

Large kings with small crowns: a Mediterranean Pleistocene whale barnacle

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KEY WORDS - Whale barnacles, Coronulidae, Balaenopteridae, Balaenidae, Tuscany, commensalism, Pleistocene.

ABSTRACT - A large complete wall of the whale barnacle *Coronula diadema* (Linnaeus, 1767) occurring in early Pleistocene (Calabrian) mudstones near Riparbella (Tuscany, Italy) is described. Sedimentary facies analysis indicates that these deposits represent an open shelf setting, similar to many of those reported for whale fossils to date. The extant and fossil record of *C. diadema* and other species belonging to the genus and family are revised herein. The study confirms a global distribution for *C. diadema* and dates its presence in the Mediterranean from the early Pleistocene (Calabrian). A global distribution is attributed to the only other well-known fossil coronulid, *Coronula bifida* Bronn, 1831, which is common within the Pliocene record of the Mediterranean, and is documented in the Pliocene of the Pacific domain and in the earliest Pleistocene of the Atlantic [as *C. barbara* (Darwin, 1854)]. No overlap of stratigraphic ranges has been noted: *C. bifida* occurs in the Piacenzian-Gelasian and *C. diadema* is recorded from the Calabrian to the present. It is therefore suggested herein that *C. diadema* is a direct descendant of *C. bifida* and that the evolution of the former included a pronounced increase in size of the adult shell. The fossil record of large whales supports this hypothesis, which is further reinforced by the global character of its hosts such as the ocean-going humpback, blue, fin, and sperm whales. The general high host specificity of whale barnacles, which today include *Cetopirus complanatus* (Mörch, 1853) of the same family, can be extended back to the Pliocene. Considering these aspects, a coevolutionary trend towards an increase in size linking oceanic whales with coronulids is proposed.

RIASSUNTO - [Grandi re con piccole corone: un coronulide pleistocenico nel Mediterraneo] - Un esemplare completo e articolato del balanomorfo coronulide *Coronula diadema* (Linneo, 1767) è stato raccolto in depositi pleistocenici di età calabrianiana nei pressi di Riparbella, in provincia di Pisa. L'analisi di facies e della dinamica deposizionale consente di attribuire i depositi a un ambiente di piattaforma, al di sotto del livello di influenza del moto ondoso, analogo ad altri depositi in cui sono stati in precedenza ritrovati resti di grossi cetacei. Vengono riconsiderati la distribuzione geografica moderna e quella fossile della specie di coronulide, anche in confronto a quella di specie dello stesso genere e specie della stessa famiglia. La revisione conferma che *C. diadema* ha avuto dal Calabrianiano (Pleistocene inferiore) una distribuzione globale che comprendeva il Mediterraneo. Anche il secondo, altrettanto ben conosciuto coronulide fossile aveva una distribuzione globale. *Coronula bifida* Bronn, 1831 non è infatti raro nel registro fossile del Mediterraneo, ed è presente in depositi pliocenici del Pacifico e del Pleistocene inferiore più basso dell'Atlantico [come *C. barbara* (Darwin, 1854)]. La distribuzione stratigrafica delle due specie tuttavia non è coincidente, essendo *C. bifida* del Piacenziano-Gelasiano e *C. diadema* distribuita dal Calabrianiano all'attuale. Ipotizziamo che *C. diadema* sia la discendente diretta di *C. bifida* e che l'evoluzione della prima abbia incluso un pronunciato aumento nella taglia della conchiglia dell'adulto. Il registro fossile dei grandi cetacei aggiunge credibilità all'ipotesi, col sostegno del carattere globale dell'ospite preferito, la megattera conosciuta in tutti gli oceani. La generale alta specificità dei coronulidi, famiglia che oggi include *Cetopirus complanatus* (Mörch, 1853), può esser fatta risalire almeno al Pliocene. In questa visione, una tendenza coevolutiva verso l'aumento della taglia connette le balene oceaniche con i coronulidi.

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 lose 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.

