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Research article

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The oldest platylepadid turtle barnacle (Cirripedia, Coronuloidea): a new species of *Platylepas* from the Lower Pleistocene of Italy

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Abstract. Coronuloid barnacles are epibionts of several marine vertebrates (including cetaceans and sea turtles) as well as invertebrates, and are assigned to two families of turtle barnacles (Chelonibiidae Pilsbry, 1916 and Platylepadidae Newman & Ross, 1976) and one family of whale barnacles (Coronulidae Leach, 1817). Chelonibiids and coronulids have a scanty, albeit significant fossil record extending back to the Eocene and Pliocene, respectively; in turn, the fossil record of platylepadids is limited to a single record from the Upper Pleistocene. Here we report on an isolated carinolateral compartment of *Platylepas* Gray, 1825, the type genus of the family, from Lower Pleistocene (Gelasian) epibathyal deposits exposed at Milazzo (Sicily, Italy). This specimen is here designated holotype of a new species, †*Platylepas mediterranea* sp. nov. We argue that, like most extant members of *Platylepas*, †*P. mediterranea* sp. nov. lived partially embedded in the skin of a sea turtle. This record of an extinct platylepadid – the first from the Mediterranean region and the second worldwide – pushes back the fossil record of Platylepadidae to the lowermost Quaternary, thus possibly supporting an even earlier (e.g.,

Neogene) timing for the origin of this family and adding a new chapter to the evolutionary history of one of the most diverse and successful lineages of epizoic crustaceans.

Keywords. †*Platylepas mediterranea* sp. nov., sea turtles, Mediterranean Basin, evolution, symbiosis.

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Introduction

Extant turtle and whale barnacles (Cirripedia Burmeister, 1834, Thoracica Darwin, 1854, Coronuloidea Leach, 1817) are epibiotic organisms that attach themselves to the external surface of several saltwater and estuarine vertebrates (including toothed and baleen whales, sea turtles, sea cows, crocodiles, snakes and bony fish) and invertebrates (including crabs, horseshoe crabs and crayfish) (Hayashi 2013, and references therein). By living on mobile host substrates, these sessile filter-feeding crustaceans can exploit a continuous flow of water laden with nutrient particles while at the same time lowering the risk of predation (Seilacher 2005). Currently, coronuloid barnacles are assigned to three families, namely Coronulidae, Chelonibiidae and Platylepadidae (Ross & Frick 2011). Whereas coronulids are obligate phoronts of cetaceans (hence their vernacular name, whale barnacles), chelonibiids and platylepadids (collectively known as turtle barnacles) exhibit more generalist host habits, although most species live preferentially or exclusively on the skin, carapace or plastron of sea turtles. The fossil history of Chelonibiidae dates back to the Paleogene (with the earliest representative of the family, †*Emersonius cybosyrinx* Ross in Ross & Newman, 1967, from the upper Eocene Williston Limestone of Florida, USA), whereas coronulids seemingly appeared later, starting with †*Coronula bifida* Bronn, 1831 in a few Upper Pliocene deposits worldwide (e.g., Marquet *et al.* 2009). In turn, the fossil record of Platylepadidae, a widely distributed and well-diversified family of small-sized, warm-water coronuloids, with at least fourteen extant species in six genera (Ross & Frick 2011), is much less extensive and, in fact, comprises merely the holotype of †*Platylepas wilsoni* Ross, 1963 from the Upper Pleistocene Pamlico Formation of Florida, USA.

In the present paper we report on the presence of a member of *Platylepas* Gray, 1825, the type genus of the family, in Lower Pleistocene marine deposits of the central Mediterranean Basin. The single specimen known is a right carinolateral compartment; it is here designated holotype of a new species and its paleontological significance is briefly discussed.

Material and methods

The present barnacle was discovered by one of us (A.Re.) in a succession of Plio-Pleistocene marine sedimentary strata that is exposed along a coastal cliff at Cape Milazzo (Messina Province, Sicily, Italy), a peninsula located on the northeastern corner of Sicily, to the southeast of the Aeolian archipelago (Fig. 1). These deposits fill small depressions on both the underlying Paleozoic metamorphites and their Upper Miocene sedimentary cover (Fois 1990a, 1990b). These Plio-Pleistocene strata are capped by a ‘Tyrrhenian’ terrace that, in turn, is overlain by Holocene volcanic ashes (Fois 1990a, 1990b). In particular, the silty to sandy, carbonate-rich deposits referred to as “Marne Calcareae Gialle” (i.e., yellow calcareous marls; hereinafter: YCM) are rich in fossils of benthic invertebrates, including corals (scleractinians and octocorals), echinoderms (echinoids and comatulid crinoids), bryozoans, mollusks, crustaceans, foraminifera, serpulids and brachiopods. This fossil association is widely considered to be indicative of deposition in an epibathyal environment (Gignoux 1913; Lipparini *et al.* 1955; Mars 1956; Gaetani & Saccà 1984; Gaetani 1986; Violanti 1988; Langer 1989; Palazzi & Villari 1996; Rosso 2002a, 2002b, 2005; Sciuto 2003, 2005, 2009, 2012a, 2012b, 2014; Pasini & Garassino 2011; Rosso & Braga

