

Article

Ghosts of the Holobiont: Borings on a Miocene Turtle Carapace from the Pisco Formation (Peru) as Witnesses of Ancient Symbiosis

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Abstract: In spite of the widespread occurrence of epibiotic turtle barnacles (Coronuloidea: Chelonibiidae and Platylepadidae) on extant marine turtles (Chelonioidea: Cheloniidae and Dermochelyidae), and although the association between these cirripedes and their chelonian hosts has existed for more than 30 million years, only a few studies have investigated the deep past of this iconic symbiotic relationship on palaeontological grounds. We describe probable platylepadid attachment scars in the form of hemispherical/hemiellipsoidal borings on an Upper Miocene (Tortonian) fragmentary turtle carapace, identified herein as belonging to Cheloniidae, from the Pisco Lagerstätte (East Pisco Basin, southern Peru). When coupled with the available molecular data, this and other similar ichnofossils allow for hypothesising that platylepadid symbionts were hosted by sea turtles as early as in early Oligocene times and became relatively widespread during the subsequent Miocene epoch. Chelonian fossils that preserve evidence of colonisation by platylepadid epibionts in the form of pits on the turtle shell should be regarded as fossil holobionts, i.e., palaeontological witnesses of discrete communal ecological units formed by a basibiont and the associated symbionts (including the epibiota). A greater attention to the bone modifications that may be detected on fossil turtle bones is expected to contribute significantly to the emerging field of palaeosymbiology.

Keywords: Cheloniidae; Coronuloidea; epibiosis; evolution; East Pisco Basin; ichnology; *Karethraichnus lakkos*; Platylepadidae; Tortonian; turtle barnacles



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1. Introduction

Overlooked until recently, the modifications induced by the attachment of acorn barnacles (Cirripedia: Balanomorpha) on submerged bones are beginning to receive some attention by taphonomists, both in the field of forensics [1,2] and in that of palaeontology [3,4]. In fact, barnacles are known as encrusters of defleshed bones in extant as well as fossil marine settings [1,2,4–11].

Bones, however, do not need to be bare to be modified by the fouling action of barnacles. That is clearly evidenced by the turtle barnacles (Coronuloidea: Chelonibiidae and Platylepadidae, the latter being sometimes subsumed into the coronulids [12]), most of which attach on the skin and shell of living marine turtles (Chelonioidea: Cheloniidae, or hard-shelled sea turtles, and Dermochelyidae, or leatherback sea turtles), even being able to penetrate through the keratinous epidermal scutes that coat their host's skull, carapace and plastron to incise the underlying sub-epidermal bones [13–23].

In spite of the widespread occurrence of chelonibiid and platylepadid genera such as *Chelonibia*, *Cylindrolepas* and *Playtlepas* on extant marine turtles [24], and although the association between the coronuloids and their chelonian hosts has existed for more than

30 million years [25], only a few studies have investigated this symbiotic relationship on palaeontological grounds [22,26,27]. The present paper adds to this short list by describing probable platylepadid borings on a Miocene fragmentary turtle carapace from the celebrated Pisco Lagerstätte of Peru based on the recently published nomenclatural frameworks provided by Zonneveld et al. [23,28,29]. A synoptic overview of the fossil record of putative turtle barnacle attachment scars is also provided, and the palaeobiological significance of these peculiar trace fossils is briefly discussed.

2. Geological and Palaeontological Framework

The East Pisco Basin is a 180 km-long, northeastward trending Andean forearc basin that extends along the narrow coastal plain of Peru between Pisco and Nazca [30–33] (Figure 1a). The sedimentary infill of this basin includes, in ascending stratigraphic order, the lower Palaeogene Caballas Formation, the Eocene Paracas Formation, the Eo–Oligocene Otuma Formation, the Lower Miocene, Chilcatay Formation, and the Mio–Pliocene Pisco Formation [34–37]. These stratal packages are bounded by regionally extensive angular unconformities demarcated by pavements of igneous, pebble- to boulder-sized clasts that testify to periods of subaerial exposure and indicate major breaks in sedimentation [35,38]. Thus, as highlighted by Di Celma et al. [39], these ‘formations’ rather represent alloformations (as defined by the North American Commission on Stratigraphic Nomenclature [40]).

