Large kings with small crowns: a Mediterranean Pleistocene whale barnacle

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INTRODUCTION

Just like Hop-o’-My-Thumb in the Perrault fairy tale, large ocean-going whales leave small “crumbles” in the fossil record - in the form of barnacle plates - reminding us of their passage through the dark abyss of time. Among the few types of epizoans that can foul whale’s skin, the skeletonized, filter-feeding barnacles of family Coronulidae have developed an anchor device to deeply embed in the thick whale blubber, firmly occupying a position facing the rich water currents continuously created while the whale dives. Given the shape of whale barnacles and the position frequently occupied on the head of whales, to an imaginative eye they look like tiny crowns, thence their name (Seilacher, 2005). Whale barnacles are obligate commensals adapted to recognize their hosts via a chemical cue available to their larvae (Nogata & Matsumura, 2006). Probably aided by direct implantation from mother to calf, coronulids have a high specificity to their host, and possibly the same lifespan judging from the uniformity of individuals from single populations (e.g., Holthuis & Fransen, 2004). Large whales may eventually loose these barnacles by shedding during breaching (Felix et al., 2006), or other social activities. The barnacle thick calcitic plates can then become an enduring part of the fossil record, signaling the local passage of large whales even in the absence of cetacean remains (Bianucci et al., 2006b).

One large adult of the whale barnacle Coronula diadema, complete and articulated, has been recovered from a lower Pleistocene mudstone cropping out near Riparbella, in Tuscany (Italy). This discovery allowed to extend the biogeographic range of the most widespread species of whale barnacles, confirming its
global character, and possibly signaling the passage in the Mediterranean of the humpback whale, Megaptera novaeangliae, a species only rarely sighted today. The Riparbella finding gives the opportunity to reconsider the natural history of the coronulid adaptation to whale riding, small crowns on large ocean-going kings.

GEOLICAL SETTING
The studied sedimentary succession rests unconformably on a pre-Neogene bedrock and is part of the lower Pleistocene exposed in the hills around the valley of the Cecina River between Riparbella and Montescudaio (Fig. 1). This shallow marine muddy-sandy succession, up to 80 m thick, is known since more than a century (Mazzanti & Sanesi, 1987). The age is based on the occurrence of the boreal bivalve Arctica islandica within a diverse marine molluscan association (Tavani, 1954; Ragaini & Menesini, 1997). An allostratigraphic approach based on facies analysis allowed to assign these deposits to a shoreface-delta front setting, interpreting the frequent vertical facies changes in terms of relative sea-level fluctuations (Sarti et al., 2007).

STRATIGRAPHY AND PALEOENVIRONMENT
The relatively continuous section exposed along the road running from the Botra Creek to Riparbella, a classic reference section (Mazzanti & Sanesi, 1987; Sarti et al., 2007) (see Fig. 1) is intercalated by unconformable surfaces of different rank, allowing for the finescale sequence-stratigraphic interpretation based on facies analysis of the intervening deposits. Two major unconformity-bounded stratigraphic units have been recognized, the sand-dominated Botra Creek unit (BCU) and the gravel-dominated Montescudaio unit (MSU), which will not be discussed here.

BCU onlaps onto an ophiolitic bedrock forming the flanks of the Botra Creek and is characterized by the predominance of sandstone arranged in dm-to-m thick tabular beds. From the base to the top (Fig. 1), sandstone becomes coarser and primary sedimentary structures are better preserved. The basal beds are massive due to pervasive bioturbation, and rich in mollusks dominated by pectinids and glycymerids, concentrated in pockets or dispersed in the sediment. In an upward direction, beds are internally graded, occasionally showing horizontal or through-cross lamination, eventually obliterated by scattered burrows. Clay chips and disarticulated bivalve shells may occur at the base of these beds. An overall SSW sediment transport is outlined by the orientation of the occasional inclined laminasets. Two mudstone intervals punctuate the succession. A 4 m thick grey mudstone in the lower portion contains a rich and diversified molluscan assemblage dominated by venerid, ostreid, and pectinid bivalves, and by turrids and other gastropods. A large specimen of the whale barnacle Coronula diadema was collected in the topmost portion of this deposit. Eight samples were collected along the mudstone interval for the biostratigraphic analysis of the nannoflora content. The second mudstone interval is about 2.5 m thick, and characterized by two graded beds rich with articulated shells of the bivalve Arctica islandica. Two further samples were collected in the finer-grained sediments of this interval (Fig. 1).