2013; Borghi *et al.* 2014; Rosso & Di Martino 2015). The specimen described herein was collected from the Cala S. Antonino outcrop (approximate coordinates 38°15'54.9" N, 15°14'12.7" E, see Fig. 1), where the YCM reaches a maximum thickness of 13.5 meters. These strata are Early Pleistocene in age, being largely attributable to the Gelasian and, with respect to their uppermost few decimetres, to the Calabrian (Rosso *et al.* 2012, and references therein). The platylepadid compartment, recovered from the Gelasian portion of this YCM succession, is now housed in the collections of the Museo Civico di Storia Naturale di Comiso (MSNC, Comiso, Ragusa Province, Sicily, Italy). The specimen was examined and photographed using backscattered electrons under an LMU Tescan Vega II Scanning Electron Microscope (SEM) at the Università di Catania (Sicily, Italy). The following symbols and anatomical abbreviations are utilized throughout the text:

- † = extinct species
- R = rostrum
- RL = rostromedial plate

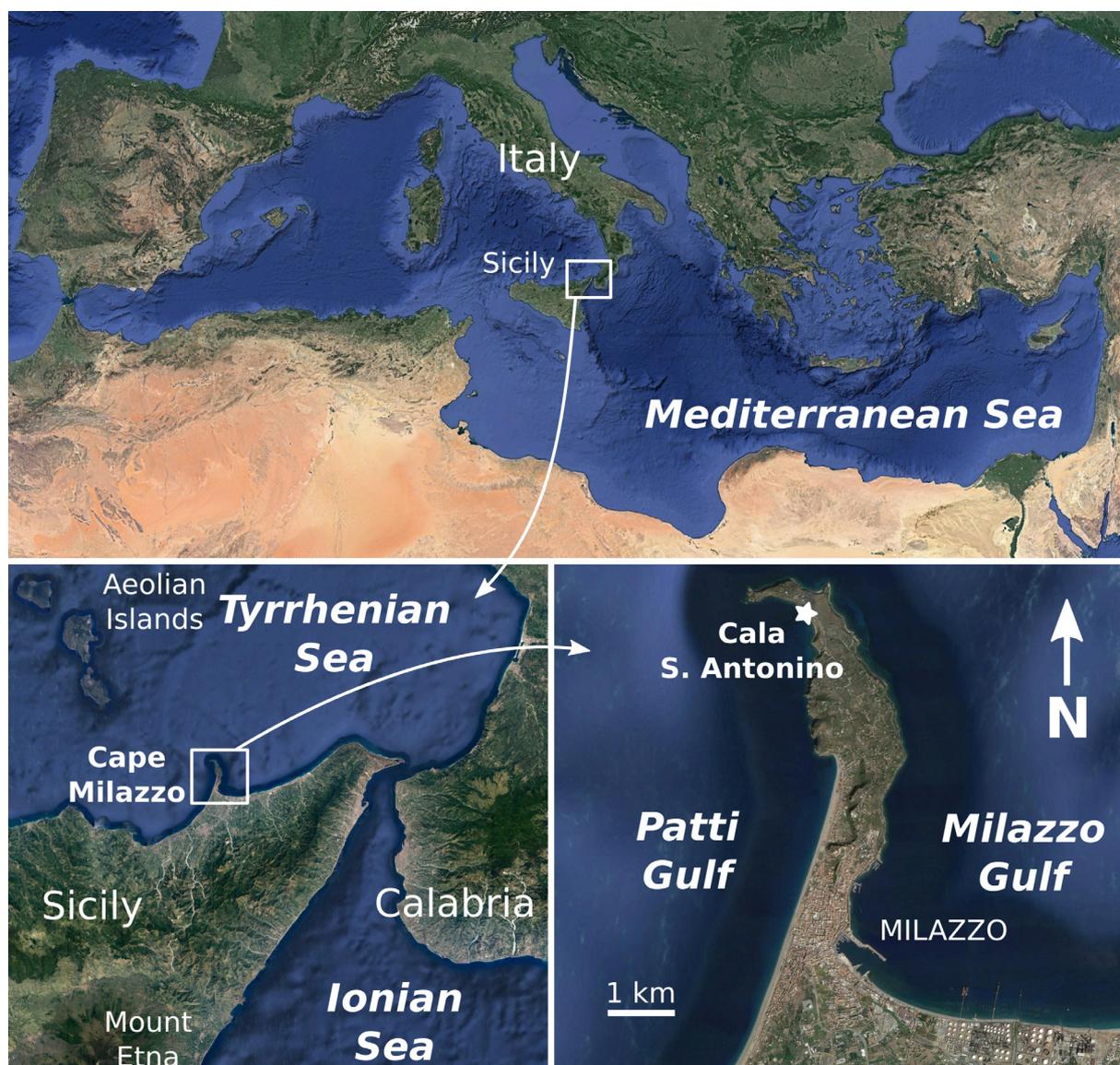


Fig. 1. Localty map, showing provenance (white star) of the holotype of the new platylepadid (MSNC 4562) described herein. All images from Google Earth.

