

JUMPING FROM TURTLES TO WHALES: A PLIOCENE FOSSIL RECORD DEPICTS AN ANCIENT DISPERSAL OF *CHELONIBIA* ON MYSTICETES

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Abstract. The barnacles included in the superfamily Coronuloidea are epizoid symbionts of various marine vertebrates (including cetaceans, sirenians, and sea turtles) and other crustaceans (crabs and horseshoe crabs). Among Coronuloidea, the so-called turtle barnacles (Chelonibiidae) are known from Paleogene times, whereas the whale barnacles (Coronulidae) likely appeared in the late Pliocene (Piacenzian). Although a derivation from the turtle barnacles (and especially from the genus *Chelonibia*) has been proposed, the evolutionary origin of Coronulidae remains to date obscure. In this work we reappraise a fossil record from upper Pliocene (Piacenzian) marine deposits at Casenuove (Empoli municipality, Tuscany, Italy) comprising various shells of *Chelonibia testudinaria* associated to a partial skeleton of a balaenid mysticete. Based on taphonomic and morpho-functional considerations, we discuss the hypothesis that the barnacles were hosted on the baleen whale, possibly on its callosities, which could have represented an analogous of the horny carapace of marine turtles. This record strongly suggests that the baleen whales can be added to the list of the possible hosts of the barnacles of the genus *Chelonibia*, thus hinting that the whale barnacles may have evolved from an ancient phase of dispersal of *Chelonibia* (or a similar ancestor) on mysticete cetaceans.

INTRODUCTION

Turtle and whale barnacles (Crustacea: Cirripedia: Coronuloidea) are known as preferential to obligate phoronts of various marine vertebrates (toothed and baleen-bearing whales, sea chelonians, and sirenians) and crustaceans (crabs and horseshoe crabs). Attaching on a motile, long-living substrate, suspension-feeding coronuloids can enjoy a continuous flow of seawater and nutrient particles. The fossil record of the turtle barnacles (family Chelonibiidae) dates back to the Paleocene (with the six-plated species *Emersonius cybosyrinx* Ross & Newman, 1967), whereas the geologically oldest evidence of sea-turtle fouling (consisting of surface imprints from the host substratum in the holotype of *Protochelonibia submersa* Harzhauser & Newman, 2011) is early Miocene in age (Harzhauser et al. 2011). In turn, the fossil history of the whale barnacles (family Coronulidae) is much younger: the Kakega-

wa group of Japan was recently recalibrated to the Pleistocene (Ishibashi 1989), so that the late Miocene record of *Coronula diadema* (Linnaeus, 1767) reported by Hatai (1939) must be rejected; therefore, unambiguous occurrences of whale barnacles are limited to the younger part of the Pliocene and the whole Quaternary.

The few, non-exhaustive phylogenetic analyses published to this date (e.g., Hayashi et al. 2013) confirmed both the tight evolutionary relationship between Chelonibiidae and Coronulidae and the basal position of the Miocene to Recent genus *Chelonibia* Leach, 1817 (the type genus of Chelonibiidae) within Coronuloidea. Little is known about the origin of the whale barnacles, although a direct derivation of Coronulidae from *Chelonibia* has been tentatively proposed by Buckeridge (1983) based on observations on the shell structure of fossil and extant coronuloid barnacles.

In this paper we reappraise a balaenid-*Chelonibia* fossil association from the Pliocene of Tuscany (Bianucci 1996) and propose that - unlike presently

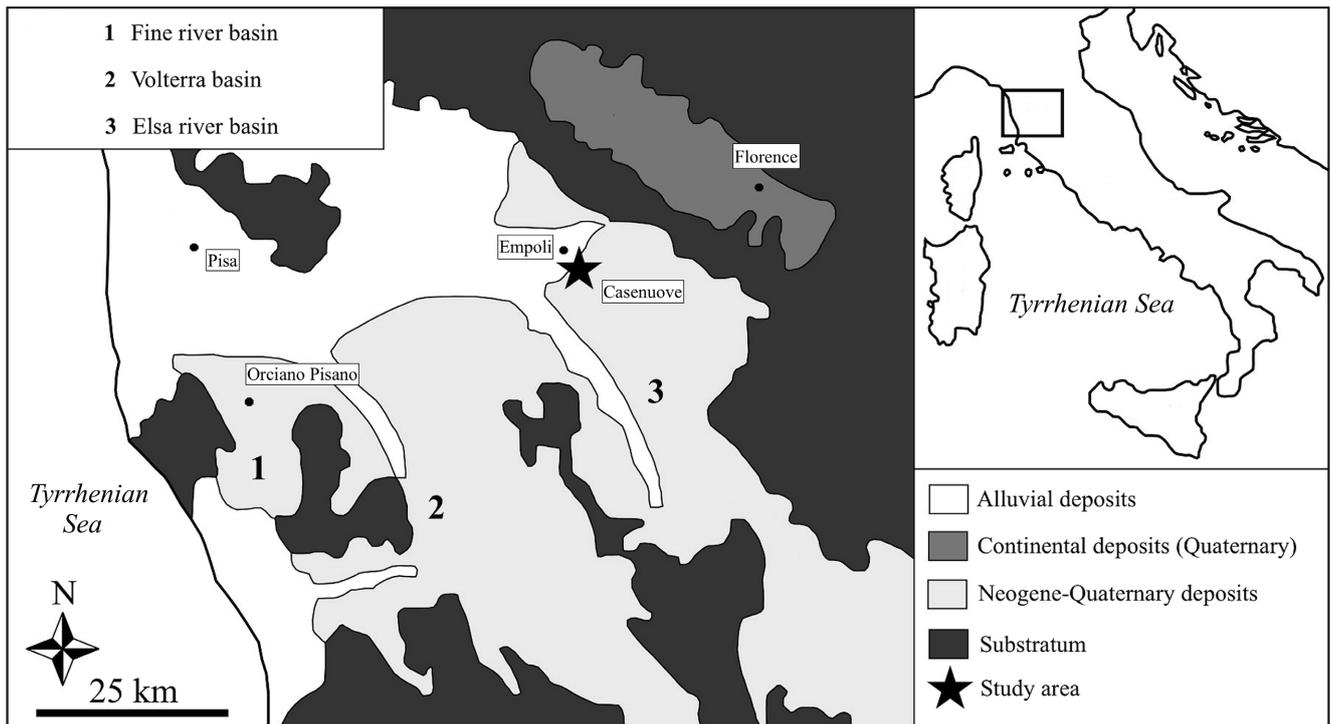


Fig. 1 - Location of the study area at Casenuove, and schematic geological map. Modified after Danise et al. (2010).

observed - this barnacle was hosted by the baleen whale, thus evoking a possible mode of origin for the whale barnacles.