Facies analysis allows a tripartite subdivision of BCU (Fig. 1). BC1 includes the basal sandstone, referred to a sediment-starved lower shoreface/delta front dominated by extensive bioturbation, overlain by inner shelf mudstone in turn followed by the sandstone of a prograding delta front. BC2 includes the overlying coarser and graded sandstone ascribed to a flood-dominated delta front. Finally, BC3 is marked by the uppermost sandstone again referred to a proximal delta front setting. The BCU facies architecture resulted from high-frequency relative sea-level fluctuations, within a delta system prograding to the SW and signaling high sediment supply in the long term. The Coronula specimen was located on top of BC1, where the maximum depth of the water column is recorded.

The nannofossil content in samples from the Coronula mudstone is not abundant. Small Gephyrocapsa and Pseudoemiliana lacunosa were however nearly ubiquitous, suggesting a biostratigraphic reference to the MNN19e Zone (Rio et al., 1990) (within the Calabrian: 0.781-1.806 Ma).

SYSTEMATICS
Family CORONULIDAE Leach, 1817
Genus Coronula Lamarck, 1802

Coronula diadema (Linnaeus, 1767) (Figs 2g-i)

Material - IGF 14647E, one complete shell kept in the Geological and Paleontological Department (=IGF) of the Museum of Natural History, University of Florence.

Occurrence - Early Pleistocene (Calabrian) mudstones near Riparbella (Tuscany, Italy).

Description - Shell of large size (7.0-6.0-4.6 cm), with a large orifice measuring 3.3-3.0 cm and a deep body cavity of 2.2 cm (Figs 2g-i). Ribs in the upper two thirds of the shell, closer to the orifice, are worn out; fine details of the rib ornamentation are instead well preserved in the lower part. These two parts of the barnacle form an angle in some of the compartments. In the upper two thirds the radii are much wider than the ribs, whereas they quickly thin out in the lower third of the shell, wholly occupied by the ribs.

Remarks - The marked difference between the upper and the lower part of the shell is a character typical of Coronula diadema (Bianucci et al., 2006a), not as yet encountered in the older Mediterranean fossil species, Coronula bifida, particularly common in Pliocene strata at Orciano Pisano in Tuscany (Figs 2a-c; see also Menesini, 1968). The relative proportions between width of radius and width of ribs observed...
during ontogeny in *C. bifida* are comparable to those of young adults of *C. diadema* (Figs 2d-f). The upper part of the Riparbella specimen corresponds to the side of the shell that in life emerged from the whale blubber, explaining the worn-out character of the ribs (see also Bianucci et al., 2006a). The association of the specimen to mudstones from an open shelf environment (the maximum depth of the water column during the Pleistocene in this area) makes the setting similar to Orciano Pisano and other Northern Apennine localities associated with fossils of large whales at paleodepths of 40-110 m (Danise, 2011).

**SMALL CROWNS**

Charles Darwin dealt at length with living and fossil *Coronula* in his 1854 monograph on barnacles, recognizing three living species (Darwin, 1854). *Coronula balaenaris* (Gmelin, 1791) is now assigned to genus *Cetopirus* Ranzani, 1817 and to the species *Cetopirus complanatus* (Mörch, 1853) (Newman & Ross, 1976; Holthius et al., 1998). The other two species discussed in the monograph, *C. diadema* and *C. reginae* Darwin, 1854, are very similar - possibly one and the same; Darwin himself having stated that “differences are so small, that at first I hesitated whether to name the species [C. reginae]” (Darwin, 1854) - although all later authors have kept them distinct (Newman & Ross, 1976).

