



Historical Biology

An International Journal of Paleobiology



ISSN: (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/ghbi20>

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To cite this article: F. Irazoqui & C. Acosta Hospitaleche (2021): Bioerosive traces in fossil penguin bones (Aves, Sphenisciformes) from the Eocene of Marambio/Seymour Island (West Antarctica), *Historical Biology*, DOI: [10.1080/08912963.2021.2017915](https://doi.org/10.1080/08912963.2021.2017915)

To link to this article: <https://doi.org/10.1080/08912963.2021.2017915>



Published online: 19 Dec 2021.



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Bioerosive traces in fossil penguin bones (Aves, Sphenisciformes) from the Eocene of Marambio/Seymour Island (West Antarctica)

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ABSTRACT

We examined a set of penguin bones from different Eocene levels of the Submeseta Formation in Marambio/Seymour Island (James Ross Basin, Antarctic Peninsula) and found the bioerosive trace fossils presented here. Traces were assigned to *Machichnus bohemicus*, *Machichnus* indeterminate, *Nihilichnus nihilicus*, Centrichnidae indeterminate, and other ambiguous structures grouped into morphologic descriptive categories such as 'shallow pits with radial scratches', 'indeterminate tunnels', 'rounded to sub-rounded shallow holes', 'oval deep traces'. According to the possible interpretations of these trace fossils, the taphonomic history of the remains, although different in all the cases, would include the primary deposition in a marine environment, transportation and subaerial exposure.

ARTICLE HISTORY

Received 19 August 2021
Accepted 9 December 2021

KEYWORDS

Pascichnia; Praedichnia;
Domichnia; Fixichnia;
Fodinichnia; Palaeogene;
James Ross Basin; Antarctic
Peninsula

Introduction

Ichnology involves the study of trace fossils produced by organisms on or within the substrate (Pemberton et al. 1992), comprising modern and fossil processes and the resulting structures. Within this field, the bioerosion structures were understood as biogenic structures produced in hard substrates (clasts, bones, or rocks) by a biological agent (Neumann 1966; Frey and Wheatcroft 1989) that is not always identified. And more recently, bioerosion was redefined as the process by which animals, plants and microbes sculpt or penetrate surfaces of hard substrates (Bromley 1994). Beyond this, trace fossils are, many times, the only evidence of the biological interaction between two or more organisms, and constitute a window to interpret dynamics of the past ecosystems.

Different approaches were historically used for the analysis of the trace fossils, alluding to the stratigraphic position of the structure (e.g. Seilacher 1964; Martinsson 1970), or the behaviour of the producer agent (Seilacher 1953). The progressive understanding of these structures encouraged the addition of new ethological categories to the later (Bromley 1996 among others). Sideways, an ichnotaxonomic classification permits the allocation of the trace fossils in a hierarchical scheme ruled by the ICZN. A discussion about the use of formal names in regards to these structures can be found in Buatois and Mangano (2011).

The ichnological studies on Seymour Island are still scarce and restricted mainly to specific cases of damaged mollusc shells (e.g. Bitner 1996; Casadío et al. 2001, Casadío, Parras et al., 2007; Harper et al. 2019) or structures disturbing the sediment (Wiedman and Feldmann 1988; Montes et al. 2019). However, during the last years, some cases of trace fossils on bones and shark teeth were briefly reported (Cione et al. 2010; Acosta Hospitaleche 2016; Gouiric-Cavalli et al. 2019; García et al. 2020).

In the present contribution, we examined a set of trace fossil-bearing penguin bones collected in Eocene levels of the Marambio/Seymour Island (West Antarctica, Figure 1). that worked as the trace carrier substrates looking for trace fossils. Penguin bones,

besides shark teeth, are the most abundant vertebrate elements in the Palaeogene of the James Ross Basin (Acosta Hospitaleche et al. 2013). These bones constitute large accumulations with different taphonomic stories (Acosta Hospitaleche 2016; Acosta Hospitaleche et al. 2016) traceable from palaeoecological indicators such as the bioerosive trace fossils. Each bioerosive structure was described, photo-documented and interpreted in regards to its genesis. It allows its allocation into an ethological category.

Material and methods

Fossil trace fossil-bearing penguin bones examined here are housed in the palaeontological collections of the Vertebrate Palaeontology Department, La Plata Museum (MLP), in La Plata (Argentina). We selected 50 specimens preserved in 36 penguin bones (18 coracoids, nine pedal phalanges, five humeri, one scapulae, one sternum, one tarsometatarsus, one femur) belonging to adult specimens that present trace fossils.

A binocular microscope Arcano ZTX Zoom (10–40X) was used for the examination of each material. Trace fossils were ichnotaxonomically determined following the ichnotaxobases proposed by Pirrone et al. (2014), Höpner and Bertling (2017), and Wisshak et al. (2019) when possible, or grouped according to morphologic criteria considering shape and size (Mikuláš et al. 2006; Britt et al. 2008; Pirrone et al. 2014). Descriptions also include information about the location on the fossil surface, and the association with other trace fossils. The ethological categories concur with Seilacher (1953), Ekdale (1985), and De Gibert et al. (2004). Measurements were taken with a Vernier Caliper of 0.01 mm of increment.