PALEONTOLOGICAL MATERIAL AND GEOLOGICAL SETTING

In summer 1995, an incomplete and largely disarticulated fossil cetacean skeleton was collected in a clay quarry near Casenuove (Fig. 1; Empoli municipality, Tuscany, Italy) (Bianucci 1996). The cetacean skeleton consists of various parts of the skull (left premaxilla, right? maxilla, left squamosal, supraoccipital, exoccipital, and possibly parts of the right? frontal and the left? maxilla) plus the right mandible, two ribs and other postcranial fragments (Bianucci 1996; Bianucci & Sorbini 2014) attributable to a mysticete (i.e., baleen-bearing) whale. Based on various osteological features (e.g., a rounded anterior outline of the supraoccipital, a ventrolaterally projected zygomatic process of the squamosal, and a greatly reduced coronoid process of the mandible), this cetacean was determined as a member of the mysticete family Balaenidae (currently including four extant species of right and bowhead whales) somewhat related to *Eubalaena* Gray, 1864 (Bianucci 1996). This fossil balaenid specimen is currently kept at the Museo di Storia Naturale dell'Università di Pisa

(MSNUP) with catalogue number MSNUP I-16839 (Bianucci & Sorbini 2014), pending to be prepared for a detailed systematic study. The associated fauna included crab remains and marine mollusks such as *Cerastoderma edule* (Linnaeus, 1758), *Conus* sp. Linnaeus, 1758, *Hadriamnia truncatula* (Foresti, 1868), *Notocochlis tigrina* (Röding, 1798), *Ostrea edulis* Linnaeus, 1758, and *Potamides tricinctus* (Brocchi, 1814); two large fossilized branches of tree were also present (Bianucci 1996). Just in the close proximity of the bones of the skull, and especially along the right mandible, a set of various fragmentary to complete shells of *Chelonibia* was found (Fig. 2) (Bianucci 1996); these specimens are currently kept at the MSNUP.

At the Casenuove clay quarry, four terrigenous marine sequences are exposed, arranged in a transgressive trend (Dominici et al. 1995). The horizon where MSNUP I-16839 was found makes part of the highstand deposits occurring near the top of the third depositional sequence and is characterized by abundant remains of the gastropods *Bittium reticulatum* (da Costa, 1778) and *Jujubinus exasperatus* (Pennant, 1777) (Dominici et al. 1995). This level, which was referred to a very shallow intertributary bay environment, also features two specimens of *Tapirus arvernensis* Croizet & Jobert, 1828. The deposition of the vertebrate-bearing sediments was tentatively attributed to the early Pliocene

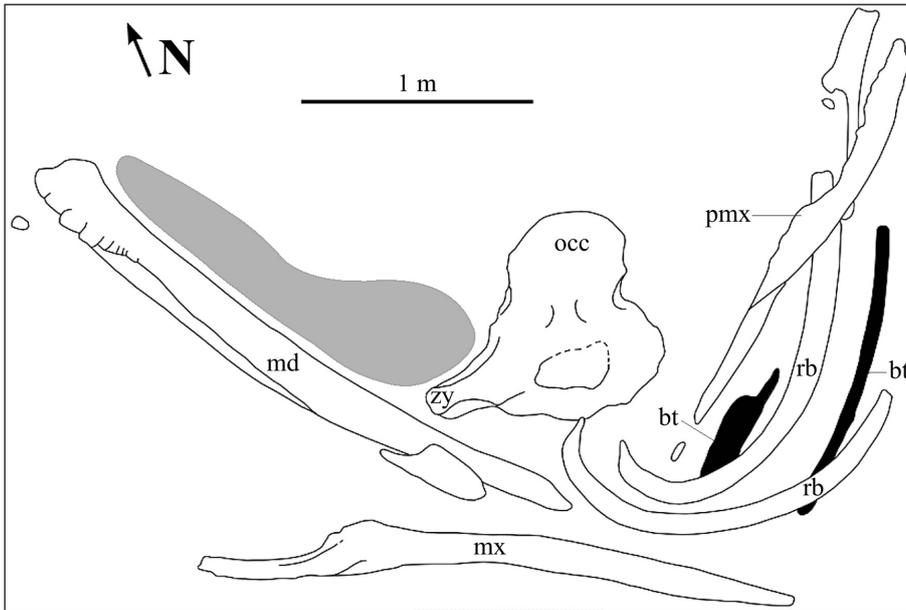


Fig. 2 - Field map of the disarticulated partial skeleton of the balaenid whale MSNUP I-16839. Casenuove (Empoli municipality Tuscany, Italy). bt = branch of tree; md = mandible; mx = maxilla; occ = occipital shield; pmx = premaxilla; rb = rib; zy = zygomatic process of the squamosal. The *Chelonibia testudinaria* remains (MSNUP I-16914 to MSNUP I-16942) were found primarily within the light grey area. Redrawn and modified after Bianucci (1996).

