

Thatchtelithichnus on a Pliocene grey whale mandible and barnacles as possible tracemakers

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With 4 figures

Abstract: The ichnogenus *Thatchtelithichnus* ZONNEVELD, BARTELS, GUNNELL & MCHUGH was created for ring-shaped, roughly circular grooves affecting the outer surface of plastral bones of Eocene geoemydid turtles. Such traces were assumed to be attachment scars of aquatic ectoparasites (possibly ticks, leeches or liver flukes). Despite its well-distinctive aspect, *Thatchtelithichnus* has only been reported subsequently by few works and mostly from the plastron-bottom of freshwater turtles. Here we provide the first record of *Thatchtelithichnus* from a fossil mammal bone, namely, a partial grey whale mandible from the Belgian Pliocene. *Thatchtelithichnus* traces from this cetacean fossil commonly penetrate into the outermost portion of the cancellous bone, achieving a maximum depth of about 2 mm. The external margin of these grooves is sharply defined and commonly follows an elliptical, somewhat festooned path. A scrutiny of recent literature in palaeontological and forensic taphonomy as well as new first-hand observations reveal that *Thatchtelithichnus*-like structures can be produced by the attachment of barnacles on the surface of mammal bones that suffered long-lasting exposure on the seafloor. When encrusting bare bones in marine settings, barnacles can thus produce a variety of traces, including *Anellusichnus* SANTOS, MAYORAL & MUÑIZ, *Thatchtelithichnus* and, possibly, *Karethraichnus lakkos* ZONNEVELD, BARTELS, GUNNELL & MCHUGH. The modes of trace formation are still largely to be understood, but observations on how barnacles damage paint coatings during growth might help us in envisaging how this kind of process works.

Key words: Actuopalaeontology, *Anellusichnus*, Belgium, bioerosion, biostratinomy, *Karethraichnus*, Lillo Formation, Oorderen Sands Member, palaeoichnology, taphonomy.

1. Introduction

The ichnogenus *Thatchtelithichnus* was created by ZONNEVELD et al. (2015) on the basis of ring-shaped, roughly circular grooves affecting the outer surface of plastral bones of geoemydid turtles from the Eocene of Wyoming (USA). These traces were interpreted by ZONNEVELD et al. (2015) as attachment scars of aquatic ectoparasites (possibly ticks, leeches, or spirorchid liver flukes) that infected the chelonians while the latter were still living. Later, WISSHAK et al. (2019) included *Thatchtelithichnus* in a list of bioclastration structures, which are not regarded as trace fossils due

to their reflecting embedment by a growing “substrate” rather than an active manipulation of the latter (BERTLING et al. 2006; but see also TAPANILA 2005 and SUÁREZ ANDRÉS et al. 2021 for different interpretations of the ichnotaxonomic and nomenclatural status of bioclastration structures). However, a reanalysis of the type material of *Thatchtelithichnus holmani* ZONNEVELD, BARTELS, GUNNELL & MCHUGH (i.e., the type and only described ichnospecies of *Thatchtelithichnus*) performed by ZONNEVELD & BARTELS (2020) revealed that no part of this ichnotaxon involves bioclastration. ZONNEVELD & BARTELS (2020) also concluded that the hypothesis formulated by ZONNEVELD et al. (2015) for



Fig. 1. IRSNB M 2316, partially preserved right mandible of *Eschrichtius* sp. from the Pliocene of Belgium, displaying a variety of ring-shaped and roughly circular grooves and fragments of the calcareous bases of balanid barnacles on its (A) labial and (B) lingual surfaces.

explaining the origin of the *Thatchtelithichnus* traces remains the most likely one and referred to *T. holmani* some traces described by [BADER et al. \(2009\)](#) from dinosaur long bones and ribs from the Jurassic of Wyoming; the latter were originally interpreted to represent the activity of beetle larvae. Finally, [COLLARETA et al. \(2020\)](#) reported on specimens of *T. holmani* from the external surface of a plastron of the geoemydid terrapin *Mauremys* from the Pliocene of Italy. [COLLARETA et al. \(2020\)](#) also re-evaluated the hypotheses regarding the origin of *Thatchtelithichnus*, reaffirming, in case of traces taking place on the plastron-bottom of turtles, a probable origin as attachment scars of aquatic ectoparasites. Finally, [ZONNEVELD et al. \(in press\)](#) reported on additional *Thatchtelithichnus* incisions from the plastron-bottom of aquatic pleurodiran turtles from the Miocene of northern Egypt. In spite of their highly idiosyncratic aspect, up to date, *Thatchtelithich-*

nus traces have only been reported by as few as four works, and mostly from the external surface of plastral bones of freshwater turtles.

