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Neoichnology of endolithic lichens: an update on the traces produced in fossil bones and teeth

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ABSTRACT

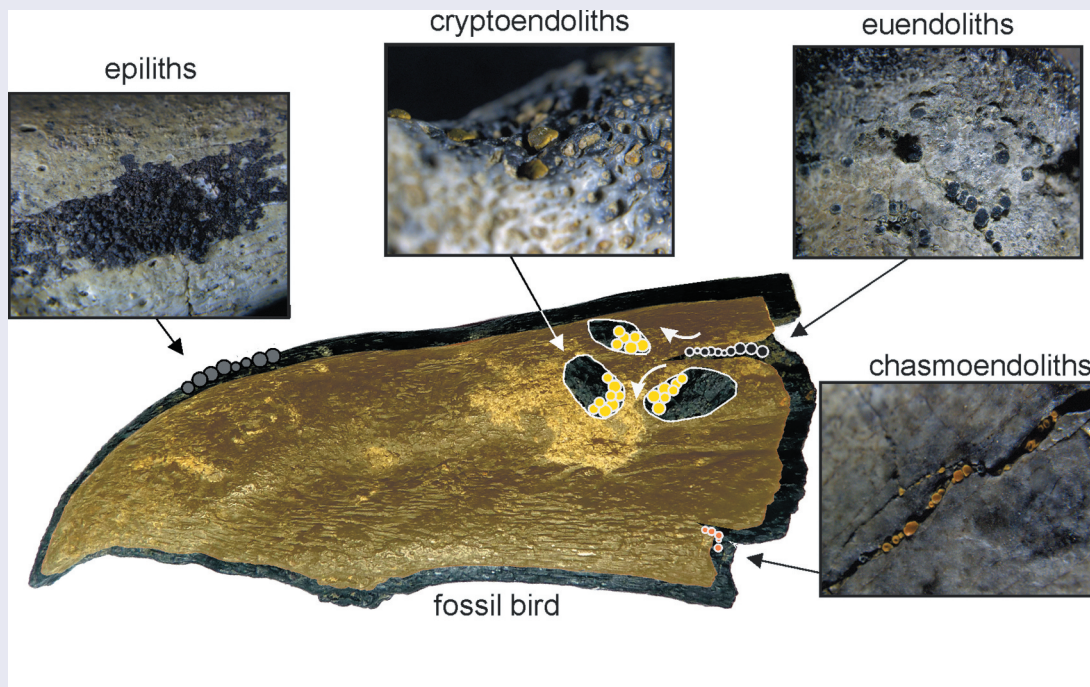
The present contribution is motivated by the frequent occurrence of traces generated by lichens on the fossil record, the usual and erroneous attribution of them to plant roots, and the scarce information published about bioerosive damage caused by lichens. As a result, two different patterns were identified on the surface and inside the fossil bones and teeth. The first one is characterised by the presence of lines clearer than the rest of the surface, produced by the hyphae and interrupted by small pits corresponding to the apothecia. These traces are often confused with *Corrossichnia* and *Sphenoichnia*, a situation that leads to taphonomic and palaeoecological misinterpretation. The second pattern, more unnoticed among other visible traces, consists of isolated pits without any other surficial trace distributed in the fossil surface. These pits can be confused with perforations made by many organisms. However, the presence of apothecia and, in some cases, also hyphae on the fossil remains, allows the accurate identification of the causal agent and the mechanism of action by which it occurs.

ARTICLE HISTORY

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Bioerosion; taphonomy;
South America; Antarctica;
Cenozoic



Introduction

Saxicolous lichens, like all bioerosive organisms, establish different relationships with the substrate (Figure 1) and have been found in epilithic (Wierzchos et al. 2011), and endolithic microhabitats (Wierzchos et al. 2012, 2018). More specifically, the endolithic habits have been subdivided into three different categories

according to their location within rocks: cryptoendolithic (occupying pore spaces in the rock), chasmoendolithic (living within cracks and fissures of the rock) and euendolithic (actively penetrating and dissolving the rock) (Salvadori and Municchia 2016). The chasmoendolithic and cryptoendolithic behaviour appears as the dominant of endolithic lichens in both cold and hot desert environments,