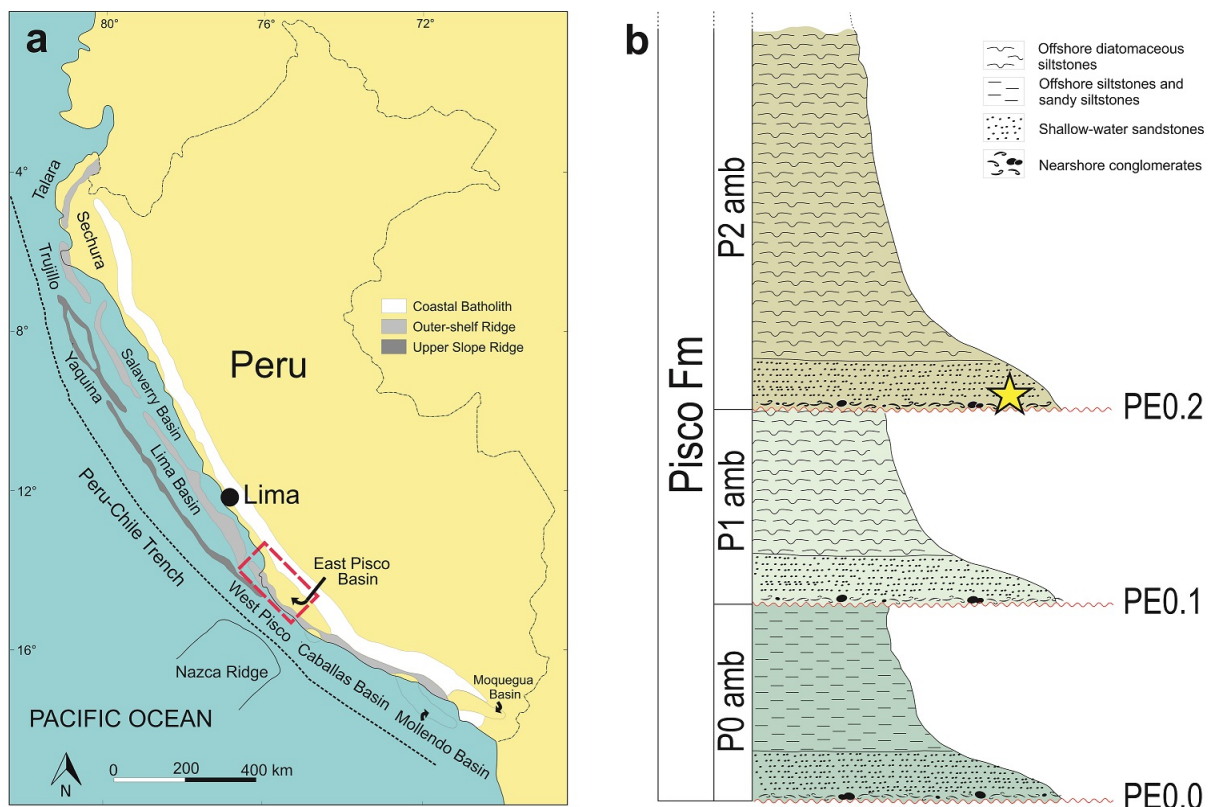


Figure 1. Cont.