With the aim of shedding new light on the tracemakers of *Thatchtelithichnus*, here we report on the occurrence of several specimens of this ichnogenus occurring on a partial grey whale (*Eschrichtius*) mandible from the Pliocene of Belgium ([TSAI et al. 2020](#)) (Fig. 1). This record is compared with similar occurrences from the surface of Recent and fossil mammal bones that suffered long-lasting exposure on the sea-floor and for which barnacle fouling has been verified or is strongly suspected. In doing so, we further discuss the possible tracemakers of *Thatchtelithichnus* and propose acorn barnacles as likely producers in case of traces occurring on bones from Recent and fossil marine settings.

Institutional abbreviations: IRSNB, Institut Royal des Sciences Naturelles de Belgique/Koninklijk Belgisch Instituut voor Natuurwetenschappen (Brussels, Belgium); NHG, Natuurhistorisch Genootschap, Koninklijk Zeeuwsch Genootschap der Wetenschappen (Middelburg, the Netherlands).

2. Systematic palaeontology

Ichnogenus *Thatchtelithichnus* ZONNEVELD, BARTELS, GUNNELL & MCHUGH, 2015

Type ichnospecies: *Thatchtelithichnus holmani* ZONNEVELD, BARTELS, GUNNELL & MCHUGH, 2015.

Thatchtelithichnus isp.
Figs. 1, 2A–E

- 2013 circular traces. – BOESSENECKER, p. 660 (*p.p.*).
2020 *Anellusichnus* SANTOS, MAYORAL & MUÑIZ, 2005. – TSAI et al., p. 191.

Ichnotaxonomic caveat: Scars assigned by ZONNEVELD et al. (2015) to *Thatchtelithichnus* are morphologically close to those known under the ichnogenetic name *Anellusichnus* (SANTOS et al. 2005), which in turn are also reminiscent of some shallowly penetrating members of *Karethraichnus* (ZONNEVELD et al. 2015). In particular, the original definition of *Anellusichnus* might prove broad enough to be arguably used to include morphologies that have been referred to *Thatchtelithichnus*. However, many ichnologists accept that there are several substrate types (such as wood, bone, rock and unconsolidated sediment) that are acceptable ichnotaxobases (e.g., HÖPNER & BERGLING 2017; but see also DONOVAN & EWING 2018 for an assessment of substrate as a poor ichnotaxonomic criterion). In consequence, in the future, the usage of the name *Anellusichnus* might be limited to traces occurring on shell substrates, with similar scars on bone being assigned straightforward to *Thatchtelithichnus*. Such a reappraisal of the scope and content of *Anellusichnus* is nevertheless beyond the purposes of the present paper, and substrate is not taken into account herein when distinguishing between the aforementioned ichnogenera. Thus, for the moment being, the below described ichnofossils are recognised as belonging to *Thatchtelithichnus* based on the observation of a distinct boss or pedestal in the central portion of

these traces – a morphological feature that characterises the type series of *T. holmani* (ZONNEVELD et al. 2015) while not being present (or at least not apparent) in the three ichnospecies of *Anellusichnus* that have been described so far (SANTOS et al. 2005; BUCKERIDGE et al. 2019).

Referred material: A total of about 30 ring-shaped traces with a clear central elevation occurring on the labial and lingual surfaces of IRSNB M 2316 (a partial mysticete dentary assigned to *Eschrichtius* sp.) (Fig. 1). The largest imprints are situated near the dorsal edge of the dentary, whereas the smallest ones are found on the linguoventral side and, labially, at mid-height.