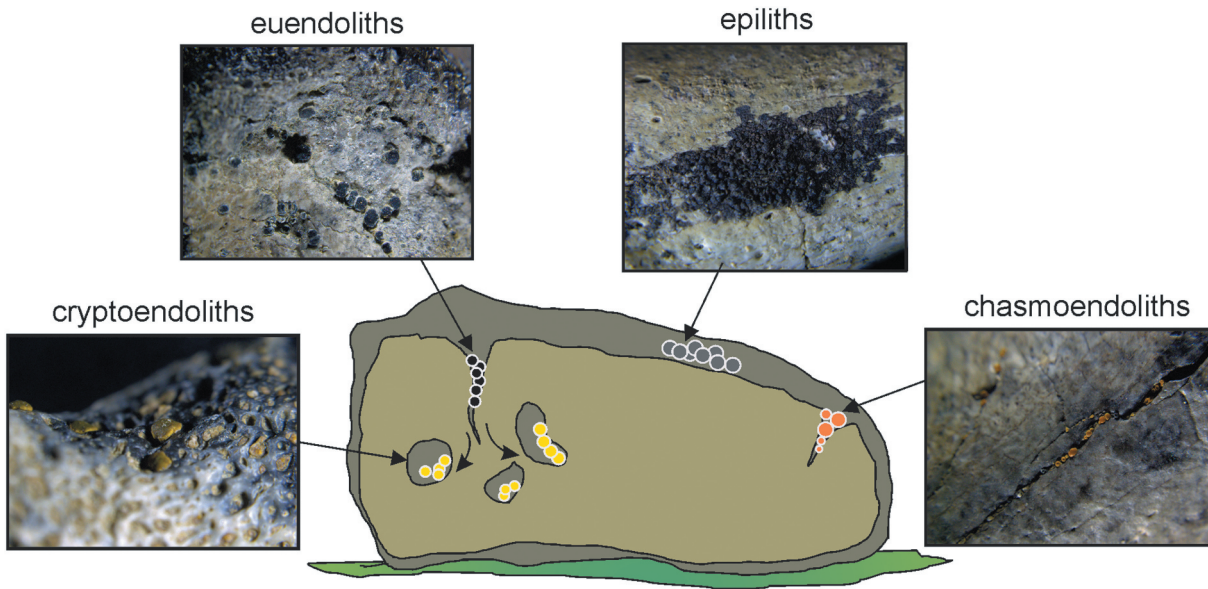


Figure 1. Schematic draw showing the habitats of the saxicolous lichens.

where they are recognised as prominent colonisers (Wierzchos et al. 2012). In recent years, the new category named autoendolithic, has been proposed. The autoendolithic organisms actively participate in mineral deposition on the rock (Marlow et al. 2015) and may contribute directly to the rock formation, through metabolic products that precipitate as minerals, or indirectly by products that promote mineralisation. It should be noted that autoendoliths remain as such until they become fully entombed by themselves as their metabolic activity ceases (Marlow et al. 2015). Although autoendolithic lichens are unusual, Bungartz et al. (2004) proposes that *Verrucaria rubrocincta* Breuss, which occurs on limestones (Breuss 2000), would generate a biomineralization that covers and protects the limestone through the formation of a layer of micrite, and thus generating a double action on the rock (Garvie et al. 2008).

The endolithic condition in lichens is not restricted to a particular taxon, on the contrary, it appears independently. For example, *Lecanora*, *Lecidea* and *Verrucaria* develop epilithic and endolithic conditions in the different species. The endolithic habit has been interpreted as an adaptation to different environmental stress conditions, allowing the species to be safe within the rock without wasting energy in a protective structure (the overlying mineral substrate provides protection). This is associated with environments exposed to high solar radiation or extreme temperatures (Friedmann 1982; Kappen et al. 1981; Omelon et al. 2006a, 2006b; Bell 1993; Kidron 2000; Walker and Pace 2007a, 2007b; Wierzchos et al. 2012). Besides, the endolithic habit has also been considered as a strategy to avoid inter-specific competition for the surface. Beyond that, endolithic lichens can be found almost anywhere in the world where rocks exist, from the poles to the tropics, in natural and urban environments (De Los Ríos et al. 2005a, 2005b; Garvie et al. 2008).