Procedence

Fossils here analysed were collected in Seymour Island, a small island near the tip of the Antarctic Peninsula, formed by the youngest sediments that filled the James Ross Basin. The Seymour Island

Group (Zinsmeister and Webb 1982) lies discordantly over the Marambio Group, and comprises the Cross Valley-Wiman Formation (Montes et al. 2008), the La Meseta Formation (lower part of the La Meseta Alloformation in Marensi 1995; Marensi et al. 1998a), and the Submeseta Formation (uppermost Allomember of the La Meseta Alloformation in Marensi 1995; Montes et al. 2013, 2019).

The La Meseta Formation (latest Palaeocene- middle Eocene) is internally divided into the six allomember, named in stratigraphic order as Valle de las focas, Acantilados I, Acantilados II, Cucullaea I, and Cucullaea II (Montes et al. 2019 and modified from; Marensi et al. 1998a, 1998b). The geometry and the architecture of these units were interpreted as the product of an incised valley and the deposition in estuary facies or inner prodelta (see Montes et al. 2019 for further details). We examined fossil penguin bones from the locality IAA 2/95, where levels of the Cucullaea I Allomember are exposed (Figure 1(b)).

The Submeseta (middle Eocene-Oligocene?) Formation is separated from the lower La Meseta Formation by an erosive discordance, and is composed of sandstones and shales with gravel intercalations. This is interpreted as shallow marine platform deposits dominated by storms shallow and represents the filling of incised valleys (Montes et al. 2019). The Submeseta Formation is divided into the three allomembers Submeseta I (SMI, level 37), Submeseta II (SMII, level 38), and Submeseta III (SMIII, level 39) according to Montes et al. (2013). More recently, these units were renamed as Laminado Allomember (LAM, level 37), Turritella Allomember (TUM, level 38), and Superior Allomember (SUM, level 39) by Montes et al. (2019).

The Submeseta Formation is the richest unit for penguin bones. Materials included in the present contribution come from the Submeseta I Allomember (level 37) in the locality IAA 1/93, the Submeseta II Allomember (level 38) in the localities DPV 10/84, DPV 13/84, DPV 14/84, and IAA 6/12, and the Submeseta III (level 39) Allomember in the localities DPV 16/84 and IAA 5/12 (Figure 1(b)).

Ichnotaxonomy

Machichnidae Wisshak et al. (2019)

Machichnus Mikuláš et al. (2006)?Machichnus bohemicus Figure 2(a,b,d,f)

Material

MLP 12-I-20-309t1 (humerus, Figure 2(a,b)), MLP 78-X-26-68t1 (coracoid, Figure 2(f)), MLP 12-I-20-157t1 (coracoid), MLP 12-I-20-307t1 (scapula, Figure 2(d)), MLP 12-I-20-217t1 (humerus).

Provenience

MLP 12-I-20-309t1 was collected in the locality IAA 5/12, MLP 78-X-26-68t1 and MLP 12-I-20-157t1 were collected in the locality DPV 13/84, Submeseta Allomember (level 38) of the Submeseta Formation, Bartonian age (late Eocene), MLP 12-I-20-307t1 and MLP 12-I-20-217t1 come from DPV 16/84 (level 39) of the Submeseta Formation, Priabonian age (late Eocene).

Description

The set of grooves on the cortical bone allows the assignment to Machichnidae, that include the genera *Machichnus*, *Nihilichnus*, *Linichnus*, *Knethichnus*, and *Mandaodonites*. The presence of shallow and subparallel grooves in MLP 12-I-20-309t1 (that according to Pirrone et al. 2014 should be more properly identified as channels given the U-shaped internal morphology) ordered in series oblique or perpendicular to the shaft supports the assignment to *Machichnus*. Slightly different are the grooves observed in MLP 12-I-20-157t1 and MLP 12-I-20-307t1 that present an internal V-shape. It also distinguishes MLP 12-I-20-309t1 from *Knethichnus* and *Linichnus* characterised by serrated grooves, or *Nihilichnus* and *Mandaodonites* represented by punctures.

MLP 12-I-20-309t1 is quite similar to *M. bohemicus* by the presence of subparallel grooves without any kind of striation, mostly shorter than 10 mm length each, and ordered in a small set that covers a low percentage of the surface. On the contrary,