Occurrence: The partial cetacean dentary IRSNB M 2316 (Fig. 1) was collected along the southwestern border of the Deurganckdok tidal dock (geographic coordinates of the finding site: N 51° 17' 23", E 4° 15' 48"), during harbour expansion at the Antwerp port (Flanders, Belgium), at a depth of about 18.5 m below the Tweede Algemene Waterpassing (TAW), the standardized (rectified) second general water level (main level of the sea at low tide at Ostend). The stratigraphic horizon of the find is located in the upper portion of the “basal shelly unit” (*sensu* LOUWYÉ et al. 2004) of the Oorderen Sands Member of the Lillo Formation, which locally marks the contact with the underlying Kattendijk Formation (= Kattendijk Sands Member *sensu* DE MEUTER et al. 1976). The deposition of the basal shelly unit has been referred to the 3.21–2.72 Ma time span (i.e., early to mid Piacenzian, late Pliocene) by means of dinoflagellate cyst biostratigraphy and sequence stratigraphy (DE SCHEPPER et al. 2009; LOUWYÉ et al. 2020). That said, a large fraction of the bioclastic and siliciclastic material that comprises the basal shelly unit of the Oorderen Sands Member seemingly originates from reworking of the Luchtbal Sands Member (LOUWYÉ et al. 2004, 2020), a geologically older unit that is not preserved at the finding site, but has been recognised at other exposures within the Deurganckdok tidal dock (TSAI et al. 2020; DECKERS et al. 2020). As the deposition of the Luchtbal Sands Member is thought to have occurred between 4.04 Ma and 3.21 Ma (DE SCHEPPER et al. 2009; LOUWYÉ et al. 2020), and considering also the fragmentary nature of IRSNB M 2316, reworking of this specimen from the Luchtbal Sands Member is possible (or even likely). Therefore, a geological age of 4.04–2.72 Ma (i.e., late

Zanclean to late Piacenzian) can be conservatively hypothesised for IRSNB M 2316.

Description: The observed traces (Fig. 2A–E) range in diameter between 3 and 15 mm, with most of them being around 6–9 mm (i.e., distinctly larger than the specimens of *Thatchtelithichnus holmani* figured by ZONNEVELD et al. 2015). Further differing from the hypodigm of *T. holmani*, the traces occurring on IRSNB M 2316 penetrate relatively deeply (up to ca. 2 mm deep) into the bone substrate, thus commonly reaching the outermost portion of the cancellous bone. The central portion of the traces consists of a relatively raised, rounded central boss or pedestal of cortical bone that often appears as obliterated by erosion (e.g., Fig. 2E). The outer edge of the traces is sharply defined; in most specimens, it follows an elliptical, distinctly festooned path (e.g., Fig. 2B) that is reminiscent of *Anellusichnus undulatus* SANTOS, MAYORAL & MUÑIZ. Most traces form clusters (e.g., Fig. 2A–C, E) that superficially resemble the recently described ichnogenus *Violinichnus* (MOURA et al. 2021). The outside wall of the trace is substantially unaffected by the borers' activities.

Associated body fossils: Six fragments of the calcareous bases of balanid barnacles were found on different areas of the eschrichtiid mandible IRSNB M 2316 (e.g., Fig. 2A, C, E). These fragmentary balanid bases are reminiscent of those of the living species *Balanus crenatus* BRUGUIÈRE. Indeed, *B. crenatus* displays a rather robust, ridged base, which persists well-fixed to the substrate even after destruction or removal of the overlying wall plates. Reaching a maximum basal diameter of 25 mm, shells of *B. crenatus* are often encountered on the surface of Pliocene vertebrate remains from the Kattendijk strata (personal observation by MB); furthermore, *B. crenatus* is likely the sole subtidal barnacle to be common in the present-day Belgian waters (KERCKHOF 2002). Interestingly, the somewhat lobed shell periphery of *B. crenatus* matches well the commonly festooned profile of many specimens of *Thatchtelithichnus* occurring on IRSNB M 2316 (e.g., Fig. 2B). However, whereas most fragmentary balanid remains are hosted within the depressed (and somewhat sheltered) portion of *Thatchtelithichnus* traces, the former are eccentric with respect to the latter. Such a coincidental association indicates that the observed barnacles colonised IRSNB M 2316 after the excavation of the *Thatchtelithichnus* scars, and likely after the mandible was affected by some kind of mineralization process which caused the subsequent

encrusting activity of episkeletozoans to leave no traces on the bone. This would agree with IRSNB M 2316 being reworked from the Luchtbal Sands Member, and thus suffering two phases of exposure on the seafloor during the Pliocene. In light of these considerations, the occurrence of fragmentary balanid bases on IRSNB M 2316 does not inform on the producers of the co-occurring *Thatchtelithichnus* traces, as the former testify to a geologically younger generation of encrusters with respect to the latter.