(Zanclean) (Dominici et al. 1995) or to the Zanclean-Piacenzian transition (Rustioni & Mazza 2001). More recently, Benvenuti et al. (2014) provided evidence that the sediments exposed at Casenuove belong to an upper Pliocene (Piacenzian) synthem (S5) recognized in the Valdelsa basin. This new interpretation is consistent with the presence of *Tapirus arvernensis*, whose last occurrence in Europe is reported at the time of the transition from the Triversa faunal unit to the Montopoli faunal unit (Dominici et al. 1995; Rustioni & Mazza 2001), about 3 Ma (Albianelli et al. 1997). An age of ca 3 Ma for the early Villafranchian mammal remains collected from deposits belonging to the synthem S5 of Benvenuti et al. (2014) had already been proposed by Benvenuti et al. (1995), based on aminochronological analyses performed on a tooth of *Anancus arvernensis* (Croizet & Jobert, 1828) found at the Piazzano farm (near Casenuove). Therefore, the Casenuove marine deposits are here regarded to be Piacenzian (ca 3 Ma) in age.

SYSTEMATIC PALEONTOLOGY

Chelonibiidae Pilsbry, 1916

Chelonibia Leach, 1817

Chelonibia testudinaria (Linnaeus, 1758)

Figs 3a-c

1758 *Lepas testudinaria* Linnaeus, p. 668.

1758 *Verruca testudinaria* Ellis, p. 852, plate 34, f. 12.

1825 *Astrolepas rotundarius* Gray, p. 105

Material: MSNUP I-16914, complete and articulated shell; MSNUP I-16915, articulated compound rostrum and first right carinolatus; MSNUP I-16916, articulated shell lacking the second right carinolatus, having an incomplete, very juvenile chelonibiid shell (MSNUP I-16917) attached to the rostrum and first right carinolatus; MSNUP I-16918, small-sized incomplete and articulated shell, constituted by the compound rostrum plus right and left first carinolatera; MSNUP I-16919, large-sized incomplete articulated shell, constituted by part of the compound rostrum, first right carinolatus, and part of the first left carinolatus, second right carinolatus, and carina; MSNUP I-16920, MSNUP I-16921, MSNUP I-16922, MSNUP I-16923, 4 incomplete compound rostra; MSNUP I-16924, 1 isolated rostrum s.s.; MSNUP I-16925, MSNUP I-16926, 2 isolated right rostrilatera; MSNUP I-16927, MSNUP I-16928, 2 isolated left rostrilatera; MSNUP I-16929, MSNUP I-16930, MSNUP I-16931, 3 right carinolatera, MSNUP I-16932, MSNUP I-16933, MSNUP I-16934, MSNUP I-16935, MSNUP I-16936, MSNUP I-16937, MSNUP I-16938, MSNUP I-16939, 8 left carinolatera; MSNUP I-16940, MSNUP I-16941, 2 carinae; MSNUP I-16942, anatomically indeterminate fragment.

Occurrence: Upper Pliocene (Piacenzian) sands in the Casenuove clay quarry (Empoli municipality, Tuscany, Italy), characterized by the co-occurrence of the gastropods *Bittium reticulatum* and *Jujubinus exasperatus*.

Description and stratigraphic remarks.

The fossil shells are nicely preserved, and the fine details of their ornamentation (e.g., both the longitudinal and the transverse striae which affect the external surface of each compartment) are generally well observable. Articulation degree spans from complete (e.g., MSNUP I-16914, found as a fully associated shell; the second left carinolatus detached during collection) to null (e.g., the isolated compartments labelled MSNUP I-16920 to MSNUP I-16942). All the collected *Chelonibia* remains are indistinguishable from modern specimens of *Chelo-*

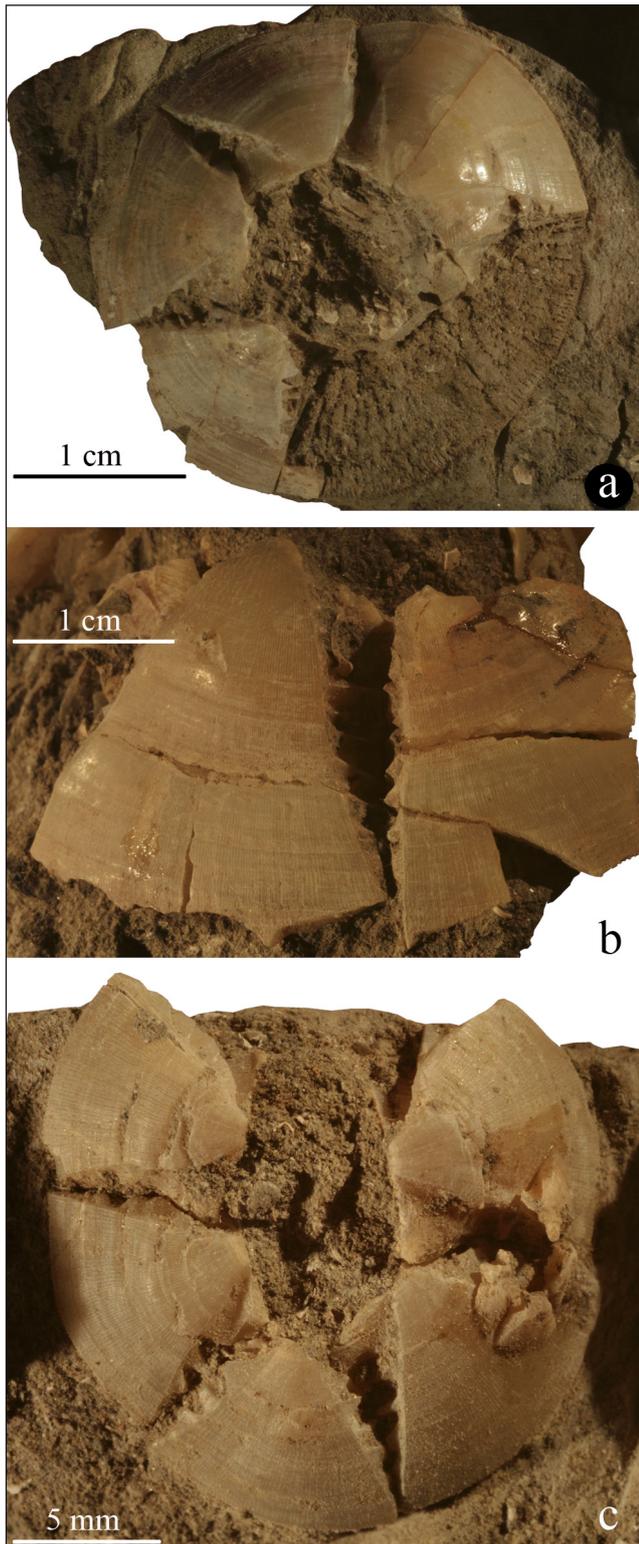


Fig. 3 - Fossil remains of *Chelonibia testudinaria* (Linnaeus, 1758) from the Pliocene of Casenuove (Empoli municipality Tuscany, Italy). a) Apical view of MSNUP I-16914 (note the star-like arrangement of the radii); b) close-up of MSNUP I-16919, showing the typically toothed edge of the radius; c) apical view of MSNUP I-16916 (note the juvenile chelonibiid shell MSNUP I-16917 attached to the rostrum and first right carinolatus of MSNUP I-16916).

