp. nov., and especially the holotype, in overall outline and outer wall microstructure (Davis 1972; fig. 38), UCMP 131832 also displays a strongly grooved sheath and remarkably thin sutural edges (Fig. 5). Whereas the occurrence of strong grooves on the sheath may be considered to be interspecific variability, the thin sutural edges of UCMP 131832 are more difficult to assess taxonomically. Indeed, in Recent *Cetopirus* shells, the compartmental sutures are not that thin, not even in carinal plates (see e.g., the carina of *Cetopirus complanatus* illustrated by Pastorino & Griffin 1996; figs 4–6). As both LACMIP 1210.158 and UCMP 131833 resemble *C. complanatus* in terms of thickness of the compartmental sutures, for the moment we do not include UCMP 131832 within the hypodigm of *C. polysyrinx* sp. nov. It is hoped that additional finds of this species will shed light

on this issue. The quest for new specimens of *C. polysyrinx* sp. nov. may also include the Middle Pleistocene remains from the Atsumi Group of Japan that were reported by Kobayashi *et al.* (2008; pl. 1, fig. 22) and Karasawa & Kobayashi (2022; pl. 2, figs. 1–2) as belonging to *Coronula* sp., as they strongly recall *Cetopirus* by displaying a short sheath, thick and narrow radii that are externally striated, and low ribs that tend to branch frequently.

A cropped CT-stack and a 3D-model of UCMP 131832 are available via MorphoSource at <https://doi.org/10.17602/M2/M432057> and <https://doi.org/10.17602/M2/M432151>, respectively.

5. Discussion and conclusions

As already observed by Davis (1972), *Cetopirus polysyrinx* sp. nov. is seemingly unique among extant and extinct coronulid species in that its secondary outer lamina (*sensu* Collareta *et al.* 2022b) comprises primary T-shaped flanges that are internally multitubiferous and somewhat spongy (Fig. 4). By contrast, the early Pleistocene species *Cetopirus fragilis* displays fewer tubules within a more calcified secondary outer lamina, whereas in the Recent form *Cetopirus complanatus* the primary T-shaped flanges are more hollowed out and plate-like septa alternate with large tubules that run parallel to the outer wall. Whether the development of tubules that alternate with longitudinal septa within the primary T-shaped flanges has an adaptive significance is not easily determined. It may have provided the basal edge of the shell with additional grasping structures to supplement the similarly shaped secondary T-shaped flanges in penetrating into a moulting substrate by cutting out thin strings of the host’s skin (Collareta *et al.* 2022b); alternatively, it could have represented a solution for enhancing shell growth rates while saving calcium carbonate and preserving structural strength, which in turn may prove useful if space competition and/or hydrodynamic energy are high (Chan & Høeg 2015; Coletti *et al.* 2019). In addition, whether or not *C. fragilis*, *C. polysyrinx* sp. nov. and *C. complanatus* comprise a lineage characterised by a progressive hollowing of the secondary outer lamina is also unclear to date.

The Recent species *C. complanatus* is currently known as an obligate epibiont of right whales (Mysticeti: Balaenidae: *Eubalaena* spp.), as no confirmed records exist to date involving other hosts (Chemnitz 1785; Darwin 1854; Watson 1981; Scarff 1986; Holthuis *et al.* 1998; Fertl & Newman 2018). A North Pacific record of *C. complanatus* was provided by Scarff (1986), who reported on shells of *Coronula diadema* (Linnaeus 1767), *Coronula reginae* Darwin, 1854 and *C. complanatus* occurring on a right whale off Half Moon Bay, California, USA. Although Scarff (1986) identified this cetacean individual as belonging to *Eubalaena glacialis* (Müller 1776), the North Pacific right whales are currently known to comprise a separate species, *Eubalaena japonica* (Lacépède 1818) (Rosenbaum *et al.* 2000); the latter is

