The occurrence of the coronuloid barnacle *Chelonibia* Leach, 1817 as an encruster on mammalian bone in the central Mediterranean Sea

Alberto COLLARETA1,2* and Giovanni BIANUCCI1,2

1Dipartimento di Scienze della Terra, Università di Pisa, via S. Maria 53, Pisa 56126, Italy
2Museo di Storia Naturale, Università di Pisa, via Roma 79, Calci 56011, Italy

*Corresponding author, e-mail: alberto.collareta@unipi.it

Among the turtle and whale barnacles (Coronuloidea: Chelonibiidae, Coronulidae, †Emersoniidae and Platylepadidae), the members of the chelonibid species *Chelonibia testudinaria* (Linnaeus, 1758) are known as epizoic barnacles that can attach to a rather wide spectrum of substrates (primarily sea turtles, crabs and sirenians). At present, three living morphs of *C*. testudinaria have been recognised; of these, the less host-specific is the *patula* morph, which also displays a remarkably simple, unspecialised shell architecture. Here we report on several chelonibiid shells, referred to the *patula* morph of *C*. testudinaria, encrusting a cetacean scapula collected from the floor of the Adriatic Sea facing Salento (Apulia Region, southeastern Italy) and tentatively referred to *Tursiops truncatus* (Montagu, 1821). This is one of the few records worldwide of a coronuloid barnacle from an inanimate substrate, as well as the second as an encruster on mammalian bone. Such an unusual occurrence is then briefly discussed in the broader framework of the coronuloid commensalism and substrate habits.

Key words: Cirripedia; Chelonibiidae; epibiosis; host preferences; symbiosis; turtle barnacle

INTRODUCTION

The acorn barnacles (Crustacea: Thoracica: Balanomorpha) included in the cirriped superfamily Coronuloidea are known as epibionts of several saltwater vertebrates and, secondarily, invertebrates (e.g., DARWIN, 1854; GRUVEL, 1905; PILSBRY, 1916; KRÜGER, 1940; NEWMAN, 1996; LIU & REN, 2007). Members of Coronuloidea are currently assigned to four families, namely, Coronulidae, Chelonibiidae, Platylepadidae, and the puzzling †Emersoniidae (NEWMAN, 1996; COLLARETA & NEWMAN, 2020). The coronulids, which are commonly referred to as the ‘whale barnacles’, are regarded as obligate commensals of cetaceans; conversely, the chelonibiids and platylepadids (collectively known as the ‘turtle barnacles’) are relatively more generalist as regards their host habits, although most of them preferentially inhabit the skin or shell of the sea turtles (chelonians) (e.g., ROSS & NEWMAN, 1967; ROSS & FRICK, 2011; HAYASHI, 2013, and references therein).

The sole living genus of Chelonibiidae, *Chelonibia*, includes two extant species, namely, *Chelonibia testudinaria* (Linnaeus, 1758) and
Chelonibia caretta (Spengler, 1790); two other living species (i.e., Chelonibia patula (Ranzani, 1817) and Chelonibia manati Gruvel, 1903) were also recognised as valid until a few years ago, but have recently been revealed as comprising peculiar morphs of C. testudinaria (CHEANG et al., 2013; ZARDUS et al., 2014). At present, Chelonibia caretta has only been reported as an epibiont on sea turtles, either on the chelonian shell or skin; in turn, C. testudinaria is an epizoic barnacle whose morphs can attach onto a relatively broad range of substrates, including marine and brackish-water turtles, crabs and horseshoe crabs, sea cows, sea snakes, crocodilians, sea snails, and even inanimate substrates such as floating plastic items (e.g., DARWIN, 1854; ROSS & JACKSON, 1972; NEWMAN & ROSS, 1976; MONROE & GARRET, 1979; FRAZIER & MARGARITOLIS, 1990; BADRUDEEN, 2000).

Here we report on several shells of the patula morph of Chelonibia testudinaria encrusting a cetacean scapula collected from the floor of the Adriatic Sea facing Salento (Apulia Region, southeastern Italy). This is one of the few records worldwide of a coronuloid barnacle from an inanimate substrate, as well as the second as an encruster on mammalian bone. The herein reported occurrence is then briefly discussed in the broader framework of the coronuloid commensalism and substrate habits.