GEOLOGICAL 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 fine-scale 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 mollusk remains 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

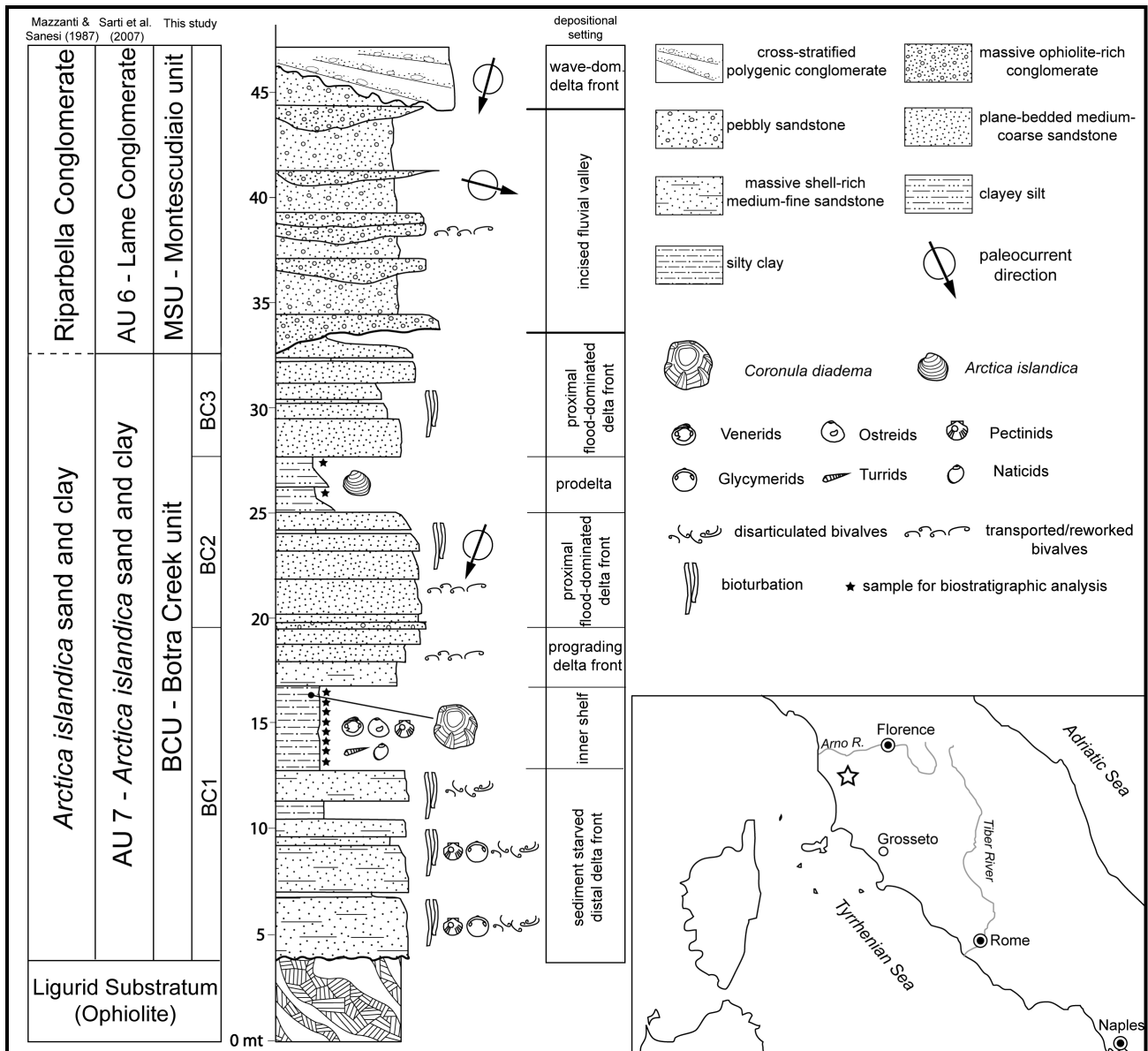


Fig. 1 - Location of the study area in central Italy and schematic log of the Botra Creek Riparbella stratigraphic section. To the left of the sedimentary log, a comparison with existing lithostratigraphic nomenclature is shown (see text for further explanation).