Associated trace fossils: Not all the traces that occur on IRSNB M 2316 exhibit the central boss or pedestal that is known to represent a diagnostic character of *T. holmani*. Scars that lack this feature (e.g., Fig. 2F) occur over some three quarters of the preserved outer bone surface (Fig. 1); they resemble either *Karethraichnus lakkos* ZONNEVELD, BARTELS, GUNNELL & MCHUGH (shallow circular or subcircular holes having a simple hemispherical profile; ZONNEVELD et al. 2015) or *Anellusichnus* ispp. (traces of circular to oval-subpolygonal shape whose boundary is revealed by a colour difference in the substrate or, more often, by the presence of a shallow outer furrow; SANTOS et al. 2005), depending on their depth. Interestingly, traces resembling *K. lakkos* on the carapacial and plastral bones of living sea turtles are produced by epizoic coronuloid barnacles such as *Platylepas* (ZONNEVELD et al. 2015; but see also HAYASHI et al. 2013: fig. 2), whereas *Anellusichnus* has been broadly reported as the attachment scar of acorn barnacles on a variety of substrates, including mammal bone (BOESSENECKER 2013). However, the absence of a central elevation in some of the traces occurring on IRSNB M 2316 might also be due to preferential erosion of this salient trace part.

3. Other examples of *Thatchtelithichnus* on mammal bones

A scrutiny of recent literature in taphonomy and forensic science reveals that *Thatchtelithichnus*-like structures, interpretable as due to the attachment of barnacles, can be observed on the surface of Recent and fossil mammal bones that suffered long-lasting exposure on the seafloor. These include a human bone that was encrusted by balanoid barnacles from the shoreline of (or ocean near) Massachusetts, eastern USA (e.g., POKINES & HIGGS 2015: fig. 15). Scars left on