MATERIAL AND METHODS

This paper describes the unusual association between a cetacean scapula and several chelonibiid barnacle shells that adhere to its outer cortical surface. This bone and its crustacean encrusters are currently kept in the zoological collection of the Museo di Storia Naturale dell’Università di Pisa (hereinafter: MSNUP) under the accession number MSNUP C 3240. They were recovered by the late Angelo Varola (†2019) from a shallow seafloor off the eastern (i.e., Adriatic) coast of Salento, between Brindisi and Santa Maria di Leuca (Apulia Region, southeastern Italy) (Fig. 1). Although the precise locality of MSNUP C 3240 is unknown, its provenance — the Adriatic Sea facing Salento — is ascertained.

RESULTS

MSNUP C 3240 consists of a partial left scapula of a cetacean that lacks most of its dorsal portion (Fig. 2). Comparisons between this bone and shoulder blades of extant Mediterranean cetaceans kept at the MSNUP allowed for highlighting strong morphological similarities with the scapula of the common bottlenose dolphin Tursiops truncatus (Montagu, 1821).

On the preserved portion of the lateral surface of the scapula (Fig. 2A), an acorn barnacle lies close to the posterior border of the blade. This is an eight-plated, truncated-conical, carinorostrally elongated shell displaying a maximum basal diameter of 9.0 mm. The true ros-
Fig. 2. MSNUP C 3240, partial cetacean scapula from the floor of the Adriatic Sea facing Salento, in (A) lateral and (B) medial views.

Fig. 3. Close-ups of five shells of Chelonibia testudinaria (patula morph) occurring as encrusters on the partial cetacean scapula MSNUP C 3240. (A) Detail of a chelonibiid specimen occurring on the medial surface of the shoulder plate (note the locally concave basal profile that indicates the adjoining occurrence of another barnacle shell that did not get preserved). (B) Detail of two chelonibiid specimens that cluster on the medial surface of the shoulder plate (note the locally concave basal profile of the larger specimen). (C) Detail of a chelonibiid specimen occurring on the medial surface of the shoulder plate (note the nearby presence of clusters of barnacle attachment traces). (D) Detail of a chelonibiid specimen occurring on the lateral surface of the shoulder plate (note the nearby presence of a barnacle attachment trace, still exhibiting shreds of the membranous basis that also reveal a dense pattern of longitudinal internal parietal septa). All the chelonibiid specimens are here depicted with their rostral end facing rightwards.
trum and rostrolaterals are partially coalescent with each other to form a tripartite rostral complex. The parietes are thin and delicate, and the substantially smooth radii are only slightly sunken. The external surfaces of the parietes are almost featureless. The opercular plates are strongly reduced. On the whole, these characters allow for the identification of the *patula* morph of *Chelonibia testudinaria*, a member of the coronuloid family Chelonibiidae (e.g., DARWIN, 1854; PILSBRY, 1916; ROSS, 1963; NEWMAN & ROSS, 1976; CHAN et al., 2009; CHEANG et al., 2013; ZAR-DUS et al., 2014).

Four similar barnacle specimens are found on the preserved portion of the medial surface of the scapula (Fig. 2B); in particular, one of them (measuring 9.3 mm in carinorostral diameter) is observed along the posterior border of the blade, two (measuring 6.4 and 4.3 mm in carinorostral diameter) cluster close to the anterior border of the blade, and the fourth (measuring 9.3 mm in carinorostral diameter) takes its place in an intermediate position. Two of the aforementioned specimens display a locally concave basal profile that indicates the adjoining occurrence of another barnacle shell that did not get preserved (Fig. 3A, B). All the observed barnacles have their carinal extremity oriented towards the unpreserved dorsal margin of the scapula.