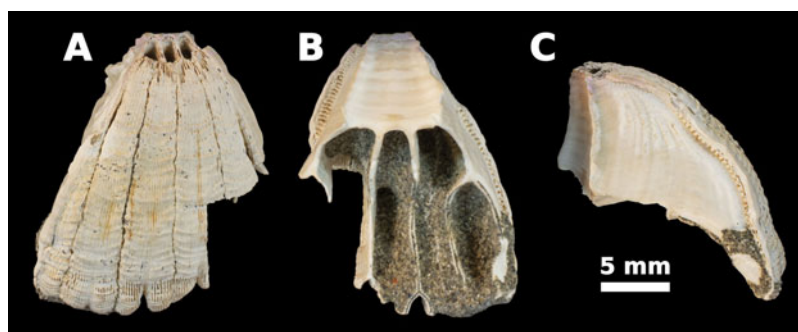


Figure 5. cf. *Cetopirus polysyrinx*, UCMP 131832, isolated carina collected near Cape Blanco (Los Angeles County, California, USA) in Middle Pleistocene (Chibanian) deposits. (a) external view; (b) internal view; and (c) right alar view. Photographs by Bob Day.

currently regarded as endangered (Cooke & Clapham 2018), as its western and eastern populations could count no more than 300 and 30 individuals, respectively (Brownell *et al.* 2001; Wade *et al.* 2010). Another record that seemingly hints at *C. complanatus* on modern North Pacific right whales is in Oyamada Tomokiyo's book 'Isanatori Ekotoba', published in Japanese in 1829 and translated into English (albeit, allegedly, not without errors) by Yamada (1983) (Omura 1986; Scarff 1986). Therein, drawings of stalked and acorn barnacles occur beside illustrations of the baleen and blubber of a right whale; the illustrated cirripedes include a depressed form that the accompanying description mentions as approximating a 'sake cup' (which is much reminiscent of the dome-like shell of *C. complanatus*, although it may also apply to *C. reginae*) (Yamada 1983; *vide* Scarff 1986). (It may also be noted that one of the coronulid specimens figured in the 'Isanatori Ekotoba' has the shell divided into five compartments; curiously, the associated text also describes whale barnacles as 'pentagonal or hexagonal' in shape.)

In light of the host specificity of extant whale barnacles, other (sub)fossil finds of *Cetopirus* have been regarded as marking the passage of ancient populations of *Eubalaena* (Álvarez-Fernández *et al.* 2014; Collareta 2016; Collareta *et al.* 2016, 2017; Bosselaers *et al.* 2017). *Cetopirus polysyrinx* sp. nov. also was, in all likelihood, an obligate commensal of right whales, either *E. japonica* or some other species of *Eubalaena*. Strengthening this interpretation, the occurrence of *Eubalaena* in the Middle or Upper Pleistocene of the broad North Pacific realm is documented by a single specimen dredged from the sea floor off Taiwan (Tsai & Chang 2019); furthermore, stratigraphically older finds referred to *Eubalaena shinshuensis* Kimura *et al.* 2007 and Balaenidae indet. are known from the Upper Miocene to Lower Pliocene of Japan (Kimura 2009), whereas specimens of cf. *Eubalaena* spp. are known from the Pliocene of central California, USA (Boessenecker 2013b).