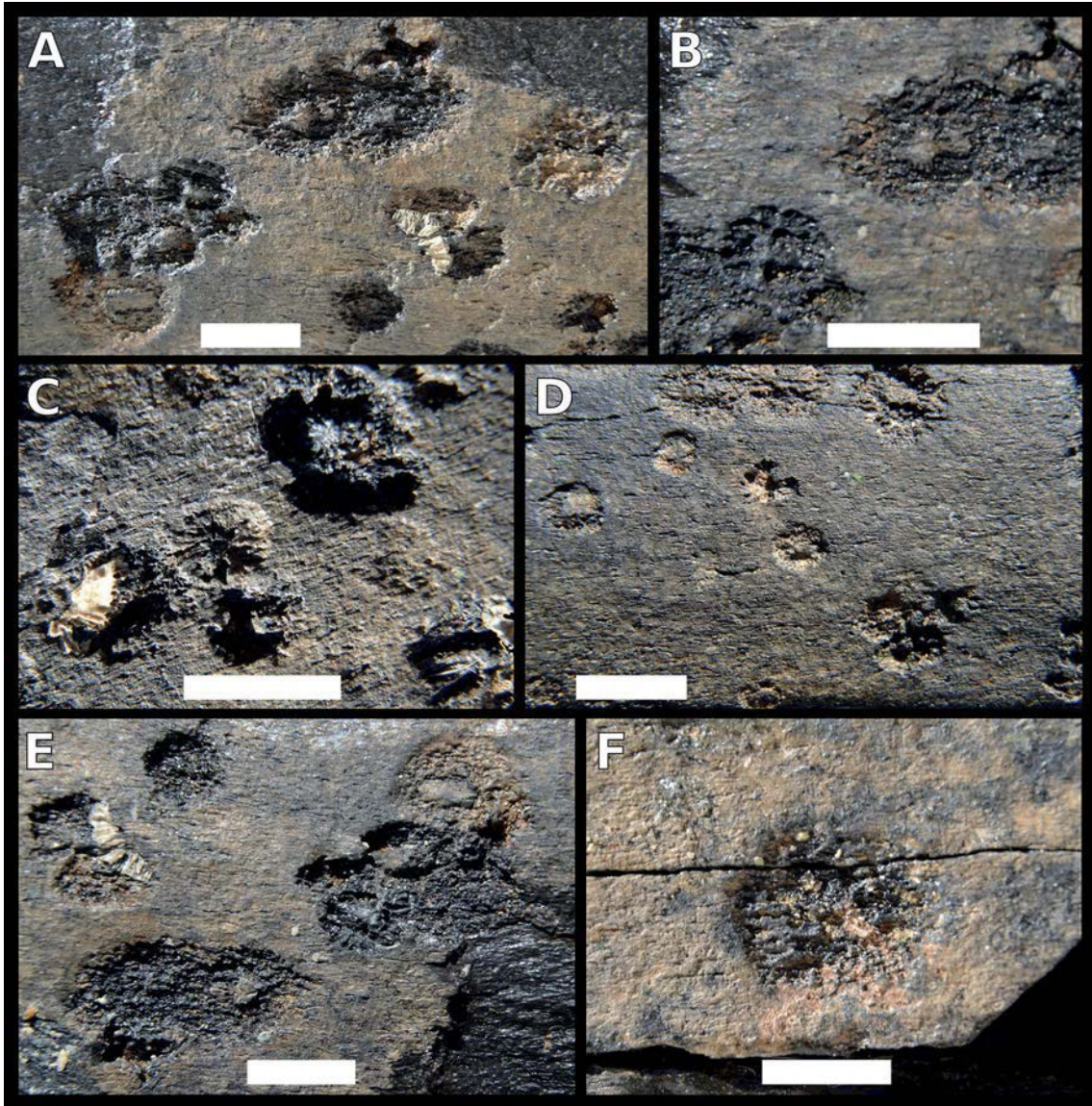


Fig. 2. Overview of the trace and body fossils occurring on IRSNB M 2316, partially preserved right mandible of *Eschrichtius* sp. from the Pliocene of Belgium. **A** – Clustering *Thatchtelithichnus* scars and fragments of the calcareous bases of balanid barnacles. **B** – Close-up of (A); clustering *Thatchtelithichnus* scars (note that the floor of these traces is comprised of cancellous bone). **C** – Clustering *Thatchtelithichnus* scars and fragments of the calcareous bases of balanid barnacles. **D** – Clustering and isolated *Thatchtelithichnus* scars. **E** – Clustering *Thatchtelithichnus* scars (alternate view of the traces depicted in panel B) and fragments of the calcareous bases of balanid barnacles (note that some traces have the central boss or pedestal clearly obliterated by erosion). **F** – *Karethraichnus lakkos*-like trace, lacking the central boss or pedestal that is typical of *Thatchtelithichnus*. All scale bars equal 1 cm.

this bone clearly consist of ring-shaped, roughly circular grooves provided with a central boss (Fig. 3A). Similar traces are present on a *Zalophus californianus* (LESSON) scapula from the middle Pleistocene of Oregon that suffered encrustation from balanids (likely belonging to *Hesperibalanus hesperius* (PILSBRY))

(BOESSENECKER 2013: fig. 4). Here, specimens of *Thatchtelithichnus* seemingly occur besides simpler traces with circular or subcircular shape and no central elevation; the latter have been assigned to *Anellusichnus circularis* SANTOS, MAYORAL & MUÑIZ by BOESSENECKER (2013).