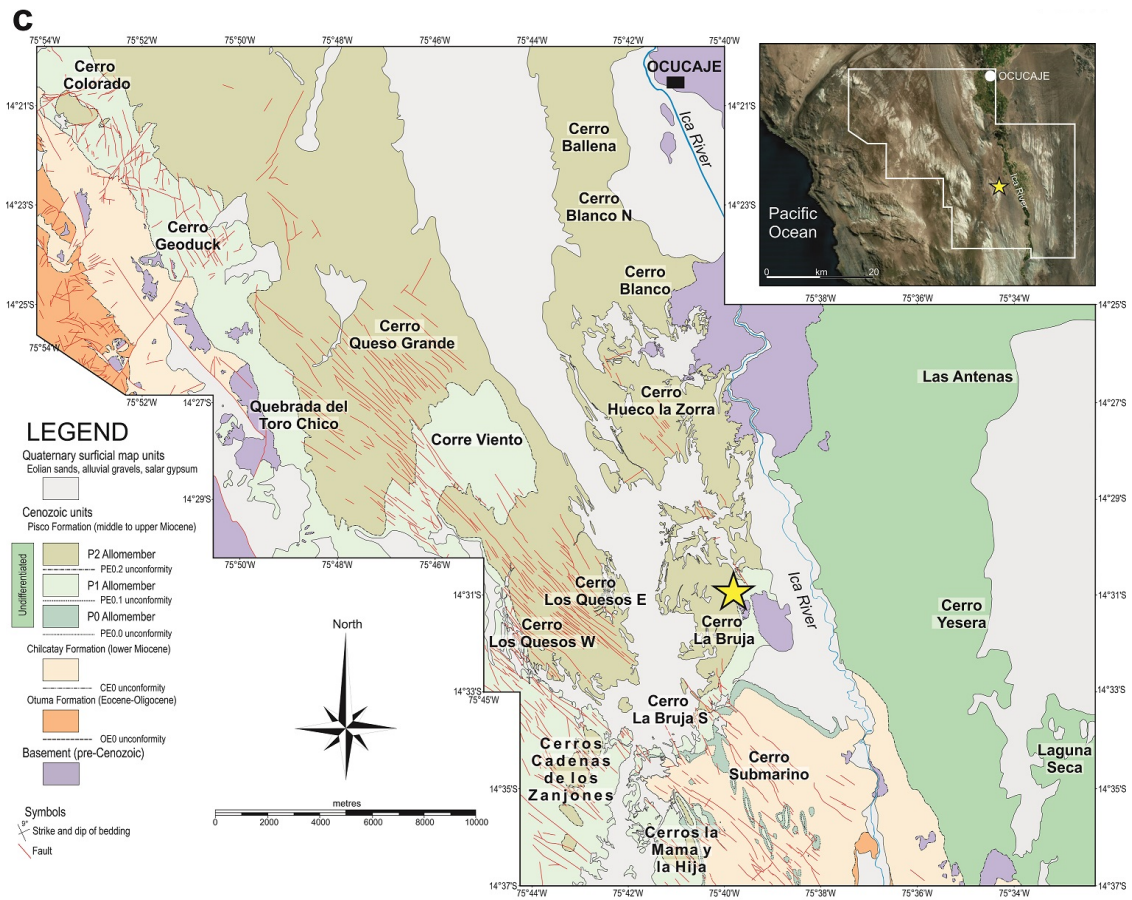


Figure 1. Geographic and geological setting. (a) Map of the major Cenozoic sedimentary basins along the coast of Peru. Redrawn and modified from Travis et al. [41] and Thornburg and Kulm [42]. (b) Schematic stratigraphic column of the Middle to Upper Miocene succession exposed in the East Pisco Basin and its internal subdivision into sequences/allomembers and facies associations. Redrawn and modified from Di Celma et al. [43]. (c) Geological map of Cerro La Bruja and surrounding areas. Redrawn and modified from Di Celma et al. [39]. The stars in panels (b,c) indicate the occurrence of the fragmentary turtle carapace MUSM 4716. Abbreviations: amb, allomember; Fm, Formation.

The fossil specimen described herein is currently stored in the vertebrate palaeontology collection of the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima, Peru) with catalogue number MUSM 4716. It originates from the Upper Miocene strata of the Pisco Formation exposed along the lower Ica River Valley, in the Ica Desert, and was identified by some previous works by means of the field number CLB-16 [10,44]. The Pisco Formation consists of conglomerates, sandstones, diatomites, diatomaceous siltstones, volcanic ash beds and dolomite horizons, testifying to deposition in coastal and inner shelf settings characterised by strong coastal upwelling and high primary productivity conditions [34,45,46]. The Pisco strata are broadly known as comprising one of the most impressive Cenozoic marine Fossil-Lagerstätten worldwide due to the exceptional abundance of marine vertebrate remains, their high taxonomic diversity and ecomorphological disparity, and the overall remarkable quality of fossil preservation [10,38,44,47–81]. Marine turtles are also part of this celebrated assemblage [10,38,44,57,67,82], but information on the Pisco chelonians is mostly limited to *Pacificchelys urbinai* Parham and Pyenson, 2010 [63], a likely durophagous Tortonian cheloniid. The outstanding record of marine vertebrates of the Pisco Formation is associated with a similarly remarkable record of fossil invertebrates [38,77,83–87], including barnacles, which represent one of the major invertebrate components of the Eo–Miocene deposits exposed in the East Pisco Basin [88–91].

Years of geological campaigning throughout the Ica Desert have led to recognizing that the Pisco Formation consists of three sequences/allomembers, designated P0 to P2 in ascending stratigraphic order, which progressively onlap northeastward onto a composite basal unconformity; each Pisco sequence/allomember is made of a coarse-grained lower portion, reflecting inshore deposition, fining upwards into offshore sediments [37,38,43,92] (Figure 1b).

MUSM 4716 was collected by one of us (R.V.-M.) at the foot of Cerro La Bruja, a prominent vertebrate locality where both P1 and P2 are exposed [38,44,47,48,54,93–95] (Figure 1c). The GPS geographic coordinates of the finding site are the following: 14°31′07.05″ S, 75°39′47.35″ W. Here, the basal sandstones of P2 are exposed. The base of P2 is assigned to the upper Tortonian, around 8.4 Ma [96].