Chelonibia testudinaria and mainly differ from all the other species of *Chelonibia* for being constituted by very

thick and deeply excavated compartments whose radii are well-diagnostically toothed along the edges and arranged in a star-like manner (Figs 3a-c). MSNUP I-16914 to MSNUP I-16919 represent six different specimens of *Chelonibia testudinaria*. The isolated rostral compartments (MSNUP I-16920 to MSNUP I-16928) belong to at least 7 more specimens. Therefore, at least 13 fossil specimens of *Chelonibia testudinaria* have been collected all around the baleen whale skeleton MSNUP I-16839.

The pre-Quaternary paleontological record of the genus *Chelonibia* is rather fragmentary and even more discontinuous than that of the type genus of the Coronulidae, *Coronula* Lamarck, 1802. The geologically oldest record of the genus *Chelonibia* is represented by 5 compartments collected from lower Oligocene deposits of Mississippi (USA); these chelonibiid remains have been selected as the type material of the new species *Chelonibia melleni* Zullo, 1982. This species shares with all the extant species of *Chelonibia* some features (e.g., the presence of a narrow true radius compared to the rostro-latera) which contribute to distinguish this genus from the other chelonibiid genera. In turn, *C. melleni* differs from the extant species of *Chelonibia* by lacking the inner lamina (at least apparently); therefore, its collocation within this genus could be questionable. Ross (1963) described two specimens of *Chelonibia patula* (Ranzani, 1817) from the Neogene Tamiami Formation of Florida (USA). Ross (1963) regarded these chelonibiid remains as late Miocene in age; however, the chronostratigraphic range of the Tamiami Formation has recently been recalibrated to the Pliocene (Missimer 1992, 1997). Withers (1928, 1929, 1953) reported the presence of extant species of *Chelonibia* (*C. testudinaria* and *C. patula*) in Miocene deposits of Zanzibar (Tanzania), Gironde (France), Austria, and Cuba; however, the geographic and stratigraphic information provided by the author is vague, and his determinations of the barnacle specimens are questionable. Therefore, these records are here considered as dubious. In 2011 Harzhauser and Newman erected the new genus and species *Protochelonibia submersa* based on two chelonibiid shells from the early Miocene of Austria (Harzhauser et al. 2011); in the same work a partial revision of the extinct species of Chelonibiidae is also provided. While reassigning *Chelonibia capellini* De Alessandri, 1895 from the upper Pliocene deposits of Orciano Pisano (Tuscany)

as *Protochelonibia cappellini* (De Alessandri, 1895), Harzhauser et al. (2011) recognized *Chelonibia hemisphaerica* Rothpletz & Simonelli, 1890 from the Miocene-Pliocene Las Palmas Formation of Gran Canaria as belonging to the genus *Chelonibia*. Since the chronostratigraphic range of the Las Palmas Formation has been recently constrained to the Tortonian-Zanclean interval by van Bogaard & Schminke (1998), this record confirms that the first appearance of *Chelonibia* is not younger than the early Pliocene, although the presence of this genus in pre-Pliocene strata is uncertain.

Among the few Italian records of fossil *Chelonibia*, the occurrence reported by De Alessandri (1906) of compartments of *Chelonibia testudinaria* along with remains of the extinct turtle barnacle *Protochelonibia cappellini* in the upper Pliocene open shelf mudstones of Orciano Pisano is noteworthy. The upper Pliocene marine deposits of Orciano Pisano feature a rich and diversified fossil association, including sea turtles and baleen whales (e.g., Bianucci & Landini 2005; Dominici et al. 2009) as well as shells of the extinct whale barnacle *Coronula bifida* Bronn, 1831 (De Alessandri 1895, 1906; Menesini 1968; Dominici et al. 2011). Dominici et al. (2009) dated a whale-bearing bed at Orciano Pisano between 3.19 and 2.82 Ma. Based on these data, a similar late Pliocene age (ca 3 Ma) could be attributed to the remains of *Coronula bifida* from Orciano Pisano, thus making them roughly coeval to the remains of *Chelonibia testudinaria* from the Casenuove clay quarry; however, the fossiliferous horizon studied and dated by Dominici et al. (2009) could be better correlated with the S4 synthem of Benvenuti et al. (2014) which predates the deposits exposed at Casenuove (personal communication by Stefano Dominici). Unfortunately, the coronulid shells from Orciano Pisano lack a precise geographic and stratigraphic collocation. A prospection led at Orciano Pisano by the Istituto di Geologia e Paleontologia dell'Università di Pisa failed to detect any fossil coronulid from the sediments cropping out around the village (Menesini 1968). It is important to consider that at the time of De Alessandri, the geographical information regarding the locations of the fossil finds was not as detailed as required today, and that very often uneducated people provided fossil material for professional paleontologists by gathering remains collected from different sites [see for example Landini (1977) and Cigala Fulgosi et al. (2009)

for a discussion about the stratigraphic position of the fossil shark teeth from Orciano Pisano in the Lawley collection]. Therefore, it is possible that the fossil materials collected during the XIX century and labeled as coming from Orciano Pisano have been collected from a larger area within the Fine river basin. Due to this uncertainty, we are not able to establish if the Orciano Pisano coronulid remains are geologically older or younger than the chelonibiid remains from the Casenuove clay quarry.