The coasts of North America represent a privileged location for investigating the evolutionary history of the coronuloid barnacles, not least because they are home to the earliest members of this superfamily (Ross & Newman 1967; Zullo 1982; Collareta & Newman 2020; Perreault *et al.* 2022). Furthermore, the Pliocene and Pleistocene deposits of the Pacific coast of North America have yielded a rather idiosyncratic fossil coronulid fauna. Indeed, two extinct whale barnacle species have been described on the basis of – and are currently limited to – a few fossil finds from the United States and Mexican West Coast, namely, *Cetolepas hertleini* Zullo, 1969 and *Cryptolepas murata* Zullo, 1961. The former is a greatly enigmatic coronuline species of sub-cylindrical shell shape that is known from the Upper Pliocene (Vendrasco *et al.* 2012) San Diego Formation of San Diego County, California, USA (Zullo 1969). There is no hint, for this extinct genus and species, of what sort of host it might have been on. *Cryptolepas murata* was described from Upper Pleistocene deposits exposed at San Quintín, Baja California, Mexico, and is currently regarded as belonging to the same genus as *Cryptolepas rhachianecti* Dall, 1872, an obligate epibiont of grey whales (*Eschrichtius robustus* (Liljeborg, 1861)) (Newman & Abbott 1980; Bradford *et al.* 2011; Hayashi 2012; Bosselaers & Collareta 2016; Taylor *et al.* 2022). (Although Bosselaers & Collareta (2016) were hesitant about the genus-level assignment of *C. murata*, the high-quality photographs provided by Taylor *et al.* (2022) clearly confirm that this extinct species belongs to *Cryptolepas*.) Remains of *C. murata* co-occur with the holotype of *C. polysyrinx* sp. nov. in the Palos Verdes Sand strata exposed at San Pedro, Los Angeles County, California, USA (pers. obs. by AC, December 2021), thus evoking the co-occurrence of grey and right whales off the Pacific North American coast during the Late Pleistocene. Zullo (1961,

1969) envisaged *C. murata* as ancestral to *C. rhachianecti*, and the former as originating through *C. hertleini* from a *Cetopirus*-like ancestor (but see e.g., Davis 1972 for an alternative hypothesis). If this inference is correct, the discovery of Pliocene representatives of *Cetopirus* could be anticipated. Whatever the likelihood of Zullo's phyletic reconstruction, the composition of the North-West Pacific coronulid fossil fauna – including *Cetolepas*, *Cryptolepas* and now *Cetopirus* – seemingly contrasts with all other coeval assemblages worldwide, which are dominated by *Coronula* spp. (e.g., Beu 1971; Bianucci *et al.* 2006a, 2006b; Buckeridge *et al.* 2018, 2019; Collareta *et al.* 2018a, 2018b).

6. Acknowledgements

The present work is meant as a homage to the seminal cirripedological work by Clark William Davis (San Francisco State University).

We warmly thank Lindsay Walker (formerly at LACM), Juliet Hook (LACM), Austin Hendy (LACM), Bob Day (UCMP volunteer), Christine Garcia (CAS) and Peter D. Roopnarine (CAS) for their invaluable support throughout the present study. Not only did they search for the specimens that have been studied herein; they also provided precious curatorial information as well as high-quality photographs.

John S. Buckeridge (Earth & Oceanic Systems Group, Royal Melbourne Institute of Technology), Ray T. Perreault (Jarreau Scientific), Giovanni Bianucci (Università di Pisa), Giovanni Coletti (Università di Milano Bicocca) and the late William A. Newman (Scripps Institution of Oceanography) deserve our most sincere gratitude for many fruitful and illuminating discussions in the fields of coronulid palaeontology and neontology. We are sincerely indebted to John W.M. Jagt (Natuurhistorisch Museum Maastricht), John S. Buckeridge and Andrew J. Ross (National Museums Scotland), whose thorough and constructive reviews greatly contributed to improve an early draft of this paper. Not least, thorough support by Susie Cox (*Earth and Environmental Science Transactions of the Royal Society of Edinburgh* Editorial Office) is also kindly acknowledged.

7. Financial support

Funding and training for computed tomography scanning was provided by the Doris O. and Samuel P. Welles Fund of the UCMP, Department of Integrative Biology, and the FAVE/Tseng Laboratory. The research of the first author is supported by a LinnéSys: Systematics Research Fund grant (funded by the Linnean Society of London and the Systematics Association).

8. Conflicts of interest

None.