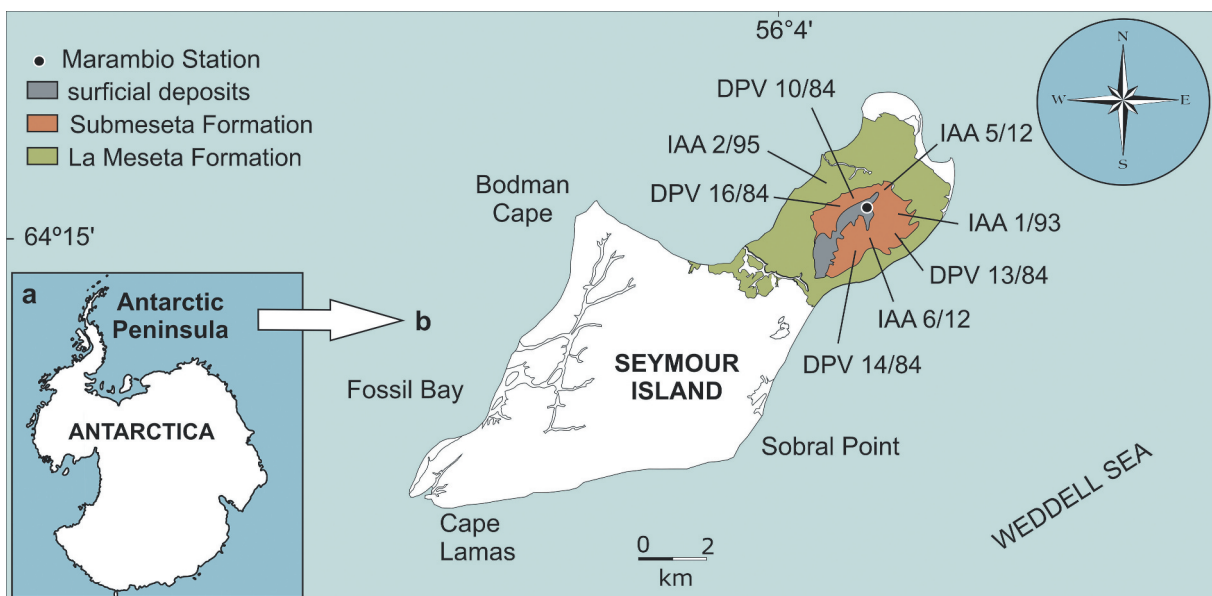


Figure 1. Simplified geological map of the Marambio/Seymour Island showing the places where La Meseta and Submeseta Formation crops out (modified from Montes et al. 2013) and the location of the fossiliferous localities cited in the text. (a) The Antarctic Peninsula in West Antarctica, (b) The Seymour/Marambio Island and areas of interest.

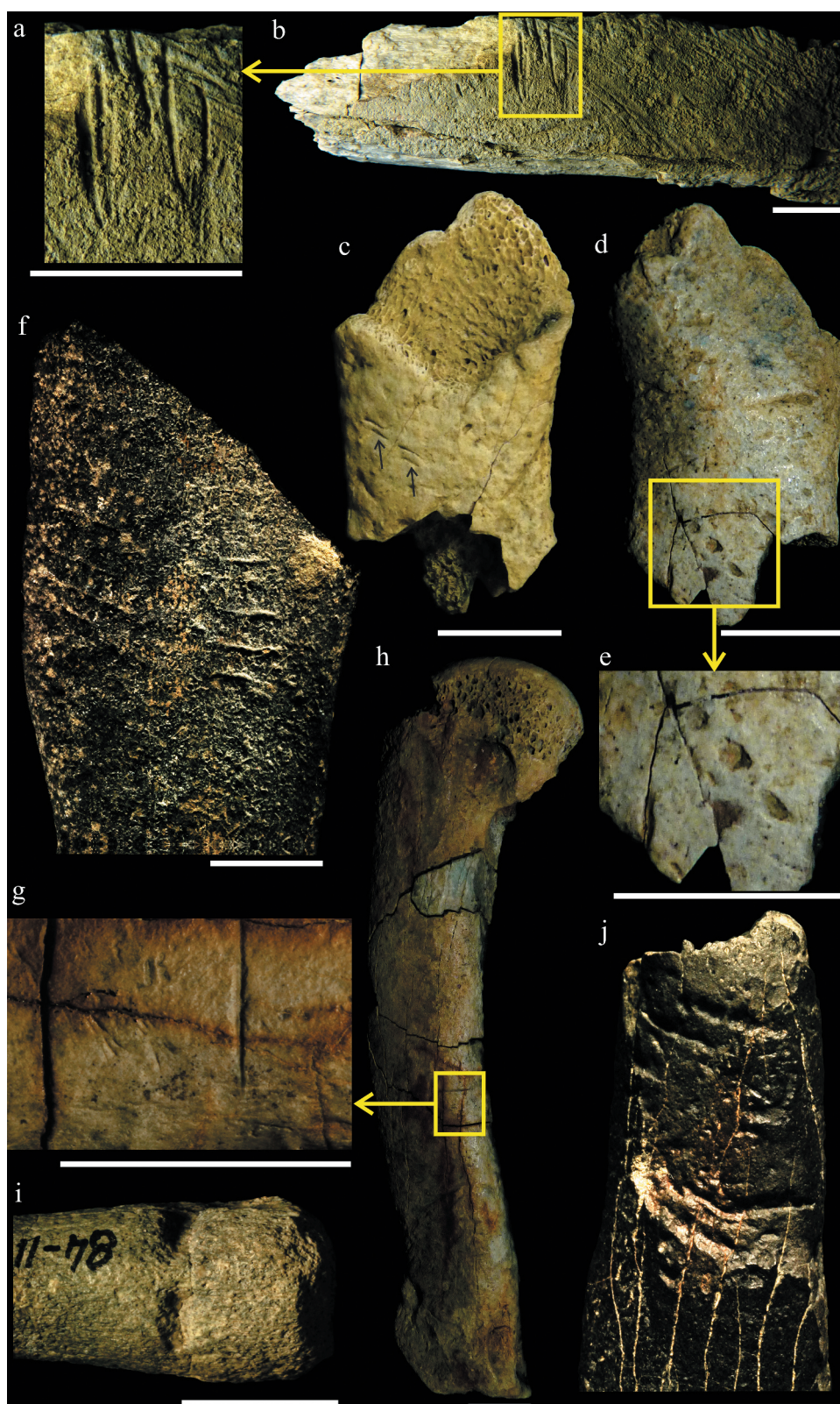


Figure 2. Bioerosive traces observed in the materials. (a-b) *Machichnus bohemicus* in MLP 12-I-20-309t1, (d) MLP 12-I-20-307t1 and (f) MLP 76-X-26-68t1. (c,g,h,i) *Machichnus* indeterminate in (c) MLP 12-I-20-307t2, (g,h) MLP 11-II-20-39t1 and (i) MLP 84-II-1-26t1. (d,e,j) *Nihilichnus nihilicus* in (d,e) MLP 12-I-20-307t3 and (j) MLP 12-I-20-308t1. Scale bar = 10 mm.