3. Results

MUSM 4716 (Figure 2) is a fragmentary chelonian carapace that measures 130 mm in maximum preserved width and 82 mm in maximum preserved length. It consists of two partial neurals and four adjoining partial costals. The reconstructed shape of the neurals conforms to the “6A” type of Pritchard [97]. The posterolateral sides are long, anteroposteriorly elongated and somewhat angular anteriorly, whereas the anterior sides are much shorter, anteromedially oriented and essentially straight. The maximum preserved width of the neurals is 30 mm. The estimated length is less than twice the maximum preserved width. No obvious scute sulci are visible, nor is any distinct sculpturing present. Although taphonomic loss of the outermost layer of cortical bone may contribute to explain the co-occurrence of these features, the observation of largely unsculptured dorsal bone surfaces recalls the condition observed in the sole known carapacial fragment of *Pacificchelys urbinai* [63], the only formally named chelonian from the Upper Miocene strata of the Pisco Formation (see Bianucci et al. [98] for an assignment of *Natemys peruvianus* Wood et al., 1996 [99], a dermochelyid, to the Lower Miocene Chilcatay Formation). The overall morphology of MUSM 4716 appears as consistent with that of carapaces of hard-shelled sea turtles, the only chelonians to have been positively identified in the Upper Miocene strata of the East Pisco Basin besides an as yet undescribed *Dermochelys*-like dermochelyid taxon [82]. Given its fragmentary nature, MUSM 4716 is identified herein at the family-level only, as belonging to Cheloniidae gen. et sp. indet., as has been done in some previous works on the Pisco Formation fossil vertebrates [10,44].

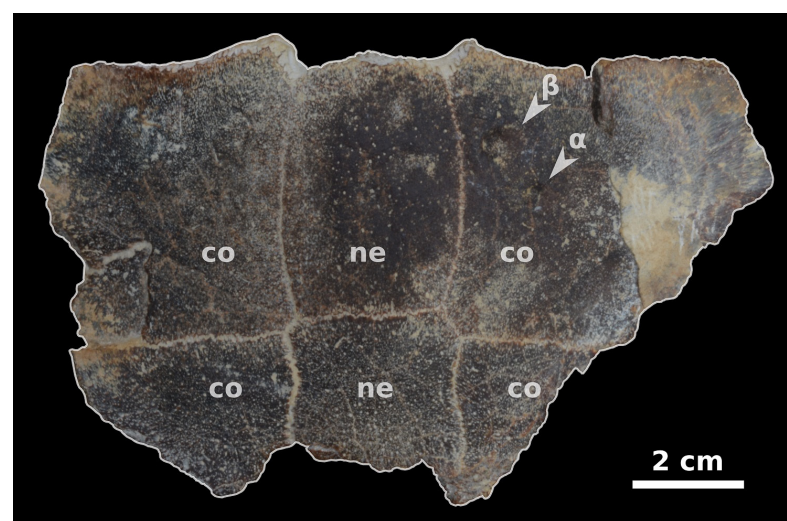


Figure 2. MUSM 4716, fragmentary turtle carapace from the Upper Miocene (Tortonian) strata of the Pisco Formation (Peru), in dorsal (external) view. The arrowheads indicate the location of two traces (α and β) detailed in Figure 3 (note that light conditions were not set with the purpose of highlighting those scars when taking this photograph). Abbreviations: co, costal plate; ne, neural plate.



Figure 3. Detail of two *Karethraichnus* borings (α and β) occurring on the exterior of the fragmentary turtle carapace MUSM 4716; (a) photograph and (b) explanatory line drawing. Abbreviations: co, costal plate; ne, neural plate. The dashed line in panel (b) indicates the position of the co–ne suture.

Two well-discernible bone modification features are observed on the exterior of MUSM 4716, being located on the same costal plate (Figures 2 and 3). One of them (α) is an almost perfectly circular depression, measuring about 3.5 mm in diameter (according to manual caliper measurements) and about 1 mm (or slightly less) in maximum depth. It occurs 10 mm lateral to the neural–costal suture (Figure 3). The other scar (β) is located some 6 mm anteromedial to α and ca. 3.5 mm lateral to the neural–costal suture (Figure 3). It is slightly elliptical, measuring ca. 7.5×6 mm. Its deepest point, slightly more than 1 mm in depth, is moderately eccentric. Both α and β display a smooth, rounded floor and may be described as roughly hemispherical or hemiellipsoidal. Scar β seemingly penetrates beneath the external bone cortex, the latter being around 1 mm in thickness; however, the transition between the cortical and cancellous bone is often hard to discern.