DISCUSSION AND CONCLUSIONS

The presence of several *Chelonibia* shells associated to a balaenid skeleton in the Pliocene marine deposits of Casenuove was originally explained by Bianucci (1996) with the presence of a sea turtle near the baleen whale remains. However, no fossil turtle was ever detected in that horizon of the quarry, although the unusually high number and concentration of the chelonibiid remains (at least 13 individuals have been recognized) strongly indicate that their phoront should have been buried with them. Here we propose that the *Chelonibia* shells from Casenuove quarry were in fact attached to the skin of the balaenid whale whose partial fossil skeleton (MSNUP I-16839) was found strictly associated to the barnacle remains. In our opinion, this hypothesis - which could contribute to enlighten the evolutionary origin of the Coronulidae - is the most reliable one. For the purposes of our discussion, the following topics are noteworthy:

- 1) The barnacles belonging to the genus *Chelonibia* are generally known as highly specific epibionts of sea turtles. However, individuals of *Chelonibia* can fix themselves on a wide spectrum of substrates, including crabs, horseshoe crabs, sirenians, mollusks, sea snakes, saltwater crocodiles, alligators, and even inanimate substrates (Newman & Ross 1976; Monroe & Garret 1979; Frazier & Margaritoulis 1990; Badrudeen 2000; Nifong & Frick 2011). In particular, the high plasticity of *Chelonibia testudinaria* with respect to variations of the substrate has been highlighted by Moriarty et al. (2008), which provided wide evidence that individuals of this species living on the carapace of sea turtles can move on their host at speeds up to 1.4 mm/day. Furthermore, the species *Chelonibia manati* Gruvel, 1903, which attaches almost exclusively to the skin

of a marine mammal (the sirenian genus *Trichecus* Linnaeus, 1758), has recently been recognized as a morphotype of *C. testudinaria* (Zardus et al. 2014). Interestingly, each compartment of *C. manati* shows “...salient longitudinal ribs which subdivide towards the base” (Pilsbry 1916), thus giving the shell an appearance which is intermediate between that of the classical turtle barnacle *C. testudinaria* (sensu stricto) and that of a rib-bearing whale barnacle such as *Cetopirus complanatus* (Mörch, 1853) or *Coronula reginae* Darwin, 1854. According to Seilacher (2005), the ribs displayed by most whale barnacle genera (e.g., *Coronula*, *Cetopirus* Ranzani, 1817, *Cryptolepas* Dall, 1872, *Cetolepas* Zullo, 1969) should be interpreted as instruments to core prongs out of the mammalian skin, thus contributing to the progressive penetration of the shell into the host’s cutis; it is therefore likely that the ribs of *C. manati* carry out the same function.

2) All the extant balaenids but *Balaena mysticetus* Linnaeus, 1758, present large, cornified patches of skin (known as callosities) on their head, and especially on their snout (Kenney 2002). Callosities start to emerge when the whale is just a fetus (Payne & Dorsey 1983), and as such, they could represent a long-lasting inheritance of the balaenid lineage which originated the extant right whales. Whereas the origin and function of these callosities are unknown, various amphipod crustaceans (cyamids, or whale lice) and whale barnacles (e.g., the coronulid genus *Tubicinella* Lamarck, 1802) take place on them (Kenney 2002; Reeb et al. 2007). Therefore, the horny callosities of the whales belonging to the genus *Eubalaena* seem to represent an excellent analogous of the horny carapace of the marine turtles, on which most extant turtle barnacles (including *Chelonibia* spp.) attach.

3) The callosity-bearing Balaenidae (i.e., the right whales) are currently known as very slow surface-swimming whales with predominantly coastal habits (e.g., Teixeira et al. 2014). Most sea turtle species gather in coastal breeding and spawning grounds in the warm summer months, and it seems that *Chelonibia testudinaria* has calibrated the timing of its reproductive activity to that of its host (Nájera-Hillman et al. 2012). Therefore, the presence of right whales in a sea turtle breeding ground during the summer season could have certainly favored the colonization of the mysticetes by *C. testudinaria* due to the huge concentration of chelonibiid cyprid larvae

in those waters. Interestingly, various Italian Neogene deposits which feature fossil sea turtles (e.g., the Pietra Leccese) also present remains of Balaenidae, thus supporting this scenario.

4) Interaction between cetaceans and turtles has been documented repeatedly (Fertl & Fulling 2007), with most interaction events being investigatory (thus involving swimming in the close proximity of the other animal and touching it with exploratory and play purposes) rather than predatory; in particular, Fertl & Fulling (2007) reported a case of possible care-giving behavior by a humpback whale [*Megaptera novaeangliae* (Borowski, 1781)] directed towards an unidentified sea turtle in Hervey Bay (Queensland, Australia). In addition, right whales are known among baleen whales for having interactions with other cetaceans, including both mysticete and odontocete species [e.g., Scarff (1986), and references therein], and there is some indirect evidence that this attitude has ancient roots (Collareta et al. 2016). More generally, right whales are highly curious towards non-conspecifics (or, at least, towards humans and human vessels) when juveniles (Lundquist et al. 2008). This investigatory tendency could have favored the interactions between balaenids and sea turtles, thus allowing the attachment of the chelonibiid cyprid larvae on the mysticetes.

5) As reported above, the exceptionally high concentration of coronuloid shells found near the mandible of the mysticete skeleton MSNUP I-16839 (at least 13 individuals detected in an area of ca 1 m²) clearly indicates that they should have been buried with their host. Although most of fossil whale barnacles were not found associated to fossil mysticete skeletons, due to spontaneous or induced detachment from a still-living cetacean [see Bianucci et al. (2006a; 2006b), and references therein], in few cases they have been described in copresence with the remains of their host. Holthuis et al. (1998) reported a complete specimen of *Cetopirus complanatus* and various bones of its host cetacean *Eubalaena glacialis* (Müller, 1776) found in a X century archaeological site in The Netherlands. Stewart et al. (2011) described various specimens of *Coronula diadema* found in association with the partial skeleton of a balaenopterid mysticete (tentatively identified as a humpback whale) in mid-Holocene intertidal deposits at Abu Dhabi (UAE). These barnacle remains “...were found associated with whale bones, generally within half a meter of the bones,

and particularly along the length of the left mandible". This taphonomic scenario strikingly evokes the balaenid-*Chelonibia* assemblage observed at Casenuove (Fig. 2).