M. regularis presents arcuate grooves in cross section that usually cover the entire surface of the bone, whereas those of *M. multilineatus* refer to grooves longitudinally striated, *M. normani* to more complex scratches grouped in two intercrossed series, *M. harlandi* to isolated scratches longitudinally striated or smooth, *M. jeansito* scratches that narrows towards one of the ends, and *M. fatimae* to large and arcuate grooves that might branch. However, our main concern is that our traces are partially located on the superficial bone like those of *M. bohemicus*, but also on the cemented sediment like *M. normani*, *M. harlandi*, and *M. jeansi*. Besides, these last three ichnospecies were nominated for depositional marine contexts like the locality where this bone was collected (Mikuláš et al. 2006; Chumakov et al. 2013; Araújo-Júnior et al. 2017).

Interpretation

Perimortem feeding traces left by the action of teeth during the soft tissues removal. We cannot be sure if these scratches were produced by carnivores or scavengers, although we know that the penguin did not survive to the attack due to the absence or remodelled tissue related to the trace fossil.

Ethological category

Praedichnia (predation or scavenging traces).

Machichnus indeterminate Figure 2(c,g,h,i)

Material

MLP 12-I-20-17t1 (coracoid), MLP 12-I-20-109t1 (pedal phalanx), MLP 94-III-15-310t1 (coracoid), MLP 94-III-15-311t1 (coracoid), MLP 11-II-20-39t1 (humerus, Figure 2(g,h)), MLP 84-II-1-26t1 (pedal phalanx, Figure 2(i)), and MLP 12-I-20-307t2 (scapula, Figure 2(c)).

Procedence

Locality DPV 13/84 Submeseta Allomember (level 38) of the Submeseta Formation, Bartonian age (late Eocene), except by MLP 12-I-20-307t2 that comes from DPV 16/84 (level 39) of the Submeseta Formation, Priabonian age (latest Eocene).

Description

Small and thin scratches that appear isolated or in reduced sets affecting the periosteal bone.

Interpretation

The three species *M. normani*, *M. harlandi*, and *M. jeansi* describe the scratches left by the teeth of fishes eating biofilms that grow on marine pebbles (Chumakov et al. 2013); the size and morphology match with the trace fossils observed here. However, MLP 11-II-20-39t1 and MLP 12-I-20-307t2 are also identical to the paired traces attributed to dermestids found in dinosaur bones by Britt et al. (2008).

Nihilichnus Mikuláš et al (2006)

Nihilichnus nihilicus Figure 2(d,e,j)

Material

MLP 12-I-20-308t1 (incomplete coracoid, Figure 2(j)), MLP 12-I-20-307t3 (scapula, Figure 2(d,e)).

Procedence

MLP 12-I-20-308t1 comes from the locality IAA 6/12 and MLP 12-I-20-307t3 comes from DPV 16/84, Submeseta Allomember (level 39) of the Submeseta Formation, Priabonian age (late Eocene).

Description

The presence of a few sets of punctures with irregular outlines supports the assignment to Machichnidae. Although obscured by the subsequent erosion of the superficial layers of bone that leaves the most internal section of the exposed traces, each puncture exhibits a circular outline, allowing its assignment to *Nihilichnus*. It precludes, at the same time, the assignment to *Machichnus*, *Knethichnus*, and *Linichnus*, that refer to grooves instead of punctures and to *Mandaodonites*, represented by sets of ovoidal individual trace fossils.

Around twelve moderately deep punctures, geometrically poorly defined, are aligned on the ventral side of the bone, while on the dorsal surface it is possible to recognise only eight, some matching in both surfaces, and one of them clearly associated with a superficial groove.

We observed strong similarities with *N. nihilicus*, that refers to solitary or grouped pits on bones like those observed here, whereas *N. covichi* was posteriorly defined to describe trace fossils only on shells.

Interpretation

Exclusively developed on the cortical bone and probably made by the teeth action.

Ethological category

Praedichnia (predation or scavenging traces).

Centrichnidae Wisshak et al. (2019) Centrichnidae indeterminate Figure 3(a,b,c,e,h,i)

Material

MLP 12-I-20-89t1 (sternum, Figure 3(h,i)), MLP 12-I-20-17t2 (coracoid, Figure 3(a,b,c,e)).

Procedence

Locality DPV 13/84 Submeseta Allomember (level 38) of the Submeseta Formation, Bartonian age (late Eocene).

Description

Isolated circular and sub-circular traces, excavated in a flat portion of cortical bone varying between 1 mm and 5 mm diameter. A pair of rounded traces of 2 mm diameter separated 45 mm from each other appear in MLP 12-I-20-17t2. These roughly circular depressions are shallower than wide, feature that distinguish them from other holes or tunnels like those assigned to Gastrochaenolithidae).