Scars α and β may be misidentified as tooth marks left by the apices of roughly conical teeth (ichnospecies *Nihilichnus nihilicus* Mikuláš et al., 2006 [100]). However, differing from our Peruvian material, such tooth marks are usually characterised by irregular jags or ring-like fractures along the trace margins and often feature crushed bone at their base [29,100,101]. In turn, both the borings that occur on the exterior of MUSM 4716 compare favourably with the ichnogenus *Karethraichnus*, which includes circular to subcircular, penetrative to non-penetrative holes bored into bone substrates [28]. More specifically, in terms of general outline, depth and lack of ornamentations, they match the diagnosis of

Karethraichnus lakkos Zonneveld et al., 2015 [28] (“shallow [. . .] *Karethraichnus* having a simple hemispherical profile with a rounded to flattened, hemispherical terminus”), as well as Zonneveld et al.’s [23] definition of the “Type II” traces (“hemispherical pits with smooth bases”). *Karethraichnus lakkos* was first described from fossil shell bones of geoemydid turtles from lower Eocene nonmarine strata of Wyoming (U.S.A.). The hypodigm of *K. lakkos* was originally interpreted as reflecting the attachment of parasites such as ticks, leeches or spirochid liver flukes [28], a hypothesis that was further elaborated by Zonneveld and Bartels [102]. As quintessentially terrestrial or freshwater organisms, the aforementioned parasites are unlikely to be the producers of the scars observed on MUSM 4716. Pholadid bivalves have been revealed to be the likely producers of *Karethraichnus* borings occurring on a sea turtle carapace from the Cretaceous of Japan, but the characteristically clavate arrangement of their homing scars (known under the ichnotaxonomic name *Karethraichnus zaratan* Sato and Jenkins, 2020 [103]) does not seem to be consistent with a shallower, *K. lakkos*-like ichnogenetic stage. According to Zonneveld et al. [23], when occurring on turtle shell bones from marine settings, scars conforming to *K. lakkos* may be suitably interpreted as due to the attachment of partially embedding turtle barnacles, including the extant platylepadids *Stomatolepas*, *Calyptolepas* and *Platylepas* (but not the even more shallowly penetrating chelonibiids). Similar traces, occurring abundantly on a modern carapace of the loggerhead turtle *Caretta caretta* (Linnaeus, 1758) [104], were also observed by Collareta et al. [27] and interpreted therein as platylepadid homing scars (Figure 4). In light of the above considerations, the rest of the present paper will regard the studied borings as representing turtle barnacle (platylepadid) attachment scars. That said, it must be stressed that there is generally no definitive one-to-one relationship between trace fossil shape and the inferred producer(s), so that alternative tracemakers cannot be definitively ruled out.

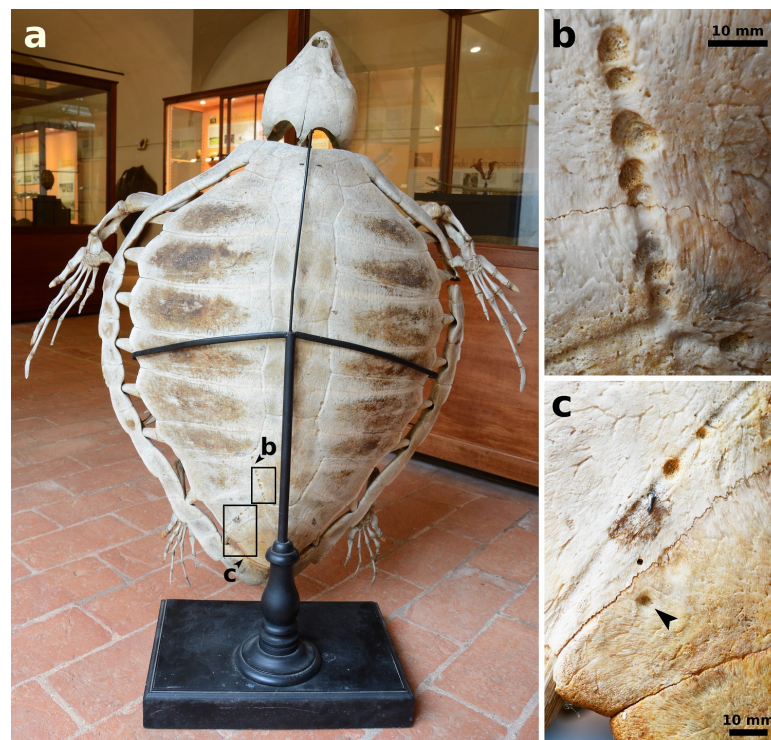


Figure 4. Recent skeleton of *Caretta caretta*, kept at Museo di Storia Naturale dell’Università di Pisa (Pisa, Italy) with catalogue number MSNUP B32, in dorsal view. (a) General view of the skeleton. (b) Close-up of some shallow hemispherical/hemiellipsoidal borings occurring along two scute sulci. (c) Close-up of an isolated shallow hemispherical boring (indicated by an arrowhead). Modified after Collareta et al. [27].