CL1 = carinolateral plate 1
CL2 = carinolateral plate 2
C = carina

Results

Class Maxillopoda Dahl, 1956
Subclass Cirripedia Burmeister, 1834
Superorder Thoracica Darwin, 1854
Order Sessilia Lamarck, 1818
Suborder Balanomorpha Pilsbry, 1916
Superfamily Coronuloidea Leach, 1817

Family **Platylepadidae** Newman & Ross, 1976

Diagnosis (after Ross & Frick 2011: 62)

Wall six-plated (R-CL1-CL2-C) or eight-plated in juvenile specimens (R-RL-CL1-CL2-C); relatively thin; parietes each with midrib and/or tooth; longitudinal tubes when present external (internal in *Chelolepas*); apertural hood absent (except in *Chelolepas*); primary or internal lamina (including the sheath) solid, outer lamina (when present) formed by joining of longitudinal T-shaped flanges extending from inner wall, thus forming external longitudinal canals.

Included subfamilies

Platylepadinae Newman & Ross, 1976; Calyptolepadinae Frick, Zardus & Lazo-Wasem, 2010; Chelolepadinae Frick & Ross, 2011; Cylindrolepadinae Frick & Ross, 2011; Stomatolepadinae Frick & Ross, 2011.

Subfamily **Platylepadinae** Newman & Ross, 1976

Diagnosis (emended after Ross & Frick 2011: 62)

Wall peltate or low-conical; mono- or bi-lamellar; parietes with a large internal midrib either with or without a corresponding external medial sulcus; midrib either smooth or having several alternating ridges incorporated into basal surface; external longitudinal sulci, when present, formed by T-shaped flanges; sutural elaborations absent; orifice worn by corrosion or abrasion, or dehiscent.

Included genus

Platylepas Gray, 1825.

Genus ***Platylepas*** Gray, 1825

Diagnosis

As for the subfamily, until new genera are referred here.

Type species

Lepas hexastylos Fabricius, 1798, by the subsequent designation of Pilsbry (1916: 264).

Included species

Platylepas hexastylos; *P. decorata* Darwin, 1854; *P. ophiophila* Lanchester, 1902; *P. indicus* Daniel, 1958; †*P. wilsoni* Ross, 1963; *P. coriacea* Monroe & Limpus, 1979; †*P. mediterranea* sp. nov.

Remarks

Following Utinomi (1970) and Hayashi (2013), we consider *Cryptolepas ophiophilus* Krüger, 1912 (= *Platylepas krügeri* sensu Pilsbry 1916) to be a junior synonym of *Platylepas ophiophila*. Moreover, we concur with various authors (e.g., Monroe & Limpus 1979; Ross & Frick 2011; Hayashi 2013) in regarding *Platylepas multidecorata* Daniel, 1962 as a junior synonym of *Platylepas decorata* Darwin, 1854.

Range and distribution

Early Pleistocene (Gelasian) to Recent. Recorded as fossil from the Lower Pleistocene (Gelasian) of Sicily, southwest Italy (present paper) and the Upper Pleistocene of Florida, southeastern USA (†*P. wilsoni*). Currently known as an epizoic phoront found on several marine vertebrates (such as turtles, sea snakes, sirenians and fish) occurring in tropical and warm-temperate seas (between ca 45° N and ca 45° S latitude).

†*Platylepas mediterranea* sp. nov.

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Figs 1–3

Diagnosis

Wall truncated conical; bi-lamellar; transverse growth lines forming principal sculpture of outer face of compartments; longitudinal septa and canals visible through outer wall, becoming more numerous peripherally; carinolatus three-lobed; sheath extending for less than half of total height of compartment, appressed, not hollowed out from behind, exhibiting distinct transverse grooves; accessory ribs present, corresponding to distinct sulci on outer face of compartments; inner face of compartments smooth, devoid of ridges or septa; radii narrow, sub-straight, and relatively robust; alae thin; inter-compartmental ornamentation absent.

Etymology

From *Mare Mediterraneum*, the Latin name of the Mediterranean Sea, in allusion to the region where the holotype was found.

Material examined**Holotype**

SICILY • a single right carinolateral compartment (CL1 or CL2); Cala S. Antonino, Cape Milazzo Peninsula; 38°15'54.9" N, 15°14'12.7" E; epibathyal deposits ("Marne Calcarea Gialle"); Lower Pleistocene (Gelasian); sole known specimen to date; MSNC 4562.

Description

MSNC 4562 is an isolated, ca 7 mm tall, near-complete right carinolateral compartment (CL1 or CL2), the external surface of which has been moderately decorticated by wear (Fig. 2a). For this reason, we describe it here starting from the better-preserved and more informative internal surface (Fig. 2b).