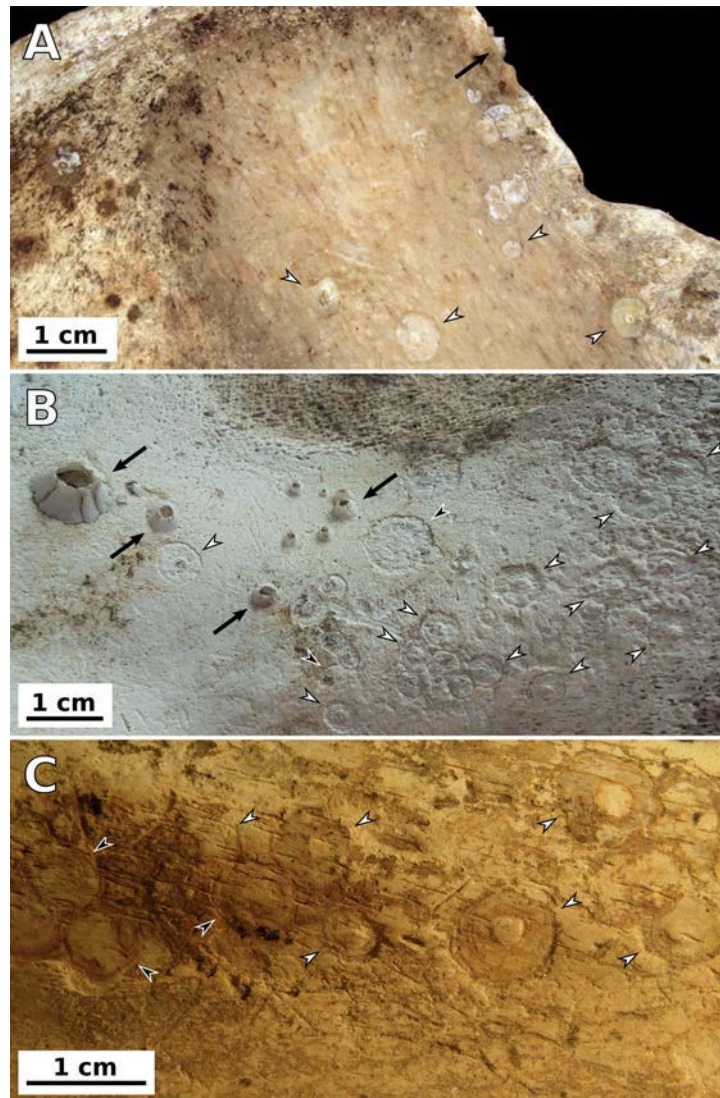


Fig. 3. *Anellusichnus*- and *Thachtelithichnus*-like scars affecting the outer surface of Recent and subfossil mammal bones that suffered long-lasting exposure on the seafloor. Black arrows indicate barnacle shells; white-filled arrowheads indicate *Thachtelithichnus* traces; black-filled arrowheads indicate *Anellusichnus* traces. **A** – Acorn barnacles and barnacle attachment scars on a Recent human bone from Massachusetts, USA (modified from [POKINES & HIGGS 2015](#): fig. 15). **B** – Acorn barnacles (*Balanus crenatus*) and barnacle attachment scars on a Recent cranium of *Balaenoptera acutorostrata* from Belgium. **C** – Putative barnacle attachment scars on NHG 26126, a (sub)fossil scapula of *Bos taurus* from the Scheldt River estuary.

Our first-hand observations on Recent and (sub)fossil mammal bones further confirm that barnacle attachment scars on mammal bones commonly conform to *Thachtelithichnus*- and *Anellusichnus*-like structures, with the former (consisting of scars provided with a distinct central boss or pedestal) being generally more abundant than the latter (in which such a central elevation is absent or not obvious). Both kinds of scars occur on a juvenile skull of *Balaenoptera acutorostrata*

LACÉPÈDE collected at the village of Bredene, just East of Ostend (Belgium), during an extreme low tide following a storm (Fig. 3B). This specimen, kept in the private collection of one of the authors (MB), still preserves some barnacle shells belonging to *Balanus crenatus* attached to it. A (sub)fossil scapula of *Bos taurus* LINNAEUS that was fished from the Scheldt River estuary (see [POST & REUMER 2016](#)) and is now kept at the Zeeuws Museum (Middelburg, the Netherlands)

also features a similar co-occurrence of traces referable to *Thatchtelithichnus* and *Anellusichnus*, with the latter resembling *Anellusichnus circularis* (Fig. 3C). No remains of barnacle shells, nor of other encrusters are currently attached to this specimen. However, the occurrence of concentric circular etched rings on the inside of some traces suggests the same origin as for similarly ornamented specimens of *A. circularis* in which subsequent phases of expansion of the calcareous bases of the producing barnacles are recorded (SANTOS *et al.* 2005). In consequence, an origin of the *Thatchtelithichnus* traces that are found on IRSNB M 2316 as attachment scars of acorn barnacles is here proposed.

4. Discussion

The present work represents the first report of *Thatchtelithichnus* from a fossil mammal bone. More generally, our results demonstrate that such traces can occur in high numbers on mammal bones from Recent and fossil marine settings. Specimens of *Thatchtelithichnus* from mammal bones are sometimes associated with shell remains of their likely tracemakers – acorn barnacles.