Interpretation

Fixation traces occasioned by invertebrates according to Wisshak et al. (2019).

Ethological category

Fixichnia (attachment traces).

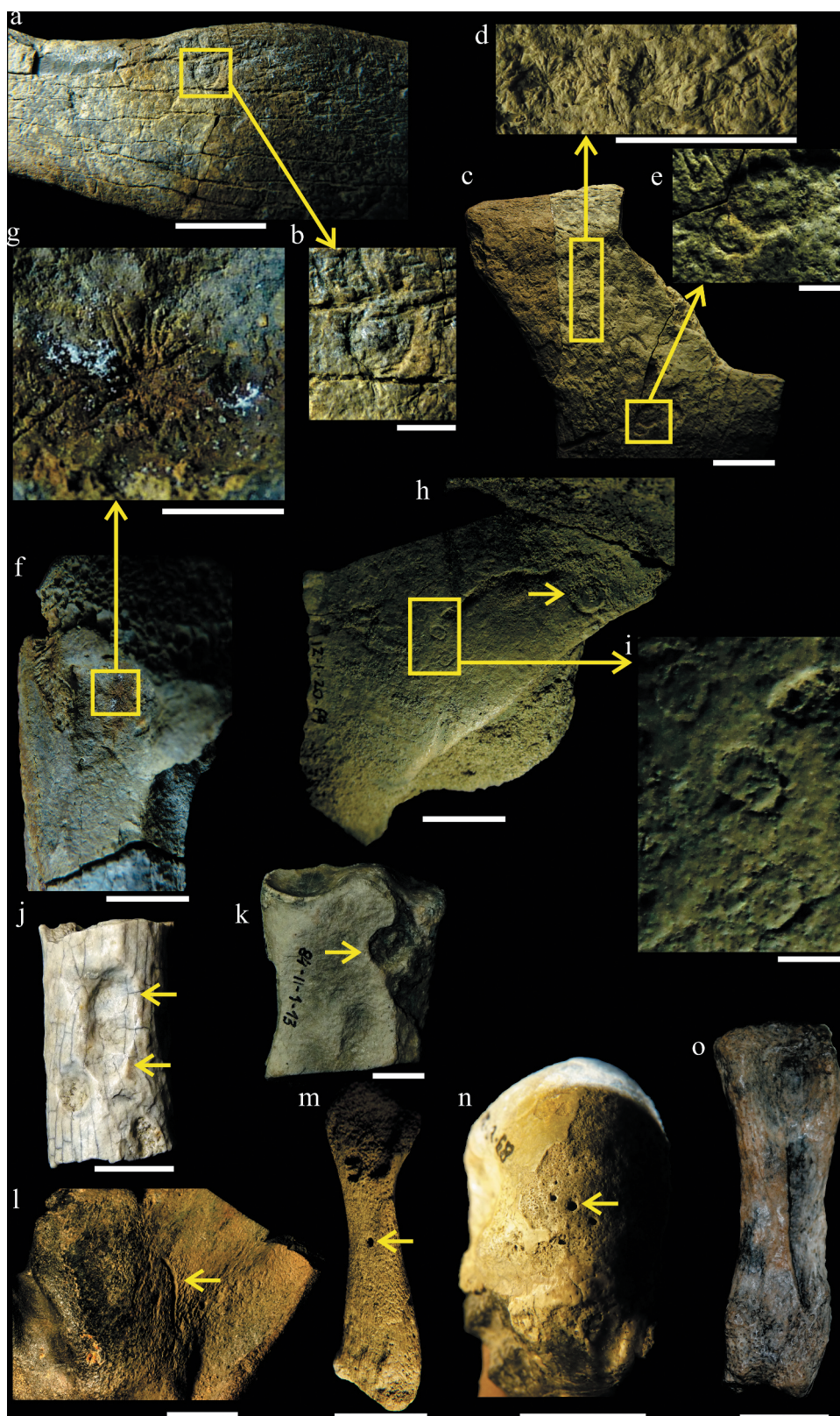


Figure 3. Bioerosive traces observed in the materials. (a,b,c,e,h,i) Centrichnidae indeterminate in (a,b,c,e) MLP 12-I-20-17t2 and (h,i) MLP 12-I-20-89t1. (c,d,f,g) Shallow pits with radial scratches in (c,d) MLP 12-I-20-17t3, and (f,g) MLP 11-II-20-39t2. (j) Oval deep traces in (j) MLP 08-XI-30-132t1. (k) External mould in (k) MLP 84-II-1-13t1. (l,o) Dubious lineal sulci in (l) MLP 91-II-4-215t1 and (o) MLP 83-V-20-10t1. (m,n) Indeterminate tunnels in (m) MLP 84-II-1-177t1 and (n) MLP 83-V-30-9t1. (b,d,e,g,i) Scale bar = 2 mm. (a,c,f,h,j,k,l,m,n,o) Scale bar = 10 mm.

Shallow pits with radial scratches **Figure 3(c,d,f,g)****Material**

MLP 96-I-6-29t1 (coracoid), MLP 12-I-20-89t2 (sternum), MLP 91-II-1-271t1 (coracoid), MLP 11-II-20-39t2 (humerus, **Figure 3(f,g)**), and MLP 93-X-1-77t1 (coracoid), MLP 12-I-20-17t3 (coracoid, **figure c, d**), MLP 12-I-20-176t1 (coracoid), MLP 12-I-20-28t1 (coracoid).