When viewed internally, MSNC 4562 exhibits a rather short sheath, extending for less than half of the total height of the compartment (Fig. 2b). The sheath is strongly appressed, i.e., it runs subparallel to the external face of the compartment; its median portion bears a low and broad longitudinal ridge which corresponds to the location of the upper part of the midrib prop (see below). The sheath exhibits a few distinct plicae (here interpreted as growth lines) that extend subparallel to the gently curved (i.e., slightly S-shaped) basal margin of the sheath (Figs 2b, 3a). The fossa for the accommodation of the ala

(hereinafter referred to as the alar depression) is shallow and its margin is rounded and roughly J-shaped. A few very weak, transversely oriented grooves are observed also within the alar depression. The sheath is massive and not hollowed out from behind. However, a very shallow depression is seen beneath the basal margin of the sheath on the radial side of the midrib prop; conversely, at the alar side of the midrib prop the sheath is solidly filled from behind, and its basal margin is just marked by a horizontal ridge forming a sort of “step” on the inner surface of the compartment (Figs 2b, 3a). Below the sheath, the inner surface of the compartment is strongly folded inwards, thus generating a prominent longitudinal midrib prop (Figs 2b–f, 3a). This hook-like structure distinctly projects inwards and downwards; it is not filled internally. The transverse section of the midrib prop is roughly drop-shaped (Fig. 3f). The midrib prop runs closer to the alar margin of the compartment than to its radial margin. Therefore, it divides the inner surface of the compartment below the sheath into two areas: the smaller one is distinctly concave and roughly shaped as a longitudinally-elongated semi-cylinder; the larger one is laterally bounded by the sutural edge of the radius (Fig. 2b, f), with a broad accessory fold parallel to the midrib prop. This accessory fold is directed downwards and starts a couple of millimeters below the basal margin of the sheath (Figs 2b, 3a). No longitudinal septa occur below the sheath, either close to its base or at the periphery (i.e., close to the preserved portions of the basal margin of the compartment), as this portion of the inner surface is substantially smooth.

On the external surface of the compartment, the midrib prop and the accessory fold correspond to two shallow, yet obvious sulci which distinguish three longitudinally-elongated lobes (Fig. 2a). Although MSNC 4562 is moderately eroded externally, its trilobate aspect is well recognized from the apex of the compartment downwards (Fig. 2e). The external surface of the compartment is ornamented by longitudinal septa, which define longitudinally elongated tubes or canals between them. MSNC 4562

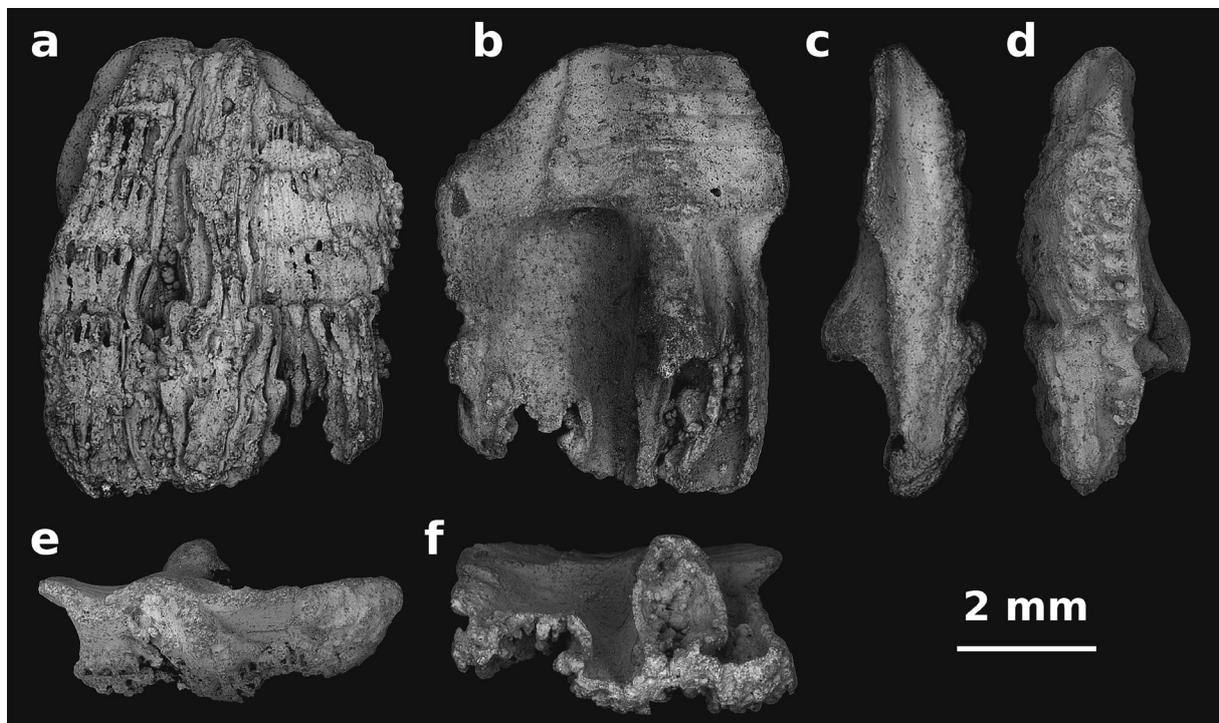


Fig. 2. †*Platylepas mediterranea* sp. nov., holotype, single right carinolateral compartment (CL1 or CL2) collected at Cala S. Antonino (Cape Milazzo, Sicily, southern Italy) from Lower Pleistocene (Gelasian) deposits (MSNC 4562). **a.** Outer view. **b.** Inner view. **c.** Alar view. **d.** Radial view. **e.** Apical view. **f.** Basal view.

is therefore tubiferous and bi-lamellar, the outer lamina being produced by the distal coalescence of the septa that extend from the inner wall. However, due to overall abrasion of the terminal T-shaped flanges of the longitudinal septa, a pristine outer wall is only locally preserved (Fig. 3b). Some septa bifurcate downwards so that the interseptal distance remains roughly constant along the whole height of the compartment. This septate sculpture is affected by prominent transverse growth ridges along which the external surface of the compartment widens distinctly (Fig. 2a, c–d). The intersection of the longitudinally elongated septa and the transversely oriented growth ridges is occasionally marked by small knobs on what remains of the outer lamina (Figs 2a, 3b).