The first report of a fossil *Coronula* is by James Parkinson in *Organic Remains of a Former World* (Parkinson, 1811) for a specimen of unknown age and provenance referred to *C. diadema*. Twenty years after (1831) Heinrich Georg Bronn briefly described a fossil found in the Jan collection at Milano, devising sufficient
differences with the extant species to establish the new species *Coronula bifida*. Concerning the four main external ribs of each compartment, he described that “a deep furrow or cleavage divides the longitudinal rib from the top to the middle, which lacks completely or is only indicated with the otherwise similar *C. diadema*. Size like the latter”. This description was deemed insufficient by Charles Darwin, who erected *C. barbara* based on three-four Pliocene specimens: “the character thus afforded [by Bronn] would not have been of specific value, as this dividing of the ribs occasionally occurs in all species, and is produced by the formation of new folds to the walls” (Darwin, 1854). Yet at another point, *C. bifida* and *C. barbara* were presented in synonymy - this time paying credit to Bronn’s description - and confirmed as close allies of *C. diadema*: “Coronula barbara, a form closely allied to *C. diadema*, existed during the Red Crag period; and Bronn has described some fossil specimens from Italy” (Darwin, 1854: 414).

Seguenza (1873) reaffirmed the validity of *Coronula bifida* based on more consistent material than available to Bronn or Darwin. Alessandri (1906) fully described and figured the Bronn specimen from the Jan collection, collected in Castell’Arquato near Piacenza (Italy). Fossils from Orciano Pisano, also from Northern Apennine Pliocene, subapennine deposits, show the typical characters of *Coronula bifida* and *C. barbara* (see Alessandri, 1906), allowing placement of the two species in synonymy (Menesini, 1968). Two new fossil species were introduced in subsequent years, *C. dormitor* Pilsbry & Olsson, 1951 (Ecuador, Pliocene) and *C. macsotayi* Weisbord, 1971 (Venezuela, Pleistocene), the first now considered as a synonym of *C. bifida*, the second of *C. diadema* (Bianucci et al., 2006b). Rich Pleistocene
collections from several stratigraphic levels outcropping on the Ecuador coast were referred to *Coronula diadema* (Bianucci et al., 2006a). The above reported fossil record suggests that all Pliocene *Coronula* belong to *Coronula bifida* and all, or most, Pleistocene, starting from the Calabrian, and modern to *Coronula diadema*. The two species appear as in phylogenetic relationship, one global Pliocene species (*Coronula bifida*) giving way approximately during the second half of the early Pleistocene [under the name of *Coronula barbara*, *Coronula bifida* is reported in the earliest Pleistocene (?Gelasian) of the Red Crag by Darwin (1854)], at the outset of very deep climatic changes, to another global species, the extant *Coronula diadema*. This hypothesis is sustained by the similarity between the two species recognized by authors (e.g., Bronn, 1831; Darwin, 1854), a similarity which is limited to young adults of *Coronula diadema* (Figs 2d-f), in later ontogenesis the modern species acquiring a bulbous character (Figs 2g-i) which is absent in all available specimens of *Coronula bifida* (Figs 2a-c). The characters shared by *Coronula bifida* and young adults of *Coronula diadema*, i.e., a truncated-conical shape and the ribs being wider than radii, are also shared with *Cetopirus*, the closest and younger genera within subfamily Coronulinae (Newman & Ross, 1976). *Cetopirus complanatus* and *Coronula diadema* thus possibly evolved different devices from a *Coronula bifida* - like ancestor allowing for a larger size, possibly as a response to size increase of large, ocean-going whales. *Cetopirus complanatus* attained a larger size by introducing during ontogeny papillae of whale skin clung to new fold pockets and increasing the number of papillae of whale skin clung to, whereas *Coronula diadema* has improved anchorage in its mature stage by drawing its basal surface deeply into the skin of the whale and accreting along the radial plate boundaries (Seilacher, 2005). *Coronula bifida*, while older than known fossil *Cetopirus*, is clearly not its direct ancestor. Rather it shares genus-level diagnostic characters with *Coronula diadema* (see Newman et al., 1969; Seilacher, 2005; Ross & Frick, 2007).