Procedence

MLP 96-I-6-29t1 comes from locality DPV 1/93 Submeseta I Allomember (level 37) of the Submeseta Formation, Lutetian age (middle Eocene). MLP 12-I-20-89t2, MLP 91-II-1-271t1, MLP 11-II-20-39t2, and MLP 93-X-1-77t1 come from the locality DPV 13/84 Submeseta Allomember (level 38) of the Submeseta Formation, Bartonian age (late Eocene). MLP 12-I-20-17t3, MLP 12-I-20-176t1, and MLP 12-I-20-28t1 come from Locality DPV 16/84 (level 39) of the Submeseta Formation, Priabonian age (latest Eocene).

Description

Two different patterns were determined. The first one (e.g. MLP 12-I-20-89t2) is a single trace developed in a flat surface and consists of a shallow depression with clear grooves radiating from the central hole. The second one (e.g. MLP 12-I-20-17t3) is established by the repetition of the trace along the surface that partially erased the radiated pattern.

Interpretation

Similar patterns occasioned by dermestid were found by Britt et al. (2008) in dinosaur bones. However, we notice that these traces could also belong to the feeding activity of sea urchins that have a complex dental apparatus, Aristotle's lantern, constituted by five calcium carbonate plates that characteristically scratched the surface. When Aristotle's lantern displaces along the surface during the feeding activity, the resulting pattern is more complex (Bromley 1975). In both cases, these trace fossils are accidentally generated on the bone surface during the grazer activity of the sea urchin.

Ethological category

Fodinichnia (feeding traces made during the larvae eating activity) Pascichnia (combined locomotion and grazing trace fossils), although some cases in which for example, the sea urchin is pre-dating on sponges living within the bone, it would be considered as Praedichnia (predation or scavenging trace fossils).

Indeterminate tunnels **Figure 3(m,n)****Material**

MLP 78-X-26-145t1 (pedal phalanx), MLP 92-II-2-204t1 (pedal phalanx), MLP 83-V-30-9t1 (proximal end of humerus, **Figure 3(n)**), MLP 12-I-20-155t1 (coracoid), MLP 84-II-1-176t1 (pedal phalanx), MLP 84-II-1-177t1 (pedal phalanx, **Figure 3(m)**), and MLP 12-I-20-47t1 (pedal phalanx).

Procedence

MLP 78-X-26-145t1, MLP 92-II-2-204t1, MLP 83-V-30-9t1, and MLP 12-I-20-155t1 come from locality DPV 13/84, and the other materials come from locality DPV 14/84, Submeseta Allomember (level 38) of the Submeseta Formation, Bartonian age (late Eocene). MLP 12-I-20-47t1 comes from locality DPV 16/84 (level 39) of the Submeseta Formation, Priabonian age (latest Eocene).

Description

Slightly oval and deep perforations of 0.2 to 0.9 mm diameter, perpendicular to slightly oblique to the bone surface. These trace fossils partially match with those of Gastrochaenolithidae, which groups holes in bones with a distal widening. We cannot clearly observe the bottom of the deeper traces (e.g. MLP 92-II-2-204t1), but in the shallower traces (e.g. MLP 84-II-1-176t1), the tunnel walls are straight and subparallel, without the characteristic distal widening.

Interpretation

Traces assigned to the Gastrochaenolithidae *Clavichnus ionasi* were assigned to the feeding activity of annelids or sipunculid worms (Muñiz et al. 2010). Although it was thought that the modern annelid *Osedax* was a specialist in the substrate choice that prefer whale carcasses (Higgs et al. 2011), its eating activity was also observed in Oligocene Plotopterids (Kiel et al. 2011), marine birds with strong adaptations to diving, like those developed in penguin skeletons. According to the observations made by Kiel et al. (2010), the shallower and smaller perforations without the characteristic distal widening could indeed correspond to failed attempts of the bone boring worms during the eating activity.

Ethological category

Domichnia (dwelling traces).

Rounded to sub-rounded shallow holes**Material**

MLP 95-I-10-260t1 (coracoid), MLP 84-II-1-44t1 (coracoid), MLP 93-X-1-113t1 (coracoid), MLP 12-I-20-155t2 (coracoid), MLP 12-I-20-157t1 (coracoid), MLP 92-II-2-166 (coracoid).

Procedence

MLP 95-I-10-260t1 comes from locality IAA 2/95 Cucullaea Allomember (level 35) of the La Meseta Formation, late Ypresian (early Eocene); MLP 84-II-1-44t1, MLP 12-I-20-155t2, and MLP 12-I-20-157t1 come from locality DPV 13/84 Submeseta Allomember (level 38) of the Submeseta Formation, Bartonian age (late Eocene).

Description

Rounded and sub-rounded holes smaller than 1 mm, with smooth margins. Modern apothecia belonging to endolithic lichens occur today within some of these holes, whereas others are empty probably due to the posterior fall of the apothecia.

Interpretation

Modern traces left by the growth of endolithic lichens that easily proliferate in fractures or rough surfaces of the fossils and other substrates. Each hole is produced by one apothecium connected to others through thin hyphae growing into shallow furrows.

Ethological category

Not defined yet for this kind of trace, although they could be considered as Fixichnia (fixation traces).