Oxalic acid secreted by epilithic lichens is commonly considered to play a crucially important role in the chemical weathering of rocks and minerals. This is confirmed by the universal occurrence of metal oxalates at the lichen–rock interface and in the lichen thallus itself, and by the fact that dissolution and precipitation of various rocks and minerals in the presence of oxalic acid can be demonstrated under experimental conditions (Chen et al. 2000). Many endolithic lichens do not produce oxalic acid but can still

exert significant chemical effects on their substrate rocks. This is because due to the secretion of other simple organic acids, such as citric, gluconic acids, which can also lead to the weathering of rocks through acidic attack and chelation (Wilson 1995). In the case of the endolithic growth within silicate rocks observed in the extreme Antarctic conditions, lichens as, for example, *Lecidea* spp. were shown to be active in chemically modifying minerals in the proximity of penetrating hyphae (De Los Ríos et al. 2005a). Jackson and Keller (1970) found that respiratory CO_2 of lichens could effectively result in a localised pH reduction in the microenvironment, and thus, contribute to promotion of the rate of chemical weathering. It has also been shown that some species can produce carbonic anhydrase, an enzyme that catalyzes the reversible hydration of CO_2 and consequently the dissolution of carbonate rocks (Favero-Longo et al. 2009, 2011). The lichens also contribute to the mechanical weathering in four ways: through the penetration of mycobiont hyphae and rhizines naturally occurring into crevices and cracks in the rock surface; by the expansion and contraction of lichen thalli due to daily and seasonal changes in the environmental temperature and humidity; by the swelling action of organic salts produced by lichens; and causing fractures during growing and incorporating mineral fragments of lichen thalli (Chen et al. 2000).

Among the hard substrates colonised by endolithic lichens are rocks and fossils that serve as an anchor point. The damage left by these lichens has been repeatedly confused in the past with the action of root traces. However, we know now that fossils provide anchorage and protection to endolithic organisms growing in extreme and hostile environments, and thus accumulate erosive damage not only on the surface, but also inside it, attacking the structural part of the bone tissues.

Mikuláš (2001) was the first who doubted about the genesis of these traces, and some years later Acosta Hospitaleche et al. (2011) documented four species of endolithic lichens with fresh apothecia growing into the bones and eroding the superficial bone, plus another one generating small perforations in the enameloid of shark teeth. Additionally, in a recent investigation, García et al. (2021), revealed the existence of euendolithic lichens that generate deep bioerosion on fossil penguin bones from Antarctica.

The presence of apothecia associated within the traces was unquestionable evidence of the bioerosive activity of the thallus within the fossil bones and constituted the first step for further analyses (Acosta Hospitaleche et al. 2011). Once these traces were clearly identified, new cases of fossils and archaeological bones were subsequently reported (García et al. 2020a,b, 2021; Gouiric-Cavalli et al. 2019), showing a wider richness of endolithic species associated with the biodegradation of fossil bones, than it was previously thought. From then on, we have focused our attention in the examination of large samples of fossil remains, to determine the lichen species certainly associated with the biodegradation observed (García et al. 2020b; see also Irazoqui and Acosta Hospitaleche 2021).

Weathering, corrosion and even the bioerosion caused by boring invertebrates, predators, and scavengers among others can blur the traces caused by the lichens or, on the contrary, be erased by the lichen traces. For that reason, to distinguish more clearly the traces assigned to lichens from all the other kinds of traces visible on the fossil surface, the taphonomic history of each remain was also a topic of interest in the present contribution.

Thus, after the examination of 151 fossil specimens collected in different localities of Patagonia and Antarctica, we can define two distinctive patterns of traces caused by endolithic lichens. The aim of this study is the characterisation of these traces, the determination of the substrates they affect, the compilation of the complete list of taxa involved as causal agents and the establishment of their habit, and the ponderation of the kind and magnitude of the damage produced on the fossils.

Material and methods

Assemblages of numerous bones and teeth belonging to the collections of the Vertebrate Palaeontology Department of La Plata Museum (MLP) were examined by naked eye looking for signs of lichen traces (see Appendix 1). Only traces directly associated with the erosive agent were positively assigned either to endolithic lichen (when apothecia and/or hyphae are still present) or to root (when roots are still preserved and associated to the trace). Also, traces previously assigned to fish (*Nihilichnus* sp.), worms (Gastrochaenolitidae) and sea urchins or dermestid coming from the same levels that the material examined here (Irazoqui and Acosta Hospitaleche 2021), were examined with comparative purposes. After that, a small group of fossils with damage provenly caused by lichens was selected to represent the spectrum of variation observed in these traces, and to characterise each morphological type (see results below).