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

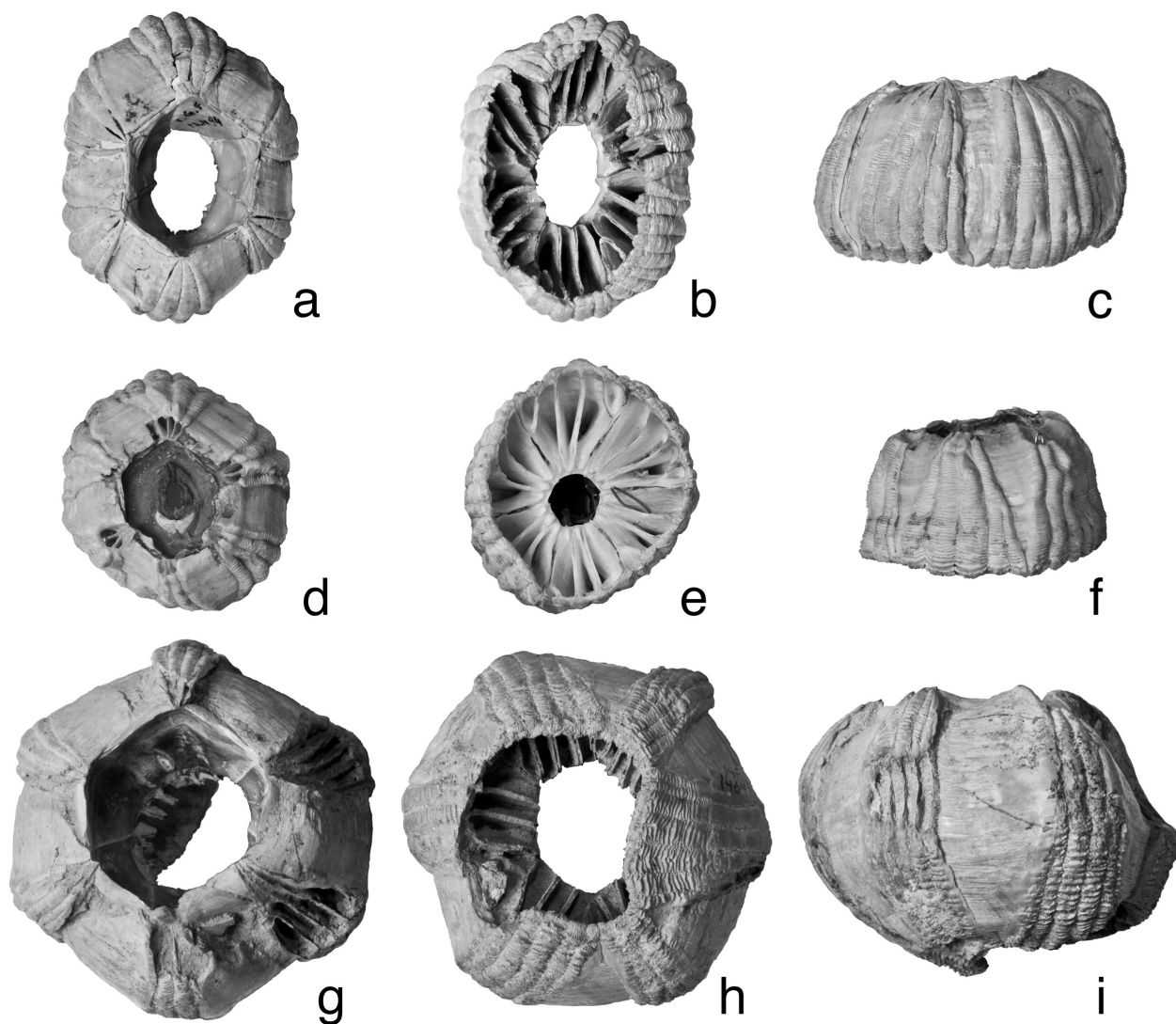


Fig. 2 - Articulated and complete shells of fossil and extant species of *Coronula*. a-c: *Coronula bifida* Bronn, 1831 (IGF 12494E), specimen from Piacenzian deposits, collected at Orciano Pisano (Pisa); d-f: *Coronula diadema* (Linnaeus, 1767) (MZUF 76), Recent specimen from the historical collections of the Zoology Department of the Museum of Natural History, University of Florence (unknown locality); g-i: *C. diadema* (Linnaeus, 1767) (IGF 14647E), specimen collected at Riparbella (PI) in Calabrian deposits. The clear-cut demarcation from upper (worn-off) and lower part of the shell is visible in the lateral view (Fig. 2i). All specimens x 0.73.

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 *C. diadema* (Bianucci et al., 2006a). The above reported fossil record suggests that all Pliocene *Coronula* belong to *C. bifida* and all, or most, Pleistocene, starting from the Calabrian, and modern to *C. diadema*. The two species appear as in phylogenetic relationship, one global Pliocene species (*C. bifida*) giving way approximately during the second half of the early Pleistocene [under the name of *C. barbara*, *C. 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 *C. 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 *C. 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 *C. bifida* (Figs 2a-c). The characters shared by *C. bifida* and young adults of *C. 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 *C. 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 *C. diadema* (see Newman et al., 1969; Seilacher, 2005; Ross & Frick, 2007).