Oval deep traces **Figure 3(j)****Material**

MLP 08-XI-30-132t1 (femur, **Figure 3(j)**)

Procedence

Submeseta Formation probably DPV 16/84 (level 39) of the Submeseta Formation, Priabonian age (latest Eocene)

Description

Oval trace (16.6 mm x 7.4 mm.), with smooth edges and bottom, parallel to the axis of the bone. It can be divided into three different parts due to the variation of the depth caused by two ridges perpendicular to the main axis. A second rounded trace (5.2 mm x 4.5 mm.) also presents smooth edges and an irregular bottom.

Interpretation

Similar traces were interpreted as the product of the feeding activity of insect larvae (see for example Xing et al. 2016).

Dubious lineal sulci **Figure 3(l,o)****Material**

MLP 91-II-4-215t1 (humerus, **Figure 3(l)**), MLP 08-XI-30-39t1 (coracoid), MLP 12-I-20-89t3 (sternum), MLP 12-I-20-17t4 (coracoid), MLP 92-II-2-166t2 (coracoid); MLP 94-III-15-310t2 (coracoid), MLP 91-II-1-271t2 (coracoid), MLP 84-II-1-178t1 (pedal phalanx), MLP 83-V-20-10t1 (pedal phalanx, **Figure 3(o)**), MLP 12-I-20-307t4 (scapula).

Procedence

MLP 91-II-4-215t1 comes from locality DPV 10/84, MLP 08-XI-30-39t1, MLP 12-I-20-89t3, MLP 12-I-20-17t4, MLP 92-II-2-166t2, MLP 94-III-15-310t2, and MLP 91-II-1-271t2 comes from locality DPV 13/84; MLP 84-II-1-178t1, and MLP 83-V-20-10t1 come from locality DPV 14/84, all of them assigned to Submeseta II Allomember (level 38) of the Submeseta Formation, Bartonian age (late Eocene). MLP 12-I-20-307t4 comes from locality DPV 16/84 (level 39) of the Submeseta Formation, Priabonian age (latest Eocene).

Description

Isolated, straight or slightly curved traces under relief of variable size affecting the cortical bone. For example, thin and short sulci are in MLP 84-II-1-178t1, whereas a single and shallow sulcus that narrows towards the distal end of the bone is observed in MLP 83-V-20-10t1.

Interpretation

They might correspond to the teeth action of small vertebrates, although the mechanical action against the hard substrate during transport cannot be ruled out.

Ethological category

Praedichnia? (predation or scavenging traces).

Inner moulds of tubes**Material**

MLP 12-I-20-156t1 (coracoid)

Procedence

Locality DPV 13/84 Submeseta Allomember (level 38) of the Submeseta Formation, Bartonian age (late Eocene).

Description

A pair of cylindrical structures like tubes of different sizes (1.6 mm width x 24 mm length and 1.5 mm width x 13 mm length), cemented on the bone surface.

Interpretation

The tubes are attributed to the filling of galleries made by any indeterminate macroinvertebrate.

Ethological category

Domichnia? (dwelling traces).

External mould **Figure 3(k)****Material**

MLP 84-II-1-13t1 (tarsometatarsus, **Figure 3(k)**)

Procedence

Locality DPV 13/84 Submeseta Allomember (level 38) of the Submeseta Formation, Bartonian age (late Eocene).

Description

A short tunnel or a hole of 0.8 mm of diameter crosses a pelitic layer and reaches a psamitic one of the sediments that still cover the ventral surface.

Interpretation

The sediment attached to the bone constitutes the external mould of a dwelling trace.

Ethological category

Domichnia (dwelling traces).

Discussion and conclusions

Concurring with modern proposals (Wisshak et al. 2019), we analysed the materials from an ichnotaxonomical perspective, providing the first report of bioerosive trace fossils from Antarctica arranged in ichnofamilies. Ichnotaxa here identified belong to Machichnidae *Machichnus bohemicus*, *Machichnus* indeterminate and *Nihilichnus nihilicus*, and Centrchnidae indeterminate. Other fossil traces, not certainly assigned to any ichnotaxon, were discussed from a morphological and biological perspectives, comparing with previous reports.

One of the most puzzling trace fossils correspond to those assigned to 'shallow pits with radial scratches'. Previous reports suggest that they could correspond to dermestids (Britt et al. 2008), although strong similarities have also been found with the fossil traces assigned to sea urchins. For instance, *Gnathichnus pentax* is a trace fossil generated by the feeding activity of regular echinoids. Although these echinoids are not recorded in the Submeseta Formation, where the record is restricted to the heart urchins or Spatangoida, a group without feeding lanterns, the genesis of the carrying deposits offer us an explanation. The test of regular sea urchins is extremely weak in comparison to the skeleton of the heart urchins that are widely represented in the Submeseta Formation and are also present in La Meseta Formation. The clear signs of transportation that the penguin bones exhibit, would have been too destructive for the regular echinoid preservation. In other words, the absence of these elements in the localities sampled here does not constitute conclusive evidence regarding the composition of the Eocene communities that lived in the James Ross Basin.