**LARGE KINGS**

*Coronula diadema* is most commonly associated with the balaenopterid *Megaptera novaeeangliae*, the humpback whale (Pilsbry, 1916; Scarff, 1986; Holthuis & Fransen, 2004), whereas *Cetopirus complanatus* is reported on the skin of the North Atlantic right whale, *Eubalaena glacialis* (see Holthius et al., 1998), occasionally on the Southern right whale *Eubalaena australis*, both of family Balaenidae (see Fertl & Newman, 2009). *Coronula diadema* is occasionally reported on cetaceans other than the humpback whale, such as the sperm whale *Physeter macrocephalus* and the right whales (Newman & Ross, 1976), although possibly never in high numbers (see Scarff, 1986). The North Atlantic right whale is an endangered species (Reilly et al., 2008), a fate that *Cetopirus* can better escape being associated also with Southern right whales. Humpback and right whales are among the largest animals living, both commonly attaining a length of around 15 m, and a weight up to 30 (*Megaptera*) or 80 tons (*Eubalaena*). The humpback whale has a global distribution, although it is now rare in the Mediterranean (Aguilar, 1989; Frantzis et al., 2004). Right whales are global at the genus level, differentiated in three species each with a more limited domain, the North Atlantic (but not recorded in the Mediterranean), North, and South Pacific respectively (Committee on Taxonomy, 2009). In sum, living coronulids show high specificity to large baleen whale genera with a global distribution. Possible commensalism between *Coronula diadema* and humpbacks dates back at least to the early Pleistocene (Bianucci et al., 2006b). Consistently, we confirm its global character since at least the Calabrian (0.781-1.806 million years).

The specificity of *Coronula bifida* to large whale dates at least to the Pliocene and was hypothesized in the Mediterranean by the Orciano Pisano record (Bianucci et al., 2006b), a locality associated with skeletons of large whales dated at around 3 Ma (Dominici et al., 2009; Danise et al., 2010). The good whale fossil record in the Miocene (Lambert et al., 2010; Marx & Uhen, 2010), coupled with scanty evidences for whale barnacles - except perhaps for the Late Miocene (Bianucci et al. 2006a) - suggests that large whales have acquired their dwarf riders relatively late in their evolutionary history, contrary to expectations (Seilacher, 2005), and in relationship with the global character of the routes they followed (Bianucci et al., 2006b). Like their barnacles, balaenopterid and balaenid whales show an increase in maximum size from the Miocene to the Recent (Lambert et al., 2010: fig. 4b). Strict coevolution is thus a strong case, connecting large ocean-going whales with their odd small riders.

**CONCLUSIONS**

The finding of a large specimen of the whale barnacle *Coronula diadema* in early Pleistocene open shelf deposit at Riparbella (Tuscany), coupled with published data on slightly older occurrences in the Eastern Pacific, confirms that the species has had a global distribution that spanned the Mediterranean, since the Calabrian. A global distribution is also consistent with the distribution of the only other well-known fossil coronulid, *Coronula bifida*, common in the Mediterranean record and possibly present in Pliocene deposits of the Eastern Pacific. The two whale barnacles never occur together and, whereas *Coronula diadema* has a range extending from the early Pleistocene (Calabrian) to the present, *Coronula bifida* occurs only in the Pliocene and perhaps in the earliest Pleistocene (Gelasian). No knowledge on other fossil *Coronula* is firmly established, only species based on scanty material and in need of revision. Available data suggest that *Coronula diadema* is the direct descendant of *Coronula bifida*, a phylogenetic relationship connected to an increase in size of the adult shell. This hypothesis is sustained by the wide geographical distribution of their host, the ocean-going humpback whale, and hinted at by the fossil record of large whales associated with larger accumulations of whale barnacles. The general high host specificity of whale barnacles, including *Cetopirus complanatus* of the same family, recorded in modern oceans can be possibly extended back to the Pliocene. In evolutionary time, both large whales and their small
commensals show an average increase in size, so as to strongly suggest coevolutionary relationships connecting humpbacks and Coronula on one side, right whales and Cetopirus on another.

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