How could barnacles colonising a bone substrate give origin to scars consistent with the overall physiognomy of *Thatchtelithichnus*? In the last few decades, barnacle-substrate interactions have been extensively studied due to barnacles being ubiquitous biofoulers on ship hulls (e.g., SUN *et al.* 2004; HOLM *et al.* 2005; WENDT *et al.* 2006; HOLM 2012; WANG *et al.* 2017). However, we are not aware of studies detailing the impact of barnacle growth on Ca-phosphate materials such as bone. Recent investigations have shown that, in *Amphibalanus amphitrite* (DARWIN), the radial advancement of the mural plates precedes the deposition of the calcareous base (BURDEN *et al.* 2014). It is likely during the radial advancement of the shell that some kind of chemical and/or mechanical attack occurs on the underlying bone substrate at or about the leading edge of the wall compartments. A report on how barnacles damage paint coatings because of their growth style might help us in envisaging how (if not why) this kind of process works (WOODS HOLE OCEANOGRAPHIC INSTITUTION 1952):

“The growing edge of the shell is sharp, and wedge shaped in section [...] As the base enlarges, this edge pushes outward and, if the substrate is not too hard,

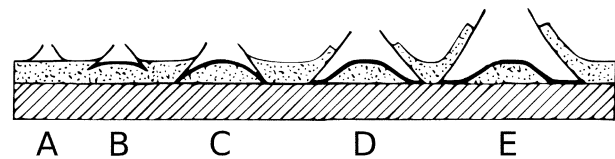


Fig. 4. Diagram showing how an acorn barnacle provided with a calcareous base plows into a paint coating. Dotted pattern indicates the paint coating; lined pattern indicates an underlying steel plate. **A** – Metamorphosed barnacle on paint surface. **B, C** – The edges of the shell grow downward until checked by the steel plate. **D, E** – Continued lateral growth forces the paint upward over the barnacle shell. Redrawn and modified from WOODS HOLE OCEANOGRAPHIC INSTITUTION (1952), after the original sketch by BÄRENFÄNGER (1939).

downward. As a result the edge of the shell tends to plow into the coating and may eventually cut down to the underlying metal. Figure 20 [i.e., Fig. 4 herein] diagrams the process.”

In light of these observations, it is tempting to speculate that the outermost layer of bone could be ploughed by the downward growing barnacle shell like the aforementioned paint coating, thus creating the central pedestal that is typical of *Thatchtelithichnus* in the process (Fig. 4). Interestingly, the calcareous base of balanid barnacles often exhibits a central area that is thinner than the rest (e.g., WANG *et al.* 2017: fig. 1B). This might also correlate with the observation of an unexcavated area in the central part of *Thatchtelithichnus*. A simple experiment of barnacle growth on bone samples is likely to shed light on several aspects of barnacle-induced bioerosion of bone.

Barnacle traces affecting bones have rarely been mentioned in previous works, and detailed characterizations and illustrations of such traces are largely wanting (e.g., BOESSENECKER 2013, and references therein). Our personal observations and a thorough literature review indicates that barnacles attaching onto a bone substrate are responsible for quite a variety of different traces, including *Anellusichnus* (BOESSENECKER 2013), *Thatchtelithichnus* (this work) and, possibly, *Karethraichnus lakkos* (ZONNEVELD *et al.* 2015). In addition to these traces, former areas of barnacle attachment on bones can be recognised as “epibiont shadows” (*sensu* PALMER *et al.* 1993), e.g. in form of oval patches where the outer cortical surface is seemingly well preserved and appears as slightly lifted above the partly abraded surrounding areas (e.g., COLLARETA & BIANUCCI 2021: fig. 3C).

Whereas preferential erosion of the central platform might lead some *Thatchtelithichnus* specimens to look similar to *Anellusichnus* (or *Karethraichnus lakkos*), the co-occurrence of *Thatchtelithichnus*- and *Anellusichnus*-like traces on unabraded Recent mammal bones is somewhat an enigma. There is no indication whatever that the two trace types originate from different settlement locations, nor that they correspond to different barnacle taxa or ontogenetic stages. In addition, whereas *Anellusichnus* traces can occur on both bones and shells, *Thatchtelithichnus* scars due to barnacle attachment are to our knowledge limited to bones. A better knowledge of the interactions that develop at the interface between different organised calcium matrices (e.g., apatite, aragonite and calcite) and the overgrowing barnacle needs to be established for cogently addressing these puzzling issues. Properly understanding these processes will certainly disclose important information on the taphonomic history of vertebrate remains that suffered prolonged exposure on the seafloor.

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