Machichnus bohemicus is a very frequent trace fossil produced by the mechanical action of teeth on the bones. This trace fossil is easily identifiable, and can be produced by a large number of agents that search for food. These traces could be generated during a predator attack, culminating in the death of the penguin, or its escape and survival. However, when the animal survives the

trauma, the injury initiates an inflammatory response that ends with the formation of a bony callus (Marsell and Einhorn 2011). These healing structures have been previously reported in other materials (see Acosta Hospitaleche et al. 2012) but are not observed in this sample. *Machichnus bohemicus* could also be produced by scavengers on the carcasses with soft tissues, or by any toothed vertebrate feeding on encrusting organisms growing on the bone. Bienkowska-Wasiluk et al. (2013) describe several fishes from the La Meseta Formation; we consider that many of them could be the producer of this kind of trace.

Nihilichnus was proposed to group triangular, circular to ovoidal holes produced by vertebrates exclusively on cortical bones (Mikuláš et al. 2006). However, *Nihilichnus covichi* was later erected for holes made on shells (Rasser et al. 2016), restricting the damage on bones to *N. nihilicus* (Mikuláš et al. 2006). In the context of our assemblages, marine mammals, reptiles, and bony fish could be responsible for these traces.

Both, the 'indeterminate tunnels' and all the other dwelling traces were probably produced by invertebrates (Wisshak et al. 2019). *Clavichnus*, identified in this sample with certain doubts, was recently established to group unbranched and claviform tunnels mainly perpendicular to the bone surface (Höpner and Bertling 2017) under the ichnospecies *Clavichnus ionasi*. Thus, this restricts the use of *Trypanites* to biogenic structures on lithic substrates. As far as we know, the fossil record of insects in Antarctica dates back to the Permian (Carpenter 1969; Tasch and Riek 1969; Tasch 1971). Particularly in the Antarctic Peninsula, coleopteran fragments identified as aquatic beetles were reported from the Jurassic Mount Flora Formation in Hope Bay (Zeuner 1959). Nonetheless, we are not sure about the producer agent identity of the trace fossils examined here.

Circular structures compatible with fixation marks were assigned to the ichnofamily Centrichnidae, although all of them are developed on bone surfaces. This is relevant because in the proposal of Wisshak et al. (2019) ichnogenera are tied to a particular hard substrate (calcareous, siliceous, xylic, and osteic, that comprises bone, teeth, and scales), and all the ichnotaxa included in Centrichnidae (*Augoichnus*, *Centrichnus*, *Lacrimichnus*, *Ophthalmichnus*, *Solealites*, and *Tremichnus*) are conditioned to calcareous skeletons. However, due to ichnofamilies address primarily morphological categories across substrate types, we believe that our structures fit anyway in this category (Wisshak et al. 2019), and suggest that the fixation marks described above could be produced by endolithic lichens.

Only a part of the trace fossils could be ichnotaxonomically identified. Nevertheless, the rest of them were grouped considering the general morphology, the relative position and distribution along the bone, and the association with similar or distinct trace fossils. These trace types were also described and photo-documented to make the information available for further examinations.

Unfortunately, a palaeoecological analysis from an ichnofacies approach is not possible due to our sample is composed by re-worked elements differently transported. Bioerosive trace fossils were more abundant in the upper levels of the sequence belonging to the Submeseta Formation than in the lower units. These levels were assigned to the Facies Association III characterised by a more uniform sandy lithology representing a non-confined tide and storm influenced nearshore environment (Marenssi et al. 1998b).

Finally, the trace fossil bearing-bones tell us about the environmental dynamics to which they were exposed and their taphonomical history. Although these bones were collected in marine levels, their taphonomical history is long and probably a little more complex. Bones were deposited in an environment located

a few kilometres away from the coast where the breeding colonies were settled down (Marenssi et al. 2002) and then subaerially exposed during a considerable time. Many penguin bones show clear signs of predation or scavenging, but also from insect larvae. Examples of praedichnia on penguin bones includes trace fossils that could have been the cause of death as for example in specimen MLP 12-I-20-309t1, and other traces significantly less marked like in MLP 91-II-4-215t1 probably made by scavengers removing remaining flesh tissues or biofilms (if not by the mechanical action against the substrate during transport). A third case of praedichnia could be attributed to the (unconfirmed) action of sea urchins feeding on other invertebrates (sponges, polychaete worms, etc.) and producing the trace fossils on the bones as a collateral damage. However, since sea urchins mainly graze on algae and undersea vegetation, these trace fossils would preferably be assigned to Pascichnia (see above). Something completely different occurs in MLP 78-X-26-145t1, when bones are deposited for a long time enough for certain invertebrates to erode their surface in search for a place to inhabit (Domichnia and Pupichnia) or just providing a surface for crusters and other organisms fixate to hard substrates (Fixichnia).

Acknowledgments

We thank to Marcelo Reguero (Museo de La Plata, La Plata, Argentina) for the invitation and coordination within the Programa Antártico Argentino, the Instituto Antártico Argentino-Dirección Nacional del Antártico (IAA-DNA), Fuerza Aérea Argentina, and the rest of the Heidi Group for the logistic support during the field trip. To La Plata University for constant support. We thank Marcelo Reguero also for the access to material and Bruno Pianzola (Museo de La Plata, La Plata, Argentina) for the pictures. The reviewers Silvina de Valais and Herminio de Araújo-Júnior improved our manuscript with their suggestions and comments.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

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CAH conceived of the presented idea, FI examined and compared the material. CAH and FI wrote the manuscript, prepared the figures, and approved the final version of the manuscript.

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