9. References

- Álvarez-Fernández, E., Carriol, R. P., Jordá, J. F., Aura, J. E., Avezueta, B., Badal, E., Carrión, Y., García-Guinea, J., Maestro, A., Morales, J. V., Perez, G., Perez-Ripoll, M., Rodrigo, M. J., Scarff, J. E., Villalba, M. P. & Wood, R. 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**, 163–9.
- Baldwin, E. M. 1945. Some revisions of the late Cenozoic stratigraphy of the southern Oregon coast. *Journal of Geology* **53**, 35–46.
- Baldwin, E. M. 1959. *The geology of Oregon*. Eugene: Distributed by the University of Oregon Cooperative Book Store.
- Beu, A. G. 1971. Further fossil whale barnacles from New Zealand. *New Zealand Journal of Geology and Geophysics* **14**, 898–904.

- Bianucci, G., Di Celma, C., Landini, W. & Buckeridge, J. S. 2006a. Palaeoecology and taphonomy of an extraordinary whale barnacle accumulation from the Plio-Pleistocene of Ecuador. *Palaeogeography, Palaeoclimatology, Palaeoecology* **242**, 326–42.
- Bianucci, G., Landini, W. & Buckeridge, J. S. 2006b. Whale barnacles and Neogene cetacean migration routes. *New Zealand Journal of Geology and Geophysics* **49**, 115–20.
- Boessenecker, R. W. 2013a. Taphonomic implications of barnacle encrusted sea lion bones from the middle Pleistocene Port Orford Formation, coastal Oregon. *Journal of Paleontology* **87**, 657–63.
- Boessenecker, R. W. 2013b. A new marine vertebrate assemblage from the Late Neogene Purisima Formation in Central California, part II: pinnipeds and cetaceans. *Geodiversitas* **35**, 815–940.
- Bosselaers, M. & Collareta, A. 2016. The whale barnacle *Cryptolepas rhachianecti* (Cirripedia: Coronulidae), a phoronit of the grey whale *Eschrichtius robustus* (Cetacea: Eschrichtiidae), from a sandy beach in The Netherlands. *Zootaxa* **4154**, 331–8.
- Bosselaers, M., Van Nieulande, F. & Collareta, A. 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**, 43–8.
- Bradford, A. L., Weller, D. W., Burdin, A. M. & Brownell, Jr., R. L. 2011. Using barnacle and pigmentation characteristics to identify gray whale calves on their feeding grounds. *Marine Mammal Science* **27**, 644–51.
- Brownell, Jr., R. L., Clapham, P. J., Miyashita, T. & Kasuya, T. 2001. Conservation status of North Pacific right whales (*Eubalaena japonica*). *Journal of Cetacean Research and Management* **2**, 269–86.
- Buckeridge, J. S., Chan, B. K. & Lee, S. W. 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**, e54.
- Buckeridge, J. S., Chan, B. K. & Lin, J. P. 2019. Paleontological studies of whale barnacles in Taiwan reveal new cetacean migration routes in the western Pacific since the Miocene. *Zoological Studies* **58**, e39.
- Chan, B. K. & Hoeg, J. T. 2015. Diversity of lifestyles, sexual systems, and larval developmental patterns in sessile crustaceans. In Thiel, M. & Watling, L. (eds) *Lifestyles and feeding biology: The natural history of the Crustacea* Vol. 2, 14–34. New York: Oxford University Press.
- Chemnitz, J. H. 1785. *Neues systematisches Conchylien-cabinet* [New systematic *Conchylia* cabinet] Vol. VIII, 1–372. Nürnberg: Raspe. [In German.]
- Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F. & Ranzuglia G. 2008. MeshLab: an open-source mesh processing tool. In Scarano, V., De Chiara, R. & Erra, U. (eds) *Sixth eurographics Italian chapter conference*, 129–36. Geneva: Eurographics Association.
- Coletti, G., Collareta, A., Bosio, G., Urbina-Schmitt, M. & Buckeridge, J. 2019. *Perumegabalanus calizai* gen. et sp. nov., a new intertidal megabalanine barnacle from the early Miocene of Peru. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **294**, 197–212.
- Collareta, A. 2016. Fossil turtle and whale barnacles (Crustacea: Cirripedia: Coronuloidea) kept at the Museo di Storia Naturale dell'Università di Pisa: an annotated catalogue. *Atti della Società Toscana di Scienze Naturali, Memorie, Serie A* **123**, 41–5.
- Collareta, A., Harzhauser, M. & Rasser, M. W. 2022a. New and overlooked occurrences of the rarely reported protochelonibiine “turtle” barnacles from the Oligocene and Miocene of Europe. *Palz* **96**, 197–206.
- Collareta, A., Insacco, G., Reitano, A., Catanzariti, R., Bosselaers, M., Montes, M. & Bianucci, G. 2018a. 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., Marean, C. W., Jerardino, A. & Bosselaers, M. 2017. *Cetopirus complanatus* (Cirripedia: Coronulidae) from the late Middle Pleistocene human settlement of Pinnacle Point 13B (Mossel Bay, South Africa). *Zootaxa* **4237**, 393–400.
- Collareta, A., Margiotta, S., Varola, A., Catanzariti, R., Bosselaers, M. & Bianucci, G. 2016. A new whale barnacle from the early Pleistocene of Italy suggests an ancient right whale breeding ground in the Mediterranean. *Comptes Rendus Palevol* **15**, 473–81.
- Collareta, A., Newman, W. A., Bosio, G. & Coletti, G. 2022b. A new chelonibiid from the Miocene of Zanzibar (Eastern Africa) sheds light on the evolution of shell architecture in turtle and whale barnacles (Cirripedia: Coronuloidea). *Integrative Zoology* **17**, 24–43.
- Collareta, A. & Newman, W. A. 2020. *Protochelonibia melleni* (Zullo, 1982) comb. nov., an archaic barnacle from the lower Oligocene of Mississippi (USA), and its impact on the stratigraphic and geographic distribution of the early coronuloids of Western Tethys. *Bollettino della Società Paleontologica Italiana* **59**, 179–81.
- Collareta, A., Regattieri, E., Zanchetta, G., Lambert, O., Catanzariti, R., Bosselaers, M., Covelo, P., Varola, A. & Bianucci, G. 2018b. New insights on ancient cetacean movement patterns from oxygen-isotope analyses of a Mediterranean Pleistocene whale barnacle. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **288**, 143–59.
- Collareta, A., Reitano, A., Rosso, A., Sanfilippo, R., Bosselaers, M., Bianucci, G. & Insacco, G. 2019. The oldest platylepadid turtle barnacle (Cirripedia, Coronuloidea): a new species of *Platylepas* from the Lower Pleistocene of Italy. *European Journal of Taxonomy* **516**, 1–17.
- Cooke, J. G. & Clapham, P. J. 2018. *Eubalaena japonica* (Lacépède, 1818). The IUCN Red List of Threatened Species 2018: e.T41711A50380694. doi: 10.2305/IUCN.UK.2018-1.RLTS.T41711A50380694.en
- 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.*, 1–684. London: Ray Society.
- Davis, C. W. 1972. *Studies on the barnacles epizoic on marine vertebrates*. Unpublished MA Thesis, 1–60. California State University, San Francisco.