LARGE KINGS

Coronula diadema is most commonly associated with the balaenopterid *Megaptera novaeangliae*, the humpback whale (Pilsbry, 1916; Scarff, 1986; Holthuis & Franssen, 2004), whereas *Cetopirus complanatus* is reported on the skin of the North Atlantic right whale, *Eubalaena glacialis* (see Holthuis et al., 1998), occasionally on the Southern right whale *Eubalaena australis*, both of family Balaenidae (see Fertl & Newman, 2009). *C. 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 *C. 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 whales 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 *C. diadema* has a range extending from the early Pleistocene (Calabrian) to the present, *C. 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 *C. diadema* is the direct descendant of *C. 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.

ACKNOWLEDGEMENTS

Thanks to Gianna Innocenti for the loan of coronulid shells hosted at the Zoology Department of the Museum of Natural History, University of Florence. Caterina Fortuna helped with updated literature on the biogeography of living whales. Thanks to the two reviewers and the editor, that helped with their comments.

REFERENCES

- Aguilar A. (1989). A record of two humpback whales, *Megaptera novaeangliae*, in the western Mediterranean Sea. *Marine Mammalian Science*, 5: 306-309.
- Alessandri G. de (1906). Studi monografici sui Cirripedi fossili d'Italia. *Palaeontographia Italica*, 12: 207-324.
- Bianucci G., Di Celma C., Landini W. & Buckeridge J. (2006a). Palaeoecology and taphonomy of an extraordinary whale barnacle accumulation from the Plio-Pleistocene of Ecuador. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 242: 326-342.
- Bianucci G., Landini W. & Buckeridge J. (2006b). Whale barnacles and Neogene cetacean migration routes. *New Zealand Journal of Geology and Geophysics*, 49: 115-120.
- Bronn H.G. (1831). Italiens Tertiär-Gebilde und deren organische Einschlüsse: vier Abhandlungen. Heidelberg, 176 pp.
- Committee on Taxonomy (2009). List of marine mammal species and subspecies. *Society for Marine Mammalogy* <www.marinemammalscience.org>, consulted on 8 July 2011.
- Danise S. (2011). Modern and fossil shallow water whale fall communities. PhD Thesis, GEO-01 XXIII Cycle, Firenze, 178 pp.
- Danise S., Dominici S. & Betocchi U. (2010). Mollusk species at a Pliocene shelf whale fall (Orciano Pisano, Tuscany). *Palaiois*, 25: 449-556.
- Darwin C. (1854). A Monograph on the subclass Cirripedia with figures of all the species. The Balanidae, The Verrucidae, etc. London: Ray Society, 684 pp.
- Dominici S., Cioppi E., Danise S., Betocchi U., Gallai G., Tangocci F., Valleri G. & Monechi S. (2009). Mediterranean fossil whale falls and the adaptation of mollusks to extreme habitats. *Geology*, 37: 815-818.
- Félix F., Bearson B. & Falconi J. (2006). Epizoic barnacles removed from the skin of a humpback whale after a period of intense surface activity. *Marine Mammal Science*, 22: 979-984.
- Fertl D. & Newman W.A. (2009). Barnacles. In Perrin W.F., Würsig B. & Thewissen J.G.M. (eds), *Encyclopedia of Marine Mammals* (2nd ed.). Academic Press, Amsterdam: 89-91.
- Frantzis A., Nikolaou O., Bompar J.-M. & Cammedda A. (2004). Humpback whale (*Megaptera novaeangliae*) occurrence in the Mediterranean Sea. *Journal of Cetacean Research and Management*, 6: 25-28.
- Gmelin J.F. (1791). *Systema naturae per regna tria naturae*, 13th ed. 1(6), cl. 6, Vermes. Leipzig: 3021-3909.
- Holthuis L.B. & Fransen C.H.J.M. (2004). Interesting records of whale epizoic crustaceans from the Dutch North Sea coast. *Nederlandse Faunistische Mededelingen*, 21: 11-16.
- 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 Verhandelingen*, 323: 349-363.
- Lamarck J.B.P.A. de M. de (1802). Mémoire sur la Tubicinelle. *Annales Muséum National D'Histoire Naturelle*, 1: 461-464.
- Lambert O., Bianucci G., Post K., de Muizon C., Salas-Gismondi R., Urbina M. & Reumer J. (2010). The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. *Nature*, 466: 105-108.