This way, the results include: 1- the assignment of the materials to a lichen trace and its morphological characterisation, 2- the determination of the substrate type (bones and/or teeth/tooth plates) and the taphonomic attributes of the selected samples (including the weathering stage, the presence of fossil diagenetic fractures, the signs of transportation, and any other relevant data observed during examination) regarding the material resistance and the damage produced by the lichens, 3 – the systematic identification of the associated lichen and their habits, and 4 – a brief comment on the regional climate and the environmental conditions of the collection areas.

The assignment of the lichen traces was made considering two morphological groups already recognised in previous contributions (e.g., Acosta Hospitaleche et al. 2011; Gouiric-Cavalli et al. 2019; García et al. 2020b, 2021) but still unnamed. Different levels of magnification were used according to the requirements of each structure. A binocular microscope Arcano ZTX Zoom (10–40X) was used for the examination of each material, whereas the pictures were taken with a microscope stereoscopic Nikon SMZ 100, in the Universidad Nacional de La Plata (UNLP) laboratories. A Scanning electron

microscopy (SEM) FEI ESEM Quanta 200, with electron source from a tungsten filament and accelerating voltage of 200 V to 30 kV, from the Laboratorio de Investigaciones en Metalúrgica Física ‘Ing. Gregorio Cusminsky’ (LIMF, UNLP) was used for further examination of the non-metallised samples in low-vacuum (LoVac) mode with precision of 0.1–1 Torr. Additionally, a qualitative, semi-quantitative and quantitative analysis of chemical elements patterns was done to compare the composition of the materials associated with the traces with an electron probe micro-analysis (energy-dispersive X-ray spectrometer) EDAX SDD Apollo 40 with light element detection from boron, and resolution of <135 eV.

Direct comparisons with fossil traces of similar morphology, and produced in the same substrate, known from the literature (Irazoqui and Acosta Hospitaleche 2021) and recognised in the materials under study, were used to distinguish and characterise the morphology of each of the lichen traces described here. The damage occasioned on and into the material was characterised considering the weathering stages proposed by Behrensmeier (1978) and Muñoz and Savanti (1998) and following the fractures superposition on the surface bone (Fernández López 2000). A Dremel Multi-Tool Mini with a diamond cutting wheel was employed to prepare the transversal sections of the fossil bones searching for bioerosive damage not visible on surface, hyphae and/or apothecia. Then, to obtain a clean picture of the traces, some of the fossils were immersed in hydrogen peroxide (H₂O₂) for cleaning, and the organic matter corresponding to the hyphae was carefully removed with cotton.

Lichens associated with the traces were systematically determined according to Øvstedal and Smith (2001) and Olech (2004). The taxonomic results constitute a compilation and review of the species previously found (see García et al. 2020b for further details). The information about the lichen trace type, the growing habit, the kind of substrate, the geographical provenance, the causal agent, and the reference of the contributions in which it was identified is summarised in Table 1.

Results

The substrate in which the traces are developed, represented by fossil bones and teeth, is subject to mechanical and chemical deterioration during burial and subaerial exposition in the field. The first step of the present investigation consisted in the assignment of the materials either to the Sulci type (characterised by clear lines on the surface with associated small pits, Figure 2) or to the Pits type (isolated pits of different sizes affecting the inner portion of the fossil, Figure 3). Additionally, epilithic lichens growing on the bone surface, but not bioeroding the substrate, were identified (see Table 1). After that, the magnitude and extension of the damage was evaluated through the examination of transversal sections of bones severely attacked by endolithic lichens (Figure 4). It allowed the determination of the maximum depth that hyphae of two lichen species extended inside the bone, established in 2.5 mm (García et al. 2021). The lichens species related to the traces were reviewed and listed in Table 1.

Sulci type lichen trace (Figs. 2a-c 4a-b, d-e;)

These traces are characterised by the presence of lines clearer than the rest of the surface produced by the hyphae (Figure 2) and interrupted by small pits corresponding to the apothecia (Figure 4a). The sulci-type lichen traces are usually confused with the fossil traces Sphenoichnia and Corrossichnia, attributed both to plant roots. However, the chemical analysis of the altered surface of the bone corresponding to the trace permits the recognition of products

Table 1. Lichen species associated with fossil remains recognised as erosive agents in previous contributions (see the reference column). The information regarding the growing type and the substrate are the results of our observations, and the type of trace is after the present work.