4. Other Turtle Barnacle Scars in the Fossil Record

A relatively small number of studies has dealt with potential barnacle attachment scars on fossil chelonians (Table 1). The oldest such trace fossils, dating back to the Late Cretaceous, were reported on by Janssen et al. [105]. They consist of shallow lesions occurring on skeletal elements of the cheloniid *Allopleuron hofmanni* (Gray, 1831) [106] from the Maastrichtian-type area (stretching across the Netherlands and Belgium). These rather irregular scars would hardly match the elliptical outline of coronuloid shells such as those of platylepadids [27] and may have been emplaced by some other turtle symbionts. Strengthening this interpretation, molecular DNA age estimates for the origin of several platylepadid lineages fall into the Cenozoic, between the early Oligocene and the Middle Miocene [22]. Other invertebrates, including boring bivalves (pholadids), may have comprised the stock of macroscopic epibionts of the Cretaceous marine turtles [103].

Table 1. Overview of the occurrences of bone modifications on fossil chelonians that are interpreted herein as reflecting barnacle attachment. See Section 4 for details.

Locality	Formation (Fm) and Age	Host Taxon	Inferred Epibiont Taxon	Key References
South Carolina, U.S. East Coast	Chandler Bridge Fm, Rupelian	<i>Carolinochelys wilsoni</i>	Platylepadidae	Weems and Sanders [107] Collareta et al. [27]
U.S. East Coast	Calvert Fm, Middle Miocene	<i>Procolpochelys grandaeva</i>	Balanidae?	Weems [108]
Maryland, U.S. East Coast	Calvert Fm, Middle Miocene	<i>Trachyaspis lardyi</i>	Platylepadidae?	Weems [108] Collareta et al. [27]
Southern Denmark	Gram Fm, Tortonian	<i>Psephophorus polygonus</i>	Chelonibiidae?	Karl et al. [109] Zonneveld et al. [23]
Southern Italy	Pietra leccese Fm, Miocene	Cheloniidae indet. (" <i>Euclastes" melii</i>)	Platylepadidae	Misuri [110] Hayashi et al. [22]
Central Italy	Arenaria di Ponsano Fm, Tortonian	Cheloniidae indet.	Platylepadidae	Collareta et al. [27]
Southern Peru	Pisco Fm, Tortonian	Cheloniidae indet.	Platylepadidae	this work
North Carolina, U.S. East Coast	Yorktown Fm, Pliocene	<i>Caretta patriciae</i>	Platylepadidae	Zug [111] this work

As regards the Palaeogene record, Weems and Sanders [107] mentioned a circular scar on a carapace of the cheloniid *Carolinochelys wilsoni* Hay, 1923 [112] from the Rupelian Chandler Bridge Formation of South Carolina (U.S.A.). They interpreted this scar, depicted in their figure 5E, as possibly caused by a sea turtle barnacle, which appears as reasonable (as well as consistent with the aforementioned divergence time estimates). Evidence that other lineages of turtle barnacles (i.e., archaic chelonibiids) inhabited the sea turtle shell as early as in early Oligocene times is provided by an exceptional cheloniid fossil, featuring *Protochelonibia* on its plastron-bottom, from the Rauenberg Fossil-Lagerstätte of southwestern Germany [25].

Besides the present work, the occurrence of potential barnacle attachment scars on Miocene turtle remains has been investigated by four studies, namely, those by Weems [108], Karl et al. [109], Hayashi et al. [22] and Collareta et al. [27]. Weems [108] mentioned the occurrence of a shallow, elliptical (or nearly circular) scar, ca. 25 mm in diameter, on a carapace of the cheloniid *Procolpochelys grandaeva* Leidy, 1851 [113] from the Middle Miocene Calvert Formation of the U.S. East Coast. Weems [108] noted similarities between the shape of this scar and the basal configuration of *Concavus concavus* (Bronn, 1831) [114], an extinct balanid. As a matter of fact, several extant members of Balanidae (which are largely known as shore barnacles) have sometimes been recorded as opportunistic epibionts of marine turtles (Epibiont Research Cooperative [115], and the many references therein). From the same formation, Weems [108] did also describe borings on bones of the cheloniid *Syllomus aegyptiacus* (Lydekker, 1889) [116] (now recognised as a junior synonym of *Trachyaspis lardyi*

Meyer, 1843 [117,118]) in the following terms: “These holes usually are shallow and well rounded inside and often are placed randomly on the outer shell surface”. We wonder whether such traces may have been emplaced by shallowly penetrating platylepadids.