- Leach W.E. (1817). Distribution systematique de la class Cirripedes. *Journal de Physique, de Chimie et d'Histoire Naturelle*, 85: 67-69.
- Linnaeus, C. (1767). *Systema naturae*, Tom. I. Pars II. 12th Revised Edition, Holmiae, Laurentii Salvii: 533-1327.
- Marx F. & Uhen G. (2010). Climate, critters, and cetaceans: Cenozoic drivers of the evolution of modern whales. *Science*, 327: 993-996.
- Mazzanti R. & Sanesi G. (1987). Geologia e morfologia della bassa Val di Cecina. *Quaderni del Museo di Scienze Naturali di Livorno*, 7 (Supplemento 1): 1-27.
- Menesini E. (1968). Osservazioni su *Coronula bifida* Bronn. *Atti della Società Toscana di Scienze Naturali*, Memorie 75(2): 387-398.
- Mörch O.A.L. (1853). *Cephalophora Catalogue Conchyliorum*: 65-68 (Cirripedia).
- Newman W.A. & Ross A. (1976). Revision of the balanomorph barnacles; including a catalog of the species. *San Diego Society of Natural History Memoir* 9: 1-108.
- Newman W.A., Zullo V.A. & Withers T.H. (1969). Cirripedia. In Moore R.C. (ed.), *Treatise on invertebrate paleontology*, Part R, 4: R206-R295.
- Nogata Y. & Matsumura K. (2006). Larval development and settlement of a whale barnacle. *Biology Letters*, 2: 92-93.
- Parkinson J. (1811). Organic remains of a former worlds: an examination of the mineralized remains of the vegetables and animals of the antediluvial world; generally termed extraneous fossils. London, vol. 3: 485 pp.
- 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. *Smithsonian Institution, United States National museum, Bulletin* 93: 366 pp.
- Pilsbry H.A. & Olsson A.A. (1951). Tertiary and Cretaceous Cirripedia from northwestern South America. *Proceeding of the Academy of Natural Sciences of Philadelphia*, 103: 197-210.
- Ragaini L. & Menesini E. (1997). Paleocomunità a molluschi nel Pleistocene inferiore della bassa Val di Cecina (Pisa). *Atti della Società Toscana di Scienze Naturali, Memorie, serie A*, 104: 67-74.
- Ranzani C. (1817). Osservazioni su i Balanidi. *Opuscoli Scientifici*, 1 (4): 276.
- Reilly S.B., Bannister J.L., Best P.B., Brown M., Brownell Jr. R.L., Butterworth D.S., Clapham P.J., Cooke J., Donovan G.P., Urbán J. & Zerbini A.N. (2008). *Eubalaena glacialis*. In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1. <www.iucnredlist.org>. Downloaded on 08 July 2011.
- Rio D., Raffi I. & Villa G. (1990). Pliocene-Pleistocene calcareous nannofossils distribution patterns in the Western Mediterranean. In Kastens, K. A., Mascle J., et al. (eds), *Proceedings of the Ocean Drilling Program, Scientific Results* 107: 513-533.
- Ross A. & Frick M.G. (2007). Systematics of the Coronuloid barnacles. In Epibiont Research Cooperative (ERC) 2007. A synopsis of the literature on the turtle barnacles (Cirripedia: Balanomorph: Coronuloidea) 1758-2007. ERC Special Publication 1: 23-30.
- Sarti G., Ciampalini A., Consoloni I. & Feroni A. (2007). I depositi del Pleistocene inferiore della bassa Val di Cecina (Toscana Italia): ricostruzione stratigrafico-deposizionale e proposta di suddivisione in unità allostratigrafiche. *Il Quaternario-Italian Journal of Quaternary Sciences*, 20: 151-162.
- 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: 129-153.
- Seguenza G. (1873). Ricerchi Paleontologiche intorno ai Cirripedi terziari della provincia de Messina. Con appendice intorno ai Cirripedi viventi nel Mediterraneo e sui fossili terziari dell'Italia Meridionale. Parte I. *Atti Accademia Pontaniana*, 10: 267-311.
- Seilacher A. (2005). Whale barnacles: exaptational access to a forbidden paradise. *Paleobiology*, 31: 27-35.
- Tavani G. (1954). Faune del Quaternario di Rosignano Marittimo (Livorno). *Atti della Società Toscana di Scienze Naturali, Memorie* 61: 241-248.
- Weisbord N.E. (1971). A new species of *Coronula* (Cirripedia) from the Lower Pliocene of Venezuela. *Bulletins of American Paleontology*, 60: 87-96.
- Manuscript received 24 July 2011
Revised manuscript accepted 4 October 2011
Published online 21 October 2011
Editor Annalisa Ferretti