Lichen species	Growing type	Substrate	Trace	Precedence	Reference
<i>Sarcogyne regularis</i> (*)	Euendolithic	Bone/teeth	Sulci type	Patagonia	Acosta Hospitaleche et al. (2011)
<i>Verrucaria</i> sp.	Epilithic	Bone	Sulci type	Patagonia	Acosta Hospitaleche et al. (2011)
<i>Buellia</i> aff. <i>punctiformis</i>	Chasmoendolithic	Bone	Sulci type	Patagonia	Acosta Hospitaleche et al. (2011)
<i>Aspicilia</i> aff. <i>aquatica</i>	Epilithic	Teeth	Pits type	Antarctica	Acosta Hospitaleche et al. (2011)
<i>Caloplaca</i> sp.	Epilithic	Bone	-	Antarctica	Acosta Hospitaleche et al. (2011)
<i>Sarcogyne privigna</i>	Euendolithic	Bone	Pits type	Antarctica	Gouiric-Cavalli et al. (2019); García et al. (2020b)
<i>Catenarina iomma</i> (**)	Epilithic	Bone	Pits type	Antarctica	Gouiric-Cavalli et al. (2019)
<i>Buellia</i> sp.	Euendolithic	Bone	Pits type	Antarctica	García et al. (2020b)
<i>Lecidea andersonii</i>	Euendolithic/chasmoendolithi	Bone	Pits type	Antarctica	García et al. (2020b, 2021)
<i>Athallia holocarpa</i>	Euendolithic	Bone	Pits type	Antarctica	García et al. (2020b, 2021)
<i>Carbonea vorticosa</i>	Euendolithic/chasmoendolithi	Bone	Pits type	Antarctica	García et al. (2020b)
<i>Polyozosia dispersa</i> (***)	Euendolithic	Bone	Pits type	Antarctica	García et al. (2020b)
<i>Polyozosia mons-nivis</i> (***)	Euendolithic	Bone	Pits type	Antarctica	García et al. (2020b)
<i>Lecanora flotoviana</i>	Euendolithic	Bone	Pits type	Antarctica	García et al. (2020b)
<i>Candelariella aurella</i>	Chasmoendolithic	Bone	Pits type	Antarctica	García et al. (2020b)
<i>Staurothele</i> aff. <i>frustulenta</i>	Epilithic	Bone	Pits type	Antarctica	García et al. (2020b)
<i>Oevstedalia antarctica</i>	Epilithic	Bone	Pits type	Antarctica	García et al. (2020b)

*As *Sarcogyne orbicularis* in Acosta Hospitaleche et al. (2011).