The radius is rather narrow and partially preserved. In radial view, it is sub-straight (Fig. 2d) and its basal termination weakly projects inwards. The sutural edge of the radius is relatively robust. The denticulation pattern of the sutural edge is largely eroded; where it is preserved, it appears simple, being in fact comprised of squat, blunt, transversely-oriented septa that originate from the inner margin of the radius and project outwards (Fig. 2d). The ala is thin and distally tapers moderately. The sutural edge of the alar portion of the compartment exhibits short, triangular, wedge-like complementary septa which project inwards from a main septum running along the outer margin of the compartment (Figs 2c, 3a).

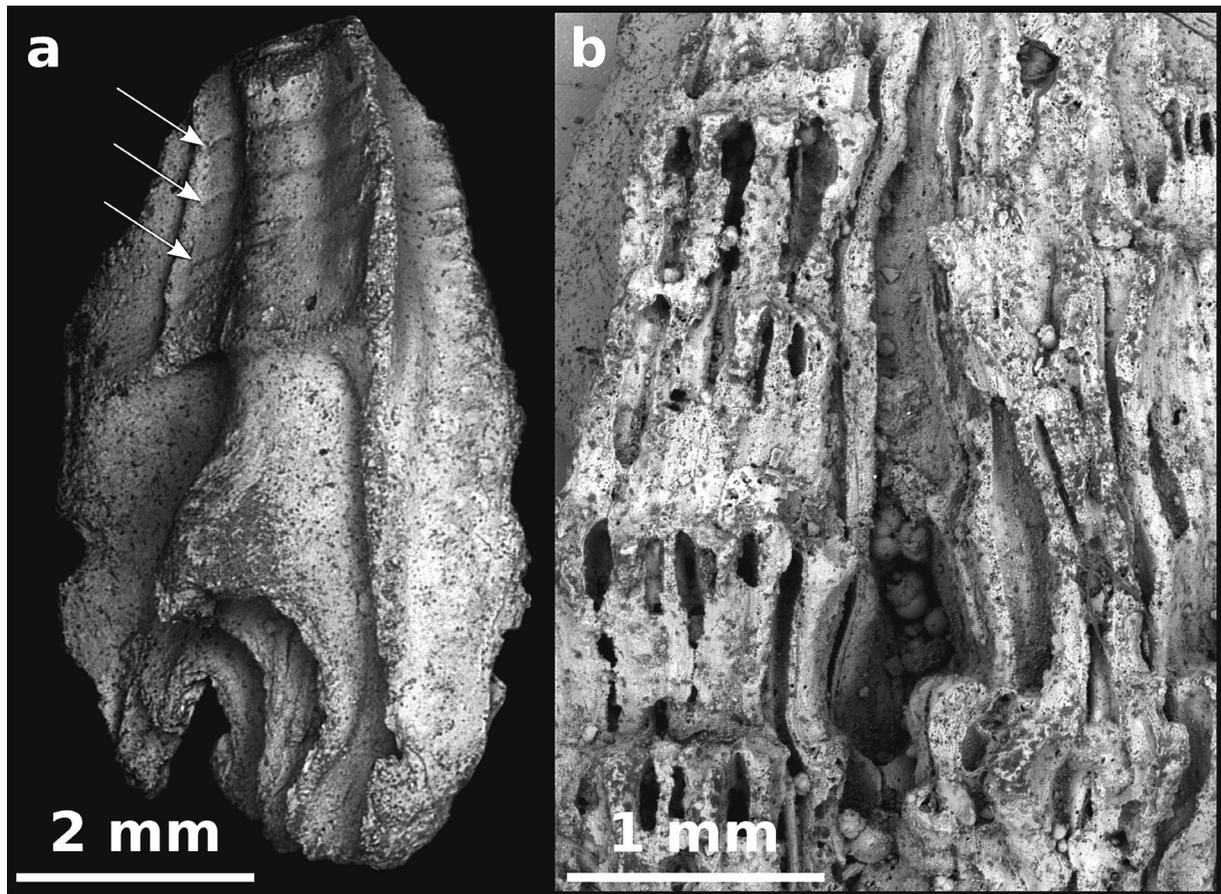


Fig. 3. †*Platylepas mediterranea* sp. nov., holotype (MSNC 4562). **a.** Interno-alar view. Note the strongly appressed sheath exhibiting distinct transverse grooves (arrows) and the short, triangular, wedge-like, transverse septa on the sutural edge of the alar portion of the compartment. **b.** Close-up of the outer surface of the compartment. The outer lamina is only locally preserved; where it is eroded, longitudinally elongated septa and canals are visible. The intersection between longitudinal septa and transverse growth ridges is occasionally marked by small knobs.