Karl et al. [109] reported on a pair of six-pointed, star-shaped marks occurring on a carapace of the extinct dermochelyid *Psephophorus polygonus* Meyer, 1846 [119] from the Upper Miocene (Tortonian) Gram Formation of southern Denmark. Karl et al. [109] tentatively interpreted these shallow traces as attachment scars left by balanid barnacles. As noted by Zonneveld et al. [23], these bone modifications may originate from a range of possible cirripede producers, including stellate barnacles (chthamalids—quintessentially littoral cirripedes that sometimes occur on turtle shells [120]) or some extinct chelonibiid morph. Interestingly, Karl et al.’s [109] traces recall the jagged outline of *Chelonibia manati lobatibasis* Pilsbry, 1916 [121], a peculiar form of *Chelonibia manati* Gruvel, 1903 [122] (now recognised as a member of the *Chelonibia testudinaria* (Linnaeus, 1758) [104] cluster of morphs [23,123,124]). Differing from most representatives of the *manati* morph of *C. testudinaria* that typically dwell on the skin of manatees, *C. manati lobatibasis* was originally described based on a specimen that was found on an extant loggerhead turtle from Florida (U.S.A.). We concur with Zonneveld et al. [23] in regarding the star-shaped traces described by Karl et al. [109] as likely reflecting attachment by some kind of acorn barnacles, possibly an extinct form of *Chelonibia*.

Hayashi et al. [22] proposed that a scar left by a *Platylepas*-like barnacle could be seen in a historical illustration of a Miocene cheloniid carapace from the Pietra leccese Formation of southern Italy [110]. That specimen is unfortunately lost, and its precise stratigraphic provenance is uncertain [125]. That said, Hayashi et al.’s [22] interpretation appears sound in light of the perfectly hemispherical outline of the trace.

Collareta et al. [27] described and referred to *Karethraichmus* cf. *lakkos*, an isolated boring on a fossil cheloniid costal plate from the Upper Miocene (Tortonian) Arenaria di Ponsano Formation of central Italy. The morphology of this scar matches well Zonneveld et al.’s [23] definition of “Type III” traces (“circular to subcircular pits with flat bases”), which nowadays are emplaced by *Platylepas*. We concur with Collareta et al. [27] in considering this boring as the probable product of marine turtle fouling by a platylepadid barnacle.

To the best of our knowledge, no Pliocene records of potential barnacle attachment traces have been published so far. That said, a peripheral of *Caretta patriciae* Zug, 2001 [111] from the Pliocene Yorktown Formation of North Carolina (U.S.A.) (Zug [111]: figure 6B) may feature a platylepadid homing scar similar to that recorded by Collareta et al. [27].

5. Discussion and Conclusions

The fragmentary fossil record of turtle barnacles mostly comprises isolated shells and disarticulated wall plates. Occurrences of barnacle remains associated with those of the putative host organism(s) are exceedingly rare [25,126–128]. Although morphofunctional considerations can provide some hints of what sort of host the extinct turtle barnacles might have been on [129–131], body fossils alone cannot disclose much information on the ancient basibionts of chelonibiids and platylepadids, nor on the nature of the intercurrent symbiotic association. Furthermore, as a likely consequence of the tiny and fragile shells they secrete [22], platylepadids are particularly rare as fossils, their fossil record being limited to a handful of Pleistocene occurrences of the extant genus *Platylepas* [132–135]. Thus, in order to provide a deep-time perspective on the symbiotic relationships of turtle barnacles (and platylepadids in particular), an alternative approach should be sought by building upon the integration of the body and trace fossil records.

When coupled with the few body fossils of *Platylepas* that are known to date, as well as with the available molecular data, the above list of potential turtle barnacle ichnofossils—scanty as it is—allows for shedding some light on the coevolutionary history of the platylepadids and sea turtles. Chelonibiids may have hosted platylepadid symbionts as early as during the early Oligocene [107], a hypothesis that fits well the most recent divergence time estimates for turtle barnacles [22]. Two Miocene carapace specimens from Italy

and Peru ([22]; this work) feature *Karethraichnus lakkos*-like scars, suggesting widespread colonization of the sea turtle shell by platylepadid epibionts not later than in Tortonian times. The Early Pleistocene saw the first known appearance of the genus *Platylepas* in the fossil record, with the extinct species *P. mediterranea* Collareta et al., 2019 [134], whereas remains of the living taxon *Platylepas hexastylus* (Fabricius, 1798) [136] are known from the Middle Pleistocene [135].