- Dubois, A., Crochet, P. A., Dickinson, E. C., Nemésio, A., Aesch, E., Bauer, A. M., Blagoderov, V., Bour, R., de Carvalho, M. R., Desutter-Grandcolas, L., Frétey, T., Jäger, P., Lavilla, E. O., Löbl, I., Louchart, A., Malécot, V., Schatz, H. & Ohler, A. 2013. Nomenclatural and taxonomic problems related to the electronic publication of new nomina and nomenclatural acts in zoology, with brief comments on optical discs and on the situation in botany. *Zootaxa* **3735**, 1–94.
- Fedorov, A., Beichel, R., Kalpathy-Cramer, J., Finet, J., Fillion-Robin, J.-C., Pujol, S., Bauer, C., Jennings, D., Fennessy, F. M., Sonka, M., Buatt, J., Aylward, S. R., Miller, J. V., Pieper, S. & Kikinis, R. 2012. 3D Slicer as an image computing platform for the quantitative imaging network. *Magnetic Resonance Imaging* **30**, 1323–41.
- Fertl, D. & Newman, W. A. 2018. Barnacles. In Würsig, B. G., Thewissen, J. G. M. & Kovacs, K. M. (eds) *Encyclopedia of marine mammals*, 3rd edn, 75–8. San Diego: Academic Press.
- Garland, M. & Heckbert, P. S. 1997. Surface simplification using quadric error metrics. *ACM Siggraph Computer Graphics* **31**, 209–16.
- 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**, 107–27.
- Holthuis, L. B., Smeenk, C. & Laarman, F. J. 1998. The find of a whale barnacle, *Cetopirus complanatus* (Mörch, 1853), in 10th century deposits in the Netherlands. *Zoologische Verhandlungen* **323**, 349–63.
- International Commission on Zoological Nomenclature 1999. *International code of zoological nomenclature*, 4th edn. London: International Trust for Zoological Nomenclature.
- Karasawa, H. & Kobayashi, N. 2022. Cirripedes from the middle Pleistocene Atsumi Group, Japan, with a reevaluation of the genus *Adna* Sowerby, 1823 (Balanoida: Pyrgomatidae). *Bulletin of the Mizunami Fossil Museum* **49**, 67–93.
- Kennedy, G. L., Lajoie, K. R. & Wehmler, J. F. 1982. Aminostratigraphy and faunal correlations of late Quaternary marine terraces, Pacific Coast, USA. *Nature* **299**, 542–7.
- Kimura, T. 2009. Review of the fossil balaenids from Japan with a re-description of *Eubalaena shinshuensis* (Mammalia, Cetacea, Mysticeti). *Quaderni del Museo di Storia Naturale di Livorno* **22**, 3–21.
- Kimura, T., Narita, K., Fujita, T. & Hasegawa, Y. 2007. A new species of *Eubalaena* (Cetacea: Mysticeti: Balaenidae) from the Gonda Formation (latest Miocene–Early Pliocene) of Japan. *Bulletin of Gunma Museum of Natural History* **11**, 15–27.
- Kobayashi, N., Goda, T., Ohira, N. & Karasawa, H. 2008. New records of crabs and barnacles (Crustacea: Decapoda and Cirripedia) from the middle Pleistocene Atsumi Group of Aichi Prefecture, Japan. *Bulletin of the Mizunami Fossil Museum* **34**, 111–5.
- Lacépède, B. G. E. 1818. Note sur des Cétacées des mers voisines du Japon [Note on cetaceans from the seas near Japan]. *Mémoires du Muséum National d'Histoire Naturelle* **4**, 467–75. [In French.]
- Leach, W. E. 1817. Distribution systématique de la classe des Cirripèdes [Systematic distribution of the class Cirripedes]. *Journal de Physique, de Chimie et d'Histoire Naturelle* **85**, 67–9. [In French.]
- Leffler, S. R. 1964. Fossil mammals from the Elk River Formation, Cape Blanco, Oregon. *Journal of Mammalogy* **45**, 53–61.