Therefore, judging from the architecture of the radial and alar sutural margins, the space between two adjacent compartments would have been completely filled.

Comparisons and remarks

MSNC 4562 unambiguously belongs to the monotypical subfamily Platylepadinae based on the presence of a large and prominent midrib prop – observable on the inner surface of the compartment – which corresponds to a distinct sulcus on the external surface of the shell. The general morphology of MSNC 4562 strongly suggests a truncated conical (i.e., volcano-like) rather than peltate shell. Based on its size, a truncated conical shell that measured ca 14 mm in carinorostral diameter could be reconstructed; a slightly larger size estimate (ca 17 mm) could be proposed if the shell were more depressed. These size estimates are largely consistent with measurements of mature specimens of extant *P. hexastylus*.

On the whole, MSNC 4562 is reminiscent of the extant species *P. hexastylus* in various aspects of the shell: the structure of the sutural margins of MSNC 4562, for instance, is rather close to that of *P. hexastylus*. In addition, the outer aspect of MSNC 4562 is similar to that of a specimen of *P. hexastylus* from Sicily as illustrated by Pilsbry (1916: pl. 67, fig. 4) and to that of numerous other truncated conical individuals of *P. hexastylus* in which the outer lamina is partially or mostly worn out, thus revealing the septate, bi-lamellar nature of the compartment wall (e.g., Darwin 1854; Pilsbry 1916; Monroe & Limpus 1916; A.C., pers. obs.). However, various characters preserved in MSNC 4562 distinguish this fossil from the extant *P. hexastylus*. First, whereas in *P. hexastylus* the shell is very light and thin, MSNC 4562 appears to have been slightly more robust. Secondly, whereas in *P. hexastylus* the sheath is generally smooth and only occasionally displays weak growth lines, that in MSNC 4562 exhibits evident transverse grooves. Thirdly, in *P. hexastylus* the sheath is hollowed out from behind, but that in MSNC 4562 is appressed and filled from behind. Fourthly, *P. hexastylus* bears septa that extend onto the internal surface of each plate up to the level of the basal margin of the sheath or even terminate within the hollowed out portion behind the sheath; in turn, the internal surface of MSNC 4562 is devoid of septa and substantially smooth. Fifthly, whereas compartments of *P. hexastylus* appear as typically bilobate externally, the external aspect of MSNC 4562 is trilobate – a character that reflects the presence of an accessory rib on the inner surface of the compartment. Although compartments belonging to adult individuals of *P. hexastylus* occasionally exhibit an accessory rib and an incipient third lobe developing near the base of the shell, the trilobate nature of the external surface of MSNC 4562 is recognizable even close to the orifice, thus suggesting that it represents a structural character rather than an incidental feature incurred during growth. This hypothesis could find some support in the above-mentioned observation that the inner face of MSNC 4562 is smooth and devoid of those ridges and septa which in extant *P. hexastylus* aid in both fixing the phoront crustacean to its substrate and preventing the collapse of the thin barnacle shell (e.g., Ross & Newman 1967). In this respect, the accessory rib observed in MSNC 4562 could be interpreted as a functional substitute of the fimbriated periphery of the compartments of *P. hexastylus*, substantially contributing to the stabilization of the relatively robust platylepadid shell to which MSNC 4562 belonged by providing firm anchorage to the underlying host tissue. If this interpretation is correct, a complete adult shell of the platylepadid species from Cala S. Antonino might have displayed up to 18 lobes on its external surface (e.g., three lobes on each CL, four on R, and two on C).

The extant species *Platylepas coriacea*, *P. indicus* and *P. ophiophila* are similar to *P. hexastylus* in shell shape and structure. MSNC 4562 further differs from *P. coriacea* by its narrower radius, longer sheath, and the trapezoidal (rather than near-triangular) outline of the paries. It differs from *P. indicus*, in which both sides of the midrib prop of each compartment bear a distinct ridge, and from *P. ophiophila* by not displaying three or more secondary ribs lateral to the midrib prop.

MSNC 4562 resembles *P. decorata* as its sheath is not hollowed out from behind and in lacking longitudinal septa on the inner surface of the compartment. However, MSNC 4562 differs markedly from *P. decorata*

by exhibiting a thinner wall, a distinctly shorter sheath, sutural edges of the compartment that lack external ornamentation, and a different aspect of the outer wall (e.g., the shell of *P. decorata* is monolamellar, each compartment being externally ornamented by fine longitudinal columns). Moreover, the shell of *P. decorata* is more or less cylindrical – a feature different from MSNC 4562, which would best match a truncated conical shell morphology.

MSNC 4562 also resembles †*P. wilsoni* in exhibiting transverse grooves on the sheath and a basal inner margin of the compartment without septa. However, MSNC 4562 clearly differs from this Late Pleistocene species by having a *P. hexastylos*-like radius (rather than a hollow tube) and by a clearly different ornamentation of the external surface of the shell (e.g., the outer wall of †*P. wilsoni* has a shingled appearance).