Furthermore, traces that are found on both the lateral and medial surfaces of the shoulder blade hint at the former presence of several more encrusting barnacle shells that detached from the scapula before it was collected from the seafloor (Fig. 3C). These traces range between 5.9 mm and 11.8 mm in maximum diameter. They consist of oval patches where the outer cortical surface is seemingly well preserved and appears as slightly lifted above the partly abraded surrounding areas. These traces superficially recall the barnacle attachment marks that have been classified under the ichnogenus name *Anel-lusichnus* (SANTOS et al., 2005; BUCKERIDGE et al., 2019), and especially *Anellusichnus circularis* Santos, Mayoral & Muñiz, 2005. A few traces still exhibit shreds of soft tissues (i.e., the membranous basis of the barnacle) attached to them, which in one case also reveal the dense pattern of longitudinal internal parietal septa that is typical of *Chelonibia* (Fig. 3D). Seven traces are observed on the lateral surface of the scapula, whereas more than 25 traces occur on the medial surface of the bone (including the medial surface of the acromion). Most of these traces form clusters (Fig. 3C). The greater abundance of barnacles and barnacle attachment traces on the medial surface of the scapula might be due to this bone having rested at the seafloor medial side-up (see also BIANUCCI & GINGERICH, 2011 in this respect).

**DISCUSSION AND CONCLUSIONS**

Encrustation of defleshed mammalian bones by acorn barnacles is a relatively common occurrence, as demonstrated by a rather conspicuous amount of observations (e.g., SACCO, 1893; DENNISON et al., 2004; BOESSENECKER, 2013; POKINES & HIGGS, 2015; TSAI et al., 2017; BOSIO et al., 2021). What is peculiar to the present report is the assignment of the encrusting barnacles to the superfamily Coronuloidea, whose members are currently understood as obligate or quasi-obligate phoronts of several different marine organisms. To our knowledge, the herein record of several chelonibiid specimens assigned to the *patula* morph of *Chelonibia testudinaria* as encrusters on mammalian bone represents the second of its kind worldwide. Indeed, a similar occurrence was reported by MONROE (1981) as follows:

“Specimen lot W7354, *Chelonibia patula*, 20 individuals, was removed (together with 20 *Balanus trigonus* W7355) from a human femur recovered in 20 m from Moreton Bay [Australia, authors’ note] near Moreton Is. on July 10th 1977. It may be that *Chelonibia patula* has a substrate preference involving organised calcium matrices.”

In another passage, MONROE (1981) characterised the bone on which the *Chelonibia* shells attached as “old”. MONROE (1981) did not figure these specimens, neither did others; in addition, no further records of *Chelonibia* or other coronuloid barnacles attaching to a bony substrate are known to the authors of the present work.
In light of these considerations, our discovery represents a rather important find that deserves to be adequately reported on.

More than 37 barnacle specimens were originally attached to the dolphin scapula. Those among them that managed to get preserved display no signs of abnormal growth as well as a much ordinary size. Therefore, coupled with the results by Monroe (1981), our observations suggest that the association between the patula morph of C. testudinaria and the defleshed mammalian bone is far from being anomalous, the latter likely representing a much suitable (although ostensibly rare) substrate for the attachment of the former. That said, the reduced opercular plates that characterise the coronuloids (including all the living members of the genus Chelonibia) and the consequent exposure of the soft parts to predators might partly explain why the patula morph of C. testudinaria is only occasionally found on motionless (but otherwise hospitable) substrates such as bone.

Whereas the testudinaria and manati morphs of C. testudinaria are largely if not exclusively confined to sea turtles and sea cows, respectively, the patula morph is capable of exploiting a broad diversity of potential substrates, including vertebrates, invertebrates and inanimate objects (both artificial ones, such as plastic, and dead biological materials, such as bone; Monroe, 1981; Frazier & Margaritoulis, 1990; this work). The greater host specialisation of the manati and testudinaria morphs of C. testudinaria is mostly achieved via a number of modifications that are related to the attachment mechanisms: for instance, the former can send finger-like ramifications of the periphery of its wall plates into the somewhat penetrable skin of its sirenian host (Ross & Newman, 1967; Frick et al., 2011), whereas the latter even displays remarkable post-settlement capabilities of locomotion that are believed to derive from specialised contractile fibrils connecting the barnacle shell to its membranous basis, which in turn contacts the underlying turtle shell (Moriarty et al., 2008). Overall, the patula morph of C. testudinaria represents the less specialised living form of coronuloid barnacles, as is also reflected by its altogether simple shell architecture (Newman & Ross, 1967; Zullo, 1982) that does not deviate strongly from the overall aspect of an ‘average’ non-epizoic, rock-dwelling balanomorph barnacle. While apparently at odds with the recent synonymisation between C. patula and C. testudinaria (Cheang et al., 2013), the persistence of a peculiar morph characterised by a generalised shell architecture allowing for diverse substrate habits and a high host plasticity might have comprised a key factor in determining remarkable species longevity in C. testudinaria as redefined by Zardus et al. (2014) (see also Collareta, 2020 in this respect). Interestingly, recruitment experiments in conditions of relatively low flow rates (i.e., those achievable on overall stationary test panels) demonstrate that larvae of C. testudinaria can successfully settle, metamorphose and grow on a wide variety of sub-optimal substrates (including pieces of carapace scutes from dead turtles, slate, and even Plexiglas®), with the resulting shells ultimately acquiring a patula-like morphology (Sloan et al., 2014). Therefore, low hydrodynamism seemingly correlates with the occurrence of the patula morph of C. testudinaria on slowly moving hosts such as molluscs, crabs and horseshoe crabs (Cheang et al., 2013; Sloan et al., 2014), and the same could be true for inanimate substrates such as bone. That said, the role and contribution of genetics, substrate nature, hydrodynamism, and other environmental parameters in controlling the adult morphology of C. testudinaria still have to be properly investigated.