**As *Caloplaca iomma* in Gouiric-Cavalli et al. (2019).

*** As *Myriolecis dispersa* and *M. mons-nivis* in García et al. (2020b).

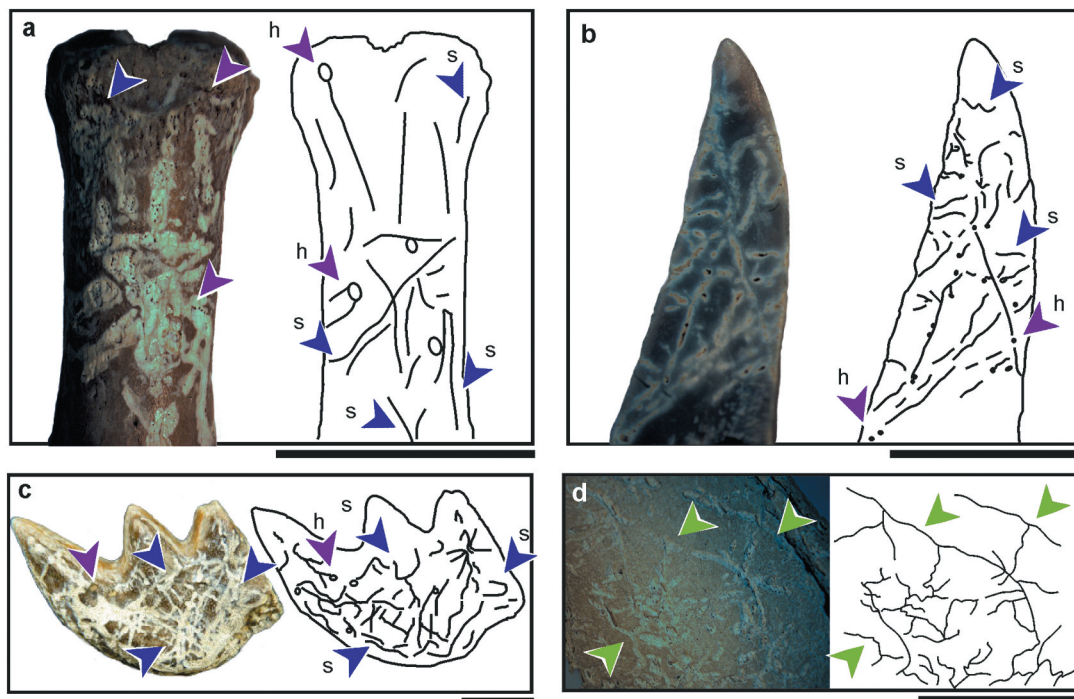


Figure 2. Lichen traces Sulci type from Patagonia and the comparison with root traces. (a) Miocene pedal phalanx of penguin MLP 09-X-15-2, (b) Miocene shark teeth MLP 09-X-15-1 (c) Cretaceous lungfish tooth-plate MACN RN 158, (d) root traces on a mammal bone from an archaeological site collected in the Río Negro Province (Argentina). Abbreviations: s, sulci; h, pits; r, root traces. Scale bar = 10 mm.

excreted as a result of lichen metabolism (Figure 4b-c), that are often lost during aerial exposure of the material in the field (Figure 4e-f).

The substrate

Differences of the substrate hardness and density are important to determine the taphonomic processes suffered for the specimen. The substrates attacked by the lichens described here include the calcium phosphate, as hydroxyapatite ($\text{Ca}_5(\text{PO}_4)_3\text{OH}$) turned into the more stable fluorapatite $\text{Ca}_5(\text{PO}_4)_3\text{F}$. It corresponds to the bone tissues of penguins (Figures 2a, 4a-b), the enamel of shark teeth (Figures 2b, 4d-e), and the enamel and dentine of lungfish tooth plates (Figure 2c).

For example, observations on enamel and enameloid include shark teeth and lungfish tooth plates. The shark teeth MLP 09-X-15-1 (Figure 2b) is preserved without any sign of weathering, and fractures. The general state of the fossil indicates a minimal transportation degree. It only presents longitudinal fissures on the labial surface running from the root to the apex. The lichen traces corroded the enameloid on both lingual and labial sides and continued on the root with a lower intensity. The tooth plate MACN RN 158 (Figure 2c) is well preserved, without any sign of weathering on the enamel, and the lichen traces extend over the entire surface, but concentrate on the margins. The tooth plate MACN RN 157 presents a diagenetic fracture, and no signs of transportation or subaerial exposure prior to final