In conclusion, MSNC 4562 looks both structurally and morphologically more similar to the type species of the genus *Platylepas* (i.e., *P. hexastylos*) than to other congeners known to date (e.g., *P. decorata*). At the same time, MSNC 4562 significantly differs from all the species of *Platylepas* known to date, thus warranting the erection of a new species – †*P. mediterranea* sp. nov.

Discussion

Following previous literature sources (e.g., Gray 1825; Costa 1838; Darwin 1854; Chevreux & de Guerne 1893; Gruvel 1912; Richard 1936; Kolosváry 1939, 1943; Pilleri 1970; Raga & Carbonell 1985; Gramentz 1988; Pasternak *et al.* 2002; Kitsos *et al.* 2003, 2005; Casale *et al.* 2004; Bakir *et al.* 2010; Fuller *et al.* 2010; Karaa *et al.* 2011; Vallini *et al.* 2011), seven species of turtle and whale barnacles are known to occur in the present-day Mediterranean Sea: three, namely *Chelonibia caretta* (Spengler, 1790), *Chelonibia testudinaria* (Linnaeus, 1758) and *Chelonibia patula* (Ranzani, 1817), belong to Chelonibiidae; three, namely *Platylepas coriacea*, *P. hexastylos* and *Stomatolepas elegans* (Costa, 1838), to Platylepadidae; and a single one (*Xenobalanus globicipitis* Steenstrup, 1852) to Coronulidae. When fossil remains are taken into account, the picture changes considerably. The Mediterranean fossil record of coronuloid barnacles is marked by a predominance of whale barnacles that are represented by at least five species in three genera (*Cetopirus* Ranzani, 1817, *Coronula* Lamarck, 1802 and *Tubicinella* Lamarck, 1802) from various Upper Pliocene to Holocene deposits in Italy, Cyprus and Spain (e.g., Aradas 1854; Seguenza 1873; Simonelli 1893; De Alessandri 1895, 1906; De Gregorio 1895; Menesini 1968; Cipolla 1978; Bossio *et al.* 1993; Bianucci *et al.* 2006; Dominici *et al.* 2011; Álvarez-Fernández *et al.* 2014; Collareta 2016; Collareta *et al.* 2016b, 2018a, 2018b; Bosselaers *et al.* 2017). In the same broad region, fossil turtle barnacles are known to start occurring from the Miocene (Seguenza 1876; De Alessandri 1895, 1906; Withers 1929; Bianucci 1996; Harzhauser *et al.* 2011; Collareta *et al.* 2016a) but, up to now, they merely comprise a few Neogene occurrences of the chelonibiid genera *Chelonibia* Leach, 1817 and †*Protochelonibia* Harzhauser & Newman 2011 in Harzhauser *et al.*, 2011. Therefore, MSNC 4562 represents the first occurrence of a fossil platylepadid in the Mediterranean Basin. Moreover, as far as we know, the global fossil record of Platylepadidae is confined to a single occurrence, namely that of †*P. wilsoni* in the Upper Pleistocene deposits of the Pamlico Formation of Florida (USA) (Ross 1963). Our record thus significantly extends downwards the stratigraphic range of *Platylepas* and, generally, that of the entire family, to the Gelasian (lowermost Pleistocene). It comes as some surprise that, in light of the rather conspicuous (albeit still scanty) fossil record of *Chelonibia* and *Coronula*, only two fossil occurrences of *Platylepas* on a global scale are known to date. As already evoked by Hayashi (2013), the paucity of members of this genus in the fossil record might be related to the fragile nature of its shell elements and the small size of its wall plates.

What kind of living substrate did the type specimen of †*P. mediterranea* sp. nov. attach to? So far, the verified hosts of extant *Platylepas* spp. include all living genera of sea turtles and sea cows, as well as several forms of sea snakes and a single genus of holostean fish, i.e., the North American gar, *Lepisosteus*