The above considerations about the specialised nature of the patula morph of C. testudinaria also suggest that the soft- and hard-part morphology of this form might represent a pivotal research target for reconstructing how and from where the unique host specialisations of the remainder of Coronuloidea (Ross & Newman, 1967; Seilacher, 2005; Kim et al., 2020) evolved. Furthermore, they raise the question of whether the earliest members of this superfamily were preferential or obligate epibionts on nektic and benthic-vagile hosts like their modern relatives, or they rather were encrusters or episkeletozoans on inanimate substrates (either biogenic...
or abiogenic). Whereas sea turtle fouling was reconstructed on the basis of indirect evidence for the early Miocene (ca. 22 million years ago) species †Protochelonibia submersa Harzhauser & Newman in HARZHAUSER et al., 2011 as well as for the early or middle Miocene †Chelonibia zanzibarensis Collareta & Newman in COLLAR- ETA et al., 2021, there is still no hint of what sort of hosts the geologically older taxa †Emersonius cybosyrinx Ross in ROSS & NEWMAN, 1967 and †Protochelonibia melleni (Zullo, 1982) might have been on (COLLARETA & NEWMAN, 2020).

All things considered, in the quest for the causes and processes beneath the emergence of epibiosis and commensalism in the so-called turtle and whale barnacles, the *patula* morph of *C. testudinaria* promises to serve as a crucial object of study.

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Pojava brumbuljka iz roda *Chelonibia* Leach, 1817, kao inkrustra na kosti sisavca u središnjem dijelu Sredozemnog mora

Alberto COLLARETA* i Giovanni BIANUCCI

*Kontakt, e-pošta: alberto.collareta@unipi.it

SAŽETAK

Među kornjačama i kitovima (Coronuloidea: Chelonibiidae, Coronulidae, † Emersoniidae i Platylepadidae), pripadnici vrste *Chelonibia testudinaria* (Linnaeus, 1758) poznati su kao epizoični brumbuljci koji se mogu pričvrstiti na prilično širok spektar podloga (prvenstveno na kornjače, rakove i velike vodene sisavce koji se hrane biljkama iz reda Sirenia).

Trenutno su prepoznate tri živa morfija *C. testudinaria*; od njih, manje specifična za domaćina je morph patula, koja također prikazuje izuzetno jednostavnu, nespecijaliziranu arhitekturu ljuske.

U ovom radu izvještavamo o nekoliko ljuski helonibiida, koje se odnose na morfe patule *C. testudinaria*, koja inkrustira lopaticu kitova sakupljenu s dna Jadranskog mora prema Salentu (regija Apulia, jugoistočna Italija) i okvirno upućenu na *Tursiops truncatus* (Montagu, 1821).

Ovo je jedan od rijetkih zapisa u svijetu o brumbuljku iz nežive podloge, a i kao drugi slučaj inkrustriranja na kosti sisavca. Takva neobična pojava potom se ukratko raspravlja u širem kontekstu komensalizma brumbuljaka i supstrata staništa.

Ključne riječi: Cirripedia; Chelonibiidae; epibiosis; preferencije domaćina; simbioza; kornjača