- Liljeborg, W. 1861. *Öfversigt af de inom Skandinavien (Sverige och Norge) anträffade Hvalartade Däggdjur (Cetacea)* [Overview of the cetacean mammals (Cetacea) found in Scandinavia (Sweden and Norway)], 1–118. Uppsala: Uppsala Universitets Årsskrift. [In Swedish.]
- Linnaeus, C. 1767. *Systema Naturae sive Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis, Tomus I. Editio duodecima, Reformata* [The System of Nature or the Three Kingdoms of Nature, according to Classes, Orders, Genera, Species, with characters, differences, synonyms, places, Volume I. Twelfth Edition, Reformed], 1–1327. Stockholm: L. Salvius. [In Latin.]
- Mörch, O. A. L. 1853. Cephalophora. In *Catalogus conchyliorum*, 65–8. Copenhagen: Typis Ludovici Kleini.
- Muhs, D. R. 2022. MIS 5e sea-level history along the Pacific coast of North America. *Earth System Science Data* **14**, 1271–330.
- Muhs, D. R., Miller, G. H., Whelan, J. F. & Kennedy, G. L. 1992. Aminostratigraphy and oxygen isotope stratigraphy of marine-terrace deposits, Palos Verdes Hills and San Pedro areas, Los Angeles County, California. In Fletcher, C. H., III & Wehmler, J. F. (eds.) *Quaternary coasts of the United States: marine and lacustrine systems*. SEPM special publication **48**, 363–76. Tulsa, OK: SEPM Society for Sedimentary Geology.
- Muhs, D. R., Wehmler, J. R., Ryan, D. D. & Rovere, A. 2021. *MIS 5e relative sea-level index points along the Pacific coast of North America (1.1)*. Zenodo [Data set]. doi: 10.5281/zenodo.5903285
- Müller, O. F. 1776. *Zoologica Danicae Prodromus seu Animalium Daniae et Norvegiae indigenarum characteres, nomine, et synonyma imprimis popularium* [Zoological Prodromus of Denmark, or the native animals of Denmark and Norway, characters, names, and synonyms of the most popular], 1–282. Copenhagen: Typis Hallageriis. [In Latin.]
- Newman, W. A. & Abbott, D. P. 1980. Cirripedia: The barnacles. In Morris, R. H., Abbot, D. P. & Haderlie, E. C. (eds) *Intertidal invertebrates of California*, 504–35. Stanford: Stanford University Press.
- Newman, W. A., Zullo, V. A. & Withers, T. H. 1969. Cirripedia. In Moore, R. C. (ed.) *Treatise on invertebrate paleontology Part R*, R206–95. Boulder: University of Kansas and the Geological Society of America.
- Omura, H. 1986. History of right whale catches in the waters around Japan. *Report of the International Whaling Commission* **10**, 35–41.
- Pastorino, G. & Griffin, M. 1996. An extant whale barnacle (Cirripedia, Coronulidae) from Holocene deposits of Buenos Aires (Argentina). *Crustaceana* **69**, 769–72.
- Perreault, R. T., Collareta, A. & Buckeridge, J. S. 2022. A new species of the archaic “turtle barnacle” genus *Protochelonibia* (Coronuloidea, Chelonibiidae) from the upper Rupelian Chickasawhay Formation of Mississippi (U.S.A.). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **305**, 225–35.
- Ranzani, C. 1817. Osservazioni sui balanidi [Observations on balanids]. *Opuscoli Scientifici* **2**, 63–9. [In Italian.]
- Rolfe, S., Pieper, S., Porto, A., Diamond, K., Winchester, J., Shan, S., Kirveslahti, H., Boyer, D., Summers, A. & Maga, A. M. 2021. SlicerMorph: an open and extensible platform to retrieve, visualize and analyse 3D morphology. *Methods in Ecology and Evolution* **12**, 1816–25.
- Rosenbaum, H. C., Brownell, Jr., R. L., Brown, M. W., Schaeff, C., Portway, V., White, B. N., Malik, S., Pastene, L. A., Pateneude, N. J., Baker, C. S., Goto, M., Best, P. B., Clapham, P. J., Hamilton, P., Moore, M., Payne, R., Rowntree, V., Tynan, C. T., Bannister, J. L. & DeSalle, R. 2000. World-wide genetic differentiation of *Eubalaena*: questioning the number of right whale species. *Molecular Ecology* **9**, 1793–802.