Lacépède, 1803 (e.g., Darwin 1854; Lanchester 1902; Krüger 1912; Pilsbry 1916; Nilsson-Cantell 1938; Daniel 1958; Stubbings 1965; Utinomi 1970; Zann 1975; Zann & Harker 1978; Monroe & Limpus 1979; Young 1991; Hernández-Vázquez & Valadez-González 1998; Jones 2004, 2010; Hayashi *et al.* 2011; Lazo-Wasem *et al.* 2011; Hayashi 2012). Lepisosteid gars and sea snakes have never been recorded from the Mediterranean region, either as living individuals or as fossil remains from Cenozoic strata. Sirenians are also absent from the present-day Mediterranean Sea; however, tens of fossil specimens are known from Paleogene and Neogene deposits, predating the latest Pliocene (ca 3 Ma; Sorbi *et al.* 2012). Having observed this, and also considering that the Italian Plio-Pleistocene record of sea turtles includes several fragmentary indeterminate cheloniids (Chesi & Delfino 2006), we argue that MSNC 4562 might have been attached to a sea turtle. If this line of reasoning is correct, †*P. mediterranea* sp. nov. could be added to the list of chelonophilic coronuloid barnacles, to which most extant representatives of the genus *Platylepas* belong. As noted above, the external aspect of MSNC 4562 strongly recalls that of a specimen of *P. hexastylos* from Sicily illustrated by Pilsbry (1916: pl. 67, fig. 4). This specimen was briefly characterized by Pilsbry (1916: 287) as follows: “It has steep, convex sides, deep median clefts in the compartments, but the internal midribs are slender and project but little [...] The septa are very numerous, sharp, and close [...] From the appearance of this barnacle I suspect that it did not live on the shell of a turtle. There is some orange-coloured skin adhering in the furrows of the lower part of the parietes”. Interestingly, the description and illustration of that particular specimen provided by Pilsbry (1916), inclusive of the presence of orange-colored shreds of the embedding tissue of its host, perfectly match the aspect of several truncated conical extant specimens of *P. hexastylos* recovered by one of us (G.I.) and partially embedded in the skin of a loggerhead turtle, i.e., *Caretta caretta* (Linnaeus, 1758), beached along the coast of Donnalucata (Ragusa, Sicily, Italy) on 25 July 2000. Personal observations by two of us (A.C. and G.I.) on platylepadid phoronts associated with this chelonian individual suggest that truncated conical individuals of *P. hexastylos* were preferentially found partially embedded in the skin of the turtle, whereas their peltate conspecifics might have been commoner on the carapace and plastron. More generally, within the genus *Platylepas*, depressed shell morphologies appear to prevail among those forms that tend to adhere superficially to a host (as observed for the typically peltate *P. coriacea*; see, e.g., Monroe & Limpus 1979), whereas less flattened (up to cylindrical) shell shapes characterize those that manage to become anchored within a soft substrate (as observed for the typically ring-like *P. decorata*; see, e.g., Zardus & Balasz 2007). Therefore, we suggest that MSNC 4562 lived partially embedded in the skin of a cheloniid sea turtle, as currently observed for many phenotypically similar individuals of *P. hexastylos* attaching to *Caretta caretta* in central Mediterranean waters.

Recent phylogenetic analyses (Hayashi *et al.* 2013; Pérez-Losada *et al.* 2014) agree in recognizing the genus *Chelonibia* as occupying a basal position within Coronuloidea, as had been proposed much earlier based simply on morphology (e.g., Foster 1979; Buckeridge 1983). Given the general lack of occurrences of fossil turtle barnacles other than chelonibiids prior to the Upper Pleistocene, some platylepadid genera have occasionally been regarded as Pleistocene or Recent offshoots of Coronulidae (Hayashi *et al.* 2013). However, morphological considerations discourage the acceptance of this hypothesis, suggesting instead that the extant genus *Platylepas* is a surviving member of an ancient group of generalist epizoic barnacles (Ross & Newman 1967). According to the divergence time analysis by Hayashi *et al.* (2013), *Platylepas* originated during the Early or Middle Miocene. Although no fossil specimen of *Platylepas* is known from sedimentary deposits from this time interval, Hayashi *et al.* (2013) argued that a trace of a *Platylepas*-like barnacle could be detected on the carapace of a fossil sea turtle, i.e., the type specimen of “*Euclastes*” *melii* Misuri, 1910, from Miocene strata of the ‘Pietra Leccese’ (Apulia, southern Italy). Hayashi *et al.* (2013) based their claim on an illustration provided by Misuri (1910) in the paper in which “*E.*” *melii* was described. Unfortunately, the whereabouts of the type material is currently unknown; the trace-bearing specimen illustrated by Misuri (1910) may have been lost (Chesi *et al.* 2007). Therefore, a direct analysis of the trace fossil hinted at by Hayashi *et al.* (2013) cannot be carried out, leaving their inference unconfirmed at this time. However, our discovery of a new species of *Platylepas* that is

phenotypically close to extant *P. hexastylus* in deposits dated as Early Pleistocene may provide some support to a ‘less shallow’ evolutionary history for the epizoic barnacles currently grouped in the family Platylepadidae. Considering also the strongly biased nature of the fossil record of thin-walled, small-sized barnacles such as *Platylepas* spp., a Neogene origin of the platylepadid lineage would appear plausible.

Concluding remarks

As already evoked elsewhere (e.g., Seilacher 1992, 2005; Bianucci *et al.* 2006; Fertl 2009; Dominici *et al.* 2011; Hayashi *et al.* 2013; Pérez-Losada *et al.* 2014; Collareta *et al.* 2016a, 2016b, 2018a; Buckeridge *et al.* 2018), the extant epibiotic organisms included in the superfamily Coronuloidea are regarded as the ultimate product of an outstanding path of co-evolution with their vertebrate hosts. Nevertheless, the fossil record of coronuloid barnacles is still fragmentary and partially unexplored. As a consequence, the Cenozoic steps of such a co-evolutionary path are only vaguely known and largely speculative. The fossil occurrence of *Platylepas* recorded in the present paper adds new data to previous studies by extending back the fossil history of Platylepadidae to the lowermost Quaternary, thus supporting an earlier (e.g., Neogene) timing for the origin of this family and substantially contributing to our views of the evolutionary history of one of the most diverse and successful lineages of epizoic crustaceans. Further additions to the fossil record of coronuloid barnacles will certainly assist in illustrating how the “evolutionary dream” (sensu Seilacher 1992, 2005) of riding a whale or a sea turtle could have come true for an amazing lineage of tiny crustaceans.

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