Turtle barnacles have alternatively been classified as commensals [21] or as parasites [28]. Depending on the extent of the infestation as well as on their growth modes, they may range from harmless to nearly deadly symbionts [18]. However eye-catching, turtle barnacles represent but a fraction of the broad and diverse spectrum of epibiotic symbionts of extant marine chelonians: for example, the loggerhead and hawksbill turtles (*Eretmochelys imbricata* (Linnaeus, 1766) [137]) are known to host more than 200 and more than 150 epibiont taxa, respectively (Frick and Pfaller [21], and the many references therein). Whereas most of these epibionts are facultative commensals that opportunistically attach onto the turtle skin and shell, others—including most chelonibiids and platylepadids—are obligate (or quasi-obligate) symbionts that display remarkable adaptations for an epibiotic lifestyle [130]. Thus, each sea turtle (the basibiont) and its symbionts (including the epibionts) comprise a single communal entity, the holobiont, which represents a discrete ecological unit [138] (Figure 5). The aforementioned chelonian fossils preserving evidence of colonization by platylepadid epibionts in the form of pits on the turtle shell should therefore be regarded as fossil holobionts.

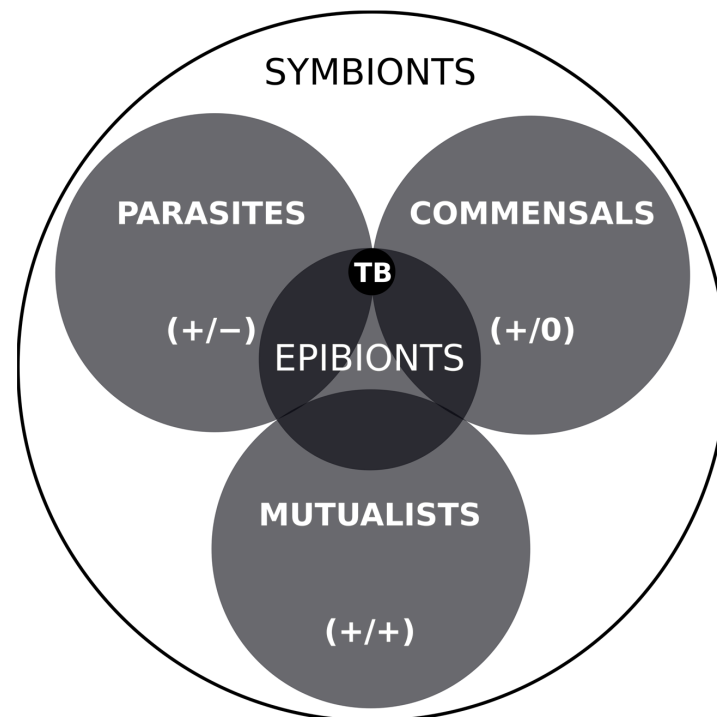


Figure 5. Venn-style diagram delineating the relationship of epibionts (i.e., organisms that live externally in association with a host partner or basibiont) to different categories of symbionts. Plus, minus and zero symbols indicate beneficial, deleterious and neutral associative outcomes for the epibiont (left of the slash) and the basibiont (right of the slash), respectively. “TB” indicates the reconstructed position of turtle barnacles, which have alternatively been classified as commensals or as parasites. All the organisms together in an epibiotic association comprise a single communal entity, the holobiont, which represents a discrete ecological unit. Redrawn and modified after Pinou et al. [138].

As unique as they may appear, the few fossil holobionts that are known to date likely represent the tip of the iceberg. In fact, despite the common and widespread occurrence of

carapacial and plastral remains of turtles in many fossil vertebrate assemblages worldwide, only a few palaeontological studies exist detailing the occurrence and significance of turtle bone modification features [23], though this is beginning to change [139]. Thus, we take advantage of this space for launching a plea to fellow palaeontologists for describing and figuring the bone modifications they detect on chelonian shell plates, some of which are expected to contribute significantly to the emerging field of palaeosymbiology. As the relevance of symbiosis as a major mechanism of macroevolution can hardly be overestimated [140], such an effort will likely result in remarkable contributions in the field of evolutionary palaeontology. At the same time, simple experiments of barnacle growth on samples of turtle shell scutes [141] and vertebrate bones [4] promise to elucidate the ichnogenetic potential of these widespread sessile cirripedes.

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