- Ross, A. & Newman, W. A. 1967. Eocene Balanidae of Florida, including a new genus and species with a unique plan of “turtle-barnacle” organization. *American Museum Novitates* **2288**, 1–21.
- Roth, B. 1979. *Late Cenozoic marine invertebrates from northwest California and southwest Oregon*. Unpublished PhD Dissertation, 1–803. University of California, Berkeley.
- Scarff, J. E. 1986. Occurrence of the barnacles *Coronula diadema*, *C. reginae* and *Cetopirus complanatus* (Cirripedia) on right whales. *Scientific Reports of the Whales Research Institute* **37**, 129–53.
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak, P. & Cardona, A. 2012. Fiji: an open-source platform for biological-image analysis. *Nature Methods* **9**, 676–82.
- Taylor, L., Abella, J. & Morales-Saldaña, J. M. 2022. New fossil remains of the commensal barnacle *Cryptolepas rhachianecti* provide evidence of gray whales in the prehistoric South Pacific. *Journal of Paleontology* **96**, 583–90.
- Tsai, C. H. & Chang, C. H. 2019. A right whale (Mysticeti, Balaenidae) from the Pleistocene of Taiwan. *Zoological Letters* **5**, 1–7.
- Vendrasco, M. J., Eernisse, D. J., Powell, C. L. & Fernandez, C. Z. 2012. Polyplacophora (Mollusca) from the San Diego Formation: a remarkable assemblage of fossil chitons from the Pliocene of Southern California. *Contributions in Science* **520**, 15–72.
- Wade, P. R., Kennedy, A., LeDuc, R., Barlow, J., Carretta, J., Shelden, K., Perryman, W., Pitman, R., Robertson, K., Rone, B., Salinas, J. C., Zerbini, A., Brownell, Jr., R. L. & Clapham, P. J. 2010. The world’s smallest whale population? *Biology Letters* **7**, 83–5.
- Watson, L. 1981. *Sea guide to the whales of the world*, 1–302. New York, E.P. Dutton.
- Wehmler, J. F., Lajoie K. R., Kvenvolden K. A., Peterson, E., Belknap, D. F., Kennedy, G. L., Addicott, W. O., Vedder, J. G. & Wright, R. W. 1977. Correlation and chronology of Pacific Coast marine terrace deposits of continental United States by fossil amino acid stereochemistry – technique evaluation, relative ages, kinetic model ages, and geologic implications. *USGS Open-File Report 77-680*, 1–196.
- Wehmler, J. F., Lajoie, K. R., Sarna-Wojcicki, A. M., Yerkes, R. F., Kennedy, G. L., Stephens, T. A. & Kohl, R. F. 1978. Amino-acid racemization dating of Quaternary mollusks, Pacific Coast United States. *USGS Open-File Report 78-701*, 445–8.
- Welton, B. J. 2015. The marine fish fauna of the Middle Pleistocene Port Orford Formation and Elk River Beds, Cape Blanco, Oregon. *New Mexico Museum of Natural History and Science Bulletin* **66**, 1–45.
- Wiley, T. J., McLaughry, J. D., Ma, L., Mickelson, K. A., Niewendorp, C. A., Stimely, L. L., Herinckx, H. H. & Rivas, J. 2014. Geologic map of the southern Oregon coast between Port Orford and Bandon, Curry and Coos Counties, Oregon. *Oregon Department of Geology and Mineral Industries Open-File Report O-2014-01*, 1–66.
- Woodring, W. P., Bramlette, M. N. & Kew, W. S. W. 1946. Geology and paleontology of Palos Verdes Hills, California. *United States Geological Survey Professional Paper* **207**, 1–181.
- Yamada, Y. 1983. Yogiotoru Eshi Vol. 2. In Pilleri, G. (ed.) *Investigations on Cetacea* **14** (Supplement), 1–119.
- Zullo, V. A. 1961. A new whale barnacle from Late Pleistocene deposits at San Quintín Bay, Baja California. *The Veliger* **4**, 13–4.
- Zullo, V. A. 1969. Thoracic Cirripedia of the San Diego Formation, San Diego County, California. *Contributions in Science of the Los Angeles County Museum of Natural History* **159**, 1–25.
- Zullo, V. A. 1982. A new species of the turtle barnacle *Chelonibia* Leach, 1817, (Cirripedia, Thoracica) from the Oligocene Mint Spring and Byram Formations of Mississippi. *Mississippi Geology* **2**, 1–6.