6) Finally, as reported in the introduction of this work, *Chelonibia* is believed to occupy a basal position within Coronuloidea (e.g., Hayashi et al. 2013); moreover, *Chelonibia* has been tentatively proposed to have originated the whale barnacles by Buckeridge (1983).

Based on the above listed topics, we propose that the fossil *Chelonibia testudinaria* specimens from the Casenuove clay quarry were hosted on the balaenid individual represented by the partial skeleton MSNUP I-16839. Therefore, the balaenid-*Chelonibia* fossil association of Casenuove most likely represents a snap-shot of an ancient phase of dispersal of *Chelonibia* on baleen whales. This interpretation helps us to depict a possible evolutionary origin for the family Coronulidae. We propose that during the Pliocene *Chelonibia* expanded its host habits from the carapace of sea turtles to another substrate: the callosities of right whales (or related mysticete taxa). This putative event would have been facilitated by various factors including the lack of competing barnacles specifically affecting the mysticetes, the coastal habits of both sea turtles and balaenid whales, and the high plasticity of various members of the genus *Chelonibia* with respect to the nature of their substrate. The subsequent conquest of a new, pulpy environment (the soft skin of the mysticetes) could have ultimately led to the origin and radiation of the extant rib-bearing whale barnacle genera (*Cetopirus*, *Coronula*, and *Cryptolepas*) via the evolution of an intermediate form somewhat resembling *Chelonibia manati*. Callosities would have become the preferred substrate of a differently designed coronulid genus, *Tubicinella*, which anchor to its host by a tubular shell that grows via the addition of new rings at its base.

As the fossil record from Casenuove does not clearly predate every unambiguous fossil record of true whale barnacles (Coronulidae) published to date, the opportunity that more than one phase of dispersal of chelonibiid barnacles on cetaceans occurred must be taken in account. Moreover, various *Chelonibia*-like turtle barnacles other than *Chelonibia* (e.g., members of the genus *Platylepas* Gray, 1825) could have accessed in a similar way the cetacean skin. Nevertheless, since the whale barnacles are widely regarded as monophyletic, only one of these

putative dispersal waves proved to be enduringly successful. In this regard, a phylogenetic analysis of the whole Coronuloidea (including both fossil and extant taxa) is overly needed, as it could both elucidate the evolutionary origin of the whale barnacles and illustrate the coevolutionary trend which is believed to have linked them to their mysticete hosts during the Pliocene-Pleistocene.

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REFERENCES

- Albianelli A., Azzaroli A., Bertini A., Ficcarelli G., Napoleone G. & Torre D. (1997) - Paleomagnetic and palynologic investigations in the Upper Valdarno Basin calibration of an Early Villafranchian fauna. *Riv. It. Paleontol. Strat.*, 103: 111-118.
- Badrudeen M. (2000) - On the occurrence of the cirriped barnacle, *Chelonibia patula* (Ranzani) on the sea snake, *Hydrophis cyanocinctus* (Daudin). *Mar. Fish. Inf. Serv. Tech. Ext. Ser.*, 164, 25 pp.
- Benvenuti M., Del Conte S., Scarselli N. & Dominici S. (2014) - Hinterland basin development and infilling through tectonic and eustatic processes: latest Messinian-Gelasian Valdelsa Basin, Northern Apennines, Italy. *Basin Res.*, 26: 387-402.
- Benvenuti M., Dominici S. & Rook L. (1995) - Inquadramento stratigrafico-deposizionale delle faune a mammiferi villafranchiane (Unità faunistiche Triversa e Montopoli) del Valdarno inferiore nella zona a sud dell'Arno (Toscana). *Il Quaternario*, 8: 457-464.
- Bianucci G. (1996) - A new record of baleen whale from the Pliocene of Tuscany (Italy). *Atti Soc. Tosc. Sci. Nat. Mem. Ser. A*, 102: 101-104.
- Bianucci G. & Landini W. (2005) - I paleositi a vertebrati fossili della Provincia di Pisa. *Atti Soc. Tosc. Sci. Nat. Mem. Ser. A*, 110: 1-21.
- 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. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 242: 326-342.
- Bianucci G., Landini W. & Buckeridge J. (2006b) - Whale barnacles and Neogene cetacean routes. *New Zealand J. Geol. Geop.*, 49: 115-120.

- Bianucci G. & Sorbini C. (2014) - Le collezioni a cetacei fossili del Museo di Storia Naturale dell'Università di Pisa. *Museol. Sci. Mem.*, 13: 93-102.
- Bogaard P. van den & Schmincke H.U. (1998) - Chronostratigraphy of Gran Canaria. *Proc. ODP, Sci. Results*, 157: 127-144.
- Borowski G.H. (1781) - *Gemmeinuzige Naturgeschichte des Theirreichs*, vol. 1. Gottlieb August Lange, Berlin.
- Brocchi G. (1814) - *Conchiologia fossile subapennina*, con osservazioni geologiche sugli Apennini e sul suolo adiacente. Stamperia Reale, Milano, 432 pp.
- Bronn H. (1831) - *Italiens Tertiär-Gebilde und deren organische Einschlüsse: vier Abhandlungen*. Groos, Heidelberg, 176 pp.
- Buckeridge J.S. (1983) - Fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia. *New Zealand Geol. Surv. Paleontol. Bull.*, 50: 1-151.
- Cigala Fulgosi F., Casati S., Orlandini A. & Persico D. (2009) - A small fossil fish fauna, rich in *Chlamydoselachus* teeth, from the Late Pliocene of Tuscany (Siena, central Italy). *Cainozoic Res.*, 6: 3-23.
- 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. *C. R. Palevol*, 15(5): 473-481.
- Croizet J.B. & Jobert A. (1828) - *Recherches sur les ossements fossiles du département du Puy-de-Dôme*. Adolphe Delahays, Paris, 224 pp.
- da Costa E.M. (1778) - *Historia naturalis testaceorum Britanniae, or, the British conchology; containing the descriptions and other particulars of natural history of the shells of Great-Britain and Ireland*. Millan, White & Elmsley, London, 254 pp.
- Dall W.H. (1872) - On the parasites of the cetaceans of the N.W. coast of America, with descriptions of new forms. *Proc. Calif. Acad. Sci.*, 4: 299-301.
- Danise S., Dominici S. & Betocchi U. (2010) - Mollusk species at a Pliocene shelf whale fall (Orciano Pisano, Tuscany). *Palaios*, 25(7): 449-456.
- Darwin C. (1854) - *A Monograph on the subclass Cirripedia with figures of all the species. The Balanidae, The Verucidae, etc.* Ray Society, London, 770 pp.
- De Alessandri G. (1895) - Contribuzione allo studio dei Cirripedi fossili d'Italia. *Boll. Soc. Geol. Ital.*, 13: 234-314.
- De Alessandri G. (1906) - Studi monografici sui cirripedi fossili d'Italia. *Palaeontographia Ital.*, 12: 207-324.
- Dominici S., Bartolini M., Benvenuti M. & Balestra B. (2011) - Large kings with small crowns: a Mediterranean Pleistocene whale barnacle. *Boll. Soc. Paleontol. Ital.*, 50: 95-101.
- Dominici S., Rook L., Benvenuti M. & Abbazzi L. (1995) - Tapir remains in paralic deposits of Pliocene age in lower Valdarno (Tuscany, Italy): Facies analysis and taphonomy. *Geobios*, 28: 131-135.
- 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(9): 815-818.
- Ellis J. (1758) - An account of several rare species of barnacles. In: A letter to Mr. Isaac Romilly, F.R.S. from John Ellis, Esq; F.R.S., *Philos. T. Roy. Soc.*, 50: 845-855.
- Fertl D. & Fulling G.L. (2007) - Interactions between marine mammals and turtles. *Mar. Turtle News.*, 115: 4-8.
- Foresti L. (1868) - Catalogo dei molluschi fossili pliocenici delle colline bolognesi. *Mem. R. Acc. Sci. Ist. Bologna*, 2 (7): 1-100.
- Frazier J.G. & Margaritoulis D. (1990) - The occurrence of the barnacle, *Chelonibia patula* (Ranzani, 1818), on an inanimate substratum (Cirripedia, Thoracica). *Crustaceana*, 59 (2): 213-218.
- Gray J.E. (1825) - A synopsis of the genera of Cirripedes arranged in natural families, with a description of some new species. *Ann. Phil. (New Ser.)*, 10: 97-107.
- Gray J.E. (1864) - On the Cetacea which have been observed in the seas surrounding the British Islands. *Proc. Zool. Soc. London*, 1864: 195-248.
- Gruvel J.A. (1903) - Revision des Cirripèdes appartenant à la collection du Muséum d'Histoire Naturelle (Operculés). II. Partie systématique. *Nouv. Arch. Mus. Nat. Hist. Nat., Ser. 4*, 5, 95-170.
- Harzhauser M., Newman W.A. & Grunert P. (2011) - A new Early Miocene barnacle lineage and the roots of sea-turtle fouling Chelonibiidae (Cirripedia, Balanomorph). *J. Syst. Palaeontol.*, 9(4): 473-480.
- Hatai K.M. (1939) - On the occurrence of *Coronula* from the Kakegawa series in Totomi, Japan. *Bull. Biogeogr. Soc. Japan*, 9: 261-265.
- Hayashi R., Chan B.K., Simon-Blecher N., Watanabe H., Guy-Haim T., Yonezawa T., Levy Y., Shuto T. & Aчитov Y. (2013) - Phylogenetic position and evolutionary history of the turtle and whale barnacles (Cirripedia: Balanomorph: Coronuloidea). *Mol. Phylogenet. Evol.*, 67(1): 9-14.
- 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. *Zool. Verhandl.*, 323: 349-363.
- Ishibashi M. (1989) - Sea-level controlled shallow-marine systems in the Plio-Pleistocene Kakegawa Group, Shizuoka, central Honshu, Japan: comparison of transgressive and regressive phases. In: Taira A. & Masuda F. (Eds) - *Sedimentary facies in the active plate margin*: 345-363. Terra Publication Company, Tokyo.
- Kenney R.D. (2002) - North Atlantic, North Pacific, and Southern right whales. In: Perrin W.F., Wursig B. & Thewissen J.G.M. (Eds) - *Encyclopedia of Marine Mammals*: 806-812. Academic Press, San Diego.
- Lamarck J.B. (1802) - Mémoire sur la Tubicinelle. *Ann. Mus. Nat. Hist. Nat.*, 1: 461-464.
- Leach W.E. (1817) - Distribution systématique de la class Cirripèdes. *J. Phys. Chim. Hist. Nat.*, 85: 67-69.
- Landini W. (1977) - Revisione degli "Ittiodontoliti pliocenici" della collezione Lawley. *Palaeontographia Ital.*, 70: 92-134.
- Linnaeus C. (1758) - *Systema Naturae sive Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis, Tomus I. Editio decima, reformata*. Stockholm, 824 pp.
- Linnaeus C. (1767) - *Systema Naturae sive Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis, Tomus I*: 533-1327.

Editio duodecima, reformata. Stockholm.

- Lundquist D., Sironi M., Würsig B. & Rowntree V. (2008) - Behavioural responses of southern right whales to simulated swim-with-whale tourism at Peninsula Valdes, Argentina. *J. Cetac. Res. Manag.*, 60: 1-15.
- Menesini E. (1968) - Osservazioni su *Coronula bifida* Bronn. *Atti Soc. Tosc. Sci. Nat., Mem. Ser. A*, 75: 387-398.
- Missimer T.M. (1992) - Stratigraphic relationships of sediment facies within the Tamiami Formation of southwest Florida: proposed intraformational correlations. In: Scott T.M. & Allmon W.D. (Eds) - The Plio-Pleistocene stratigraphy and paleontology of southern Florida: 63-92. Florida Geological Survey, Tallahassee.
- Missimer T.M. (1997) - Late Oligocene to Pliocene evolution of the central portion of the South Florida Platform: mixing of siliciclastic and carbonate sediments. University of Miami, unpublished Ph.D. thesis.
- Monroe R. & Garrett R. (1979) - *Chelonibia testudinaria* (L.) (Cirripedia, Coronulidae) on *Crocodylus porosus* Schneider, a new host record. *Crustaceana*, 36: 108.
- Mörch O.A.L. (1853) - Cephalophora. In: Catalogus conchyliorum. Typis Ludovici Kleini, Copenhagen, 170 pp.
- Moriarty J.E., Sachs J.A. & Jones K. (2008) - Directional locomotion in a turtle barnacle, *Chelonibia testudinaria*, on green turtles, *Chelonia mydas*. *Mar. Turtle News.*, 119: 1-4.
- Müller O.F. (1776) - Zoologica Danicae Prodromus seu Animalium Daniae et Norvegiae indigenarum characteres, nomine, et synonyma imprimis popularium. Typis Hallageriis, Copenhagen, 282 pp.
- Nájera-Hillman E., Bass J.B. & Buckham S. (2012) - Distribution patterns of the barnacle, *Chelonibia testudinaria*, on juvenile green turtles (*Chelonia mydas*) in Bahía Magdalena, Mexico. *Rev. Mex. Biodiv.*, 83(4): 1171-1179.
- Newman W.A. & Ross A. (1976) - Revision of the balanomorph barnacles: including a catalog of the species. *Mem. San Diego Soc. Nat. Hist.*, 9: 1-108.
- Nifong J. & Frick M.G. (2011) - First record of the American alligator (*Alligator mississippiensis*) as a host to the sea turtle barnacle (*Chelonibia testudinaria*). *Southeast. Natur.*, 10(3): 557-560.
- Payne R. & Dorsey E.M. (1983) - Sexual dimorphism and aggressive use of callosities in right whales (*Eubalaena australis*). In: Payne R. (Ed.) - Communication and Behaviour of Whales: 295-329. Westview Press, Boulder.
- Pennant T. (1777) - The British zoology, vol. 4: Crustacea, Mollusca, Testacea. 4th edition: 1-136. White, London.
- 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. *Bull. U.S. Nat. Mus.*, 93: 1-366.
- Ranzani C. (1817) - Osservazioni sui balanidi. *Opuscoli Scientifici*, 2(2): 63-69.
- Reeb D., Best P.B. & Kidson S.H. (2007) - Structure of the integument of southern right whales, *Eubalaena australis*. *Anat. Rec.*, 290(6): 596-613.
- Röding P.F. (1798) - Museum Boltenianum, Pars Secunda continens conchilia, sive Testacea univalvia, bivalvia et multivalvia. Christi, Hamburg, 199 pp.
- Ross A. (1963). *Chelonibia* in the Neogene of Florida. *Quar. J. Florida Acad. Sci.*, 26: 221-233.
- Ross A. & Newman W.A. (1967) - Eocene Balanidae of Florida, including a new genus and species with a unique plan of "turtle-barnacle" organization. *Am. Mus. Nov.*, 2288: 1-21.
- Rothpletz A. & Simonelli V. (1890) - Die marinen Ablagerungen auf Gran Canaria. *Zeitschr. Deutsch. Geol. Gesell.*, 42: 677-736.
- Rustioni M. & Mazza P. (2001) - Taphonomic analysis of *Tapiro arvernensis* remains from the lower Valdarno (Tuscany, Central Italy). *Geobios*, 34(4): 469-474.
- Seilacher A. (2005) - Whale barnacles: exaptational access to a forbidden paradise. *Paleobiology*, 31(Suppl.): 27-35.
- Scarff J.E. (1986) - Occurrence of the barnacles *Coronula diadema*, *C. reginae* and *Cetopirus complanatus* (Cirripedia) on right whales. *Sci. Rep. Whales Res. Inst.*, 37: 129-153.
- Stewart J.R., Aspinnall S., Beech M., Fenberg P., Hellyer P., Larkin N., Lokier S.W., Marx F.G., Meyer M., Miller R., Rainbow P.S., Taylor J.D., Whittaker J.E., Al-Mehsin K. & Strohmenger C.J. (2011) - Biotically constrained palaeoenvironmental conditions of a mid-Holocene intertidal lagoon on the southern shore of the Arabian Gulf: evidence associated with a whale skeleton at Musaffah, Abu Dhabi, UAE. *Quaternary Sci. Rev.*, 30: 3675-3690.
- Teixeira A., Venâncio R. & Brito C. (2014) - Archaeological Remains Accounting for the Presence and Exploitation of the North Atlantic Right Whale *Eubalaena glacialis* on the Portuguese Coast (Peniche, West Iberia), 16th to 17th Century. *PLOS ONE*, 9(2): e85971.
- Withers T.H. (1928) - The cirripede *Chelonibia caretta*, Spengler, in the Miocene of Zanzibar Protectorate. *Ann. Mag. Nat. Hist. Ser.* 10(2): 390-392.
- Withers T.H. (1929) - The cirripede *Chelonibia* in the Miocene of Gironde, France and Vienna, Austria. *Ann. Mag. Nat. Hist. Ser.* 10(4): 566-572.
- Withers T.H. (1953) - Catalogue of fossil Cirripedia in the Department of Geology. Volume 3, Tertiary. British Museum of Natural History, London, 396 pp.
- Zardus J.D., Lake D.T., Frick M.G. & Rawson P.D. (2014) - Deconstructing an assemblage of "turtle" barnacles: species assignments and fickle fidelity in *Chelonibia*. *Mar. Biol.*, 161(1): 45-59.
- Zullo V.A. (1969) - Thoracic Cirripedia of the San Diego Formation, San Diego County, California. *Contrib. Sci. Nat. Hist. Los Angeles Co.*, 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.