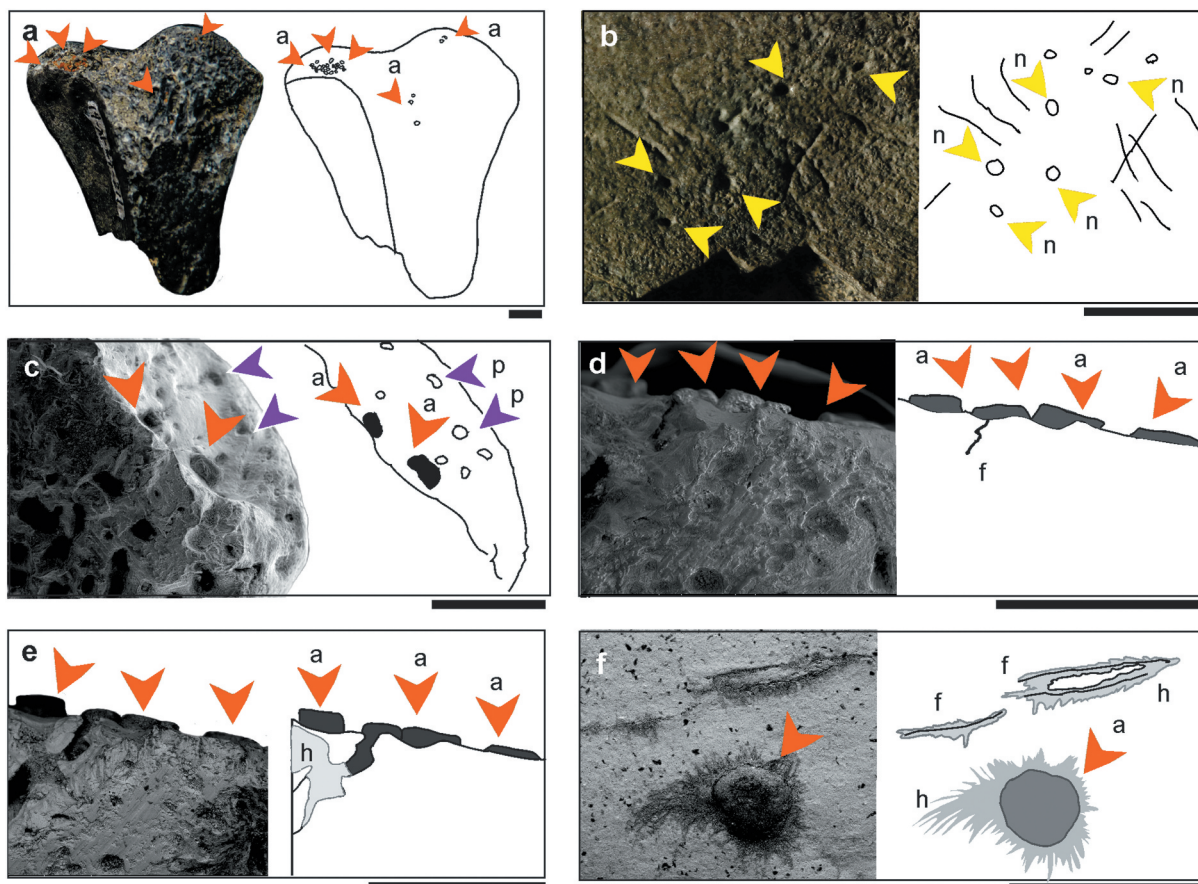


Figure 3. Lichen traces Pits type and the comparison with other traces, all from Antarctica. (a) fossil penguin bone MLP 14-XI-27-211, (b) fossil trace *Nihilichnus nihi lichnus* MLP 12- I-20-307E3, SEM images of fossil penguin bones showing the apothecia within the pits, the fractures associated with the lichen spreading, the empty pits and the hyphae growing within the bones, (c) MLP 08 XI 30 3–12 B indicating the pits (empty pits) and apothecia (*Athallia holocarpa*) still within the fossil, (d) MLP 08 XI 30 3–12 showing the apothecia (*Athallia holocarpa*) within the fossil and a thin fracture associated to the second hole filled by an apothecium, (e) MLP 08 XI 30 3–12 with hyphae growing inside the fossil, connected with the second and third apothecia (*Athallia holocarpa*) which are still immense within the bone, (f) MLP 12-1-20-34 showing two thin surficial fractures colonised by hyphae (darker areas) and an apothecium (*Lecidea andersoni*) surrounded by hyphae growing within the fossil bone. Abbreviations: a, apothecia; f, fractures; h, hyphae; n, *Nihilichnus*; p, pits. Scale bar = 1 mm.

burial. The toot plate is bioeroded on both ventral and dorsal surfaces, although the occlusal area whose dentine is softer than the marginal enamel, is completely covered by lichen traces. These traces constituted a network of grooves spread on the entire surface. Each groove is well demarcated and maintains its width throughout its length. On the marginal enamel, and the attachment surface, the traces are slightly demarcated, and the attack is weaker.

Observations on bones include penguin bones of different part of the skeleton. The tarsometatarsus MLP 69-II-29-4 preserves only the proximal half, the fractured area is rounded probably due to a moderate transportation, and the entire surface, without cracks or fractures, is widely attacked by lichens. The coracoid MLP 20–348 is also fractured, and the proximal half is missing. The surface presents small diagenetic fissures parallel to the main axis and restricted to the sternal end. The periosteal bone has signs of chemical attack as a product of the lichen bioerosion on both main surfaces. Lichen traces present a main line with lateral branching. Like the other bones, the phalanx MLP 09-X-15-2 (Figure 2a) presents the surface almost unaltered, with a moderate weathering and periosteal bone wear.

The causal agent

The lichen species found associated with the Sulci type are detailed below as a Fungi taxonomy.

Division Ascomycota (Berk.) Caval.-Sm.

Class Lecanoromycetes O. E. Erikss and Winka

Order Acarosporales Zahlbr.

Family Acarosporaceae Zahlbr.

Genus *Sarcogyne* Flot.

***Sarcogyne regularis* Körb.**

Order Caliciales Bessey

Family Caliciaceae Chevall.

Genus *Buellia* De Not.

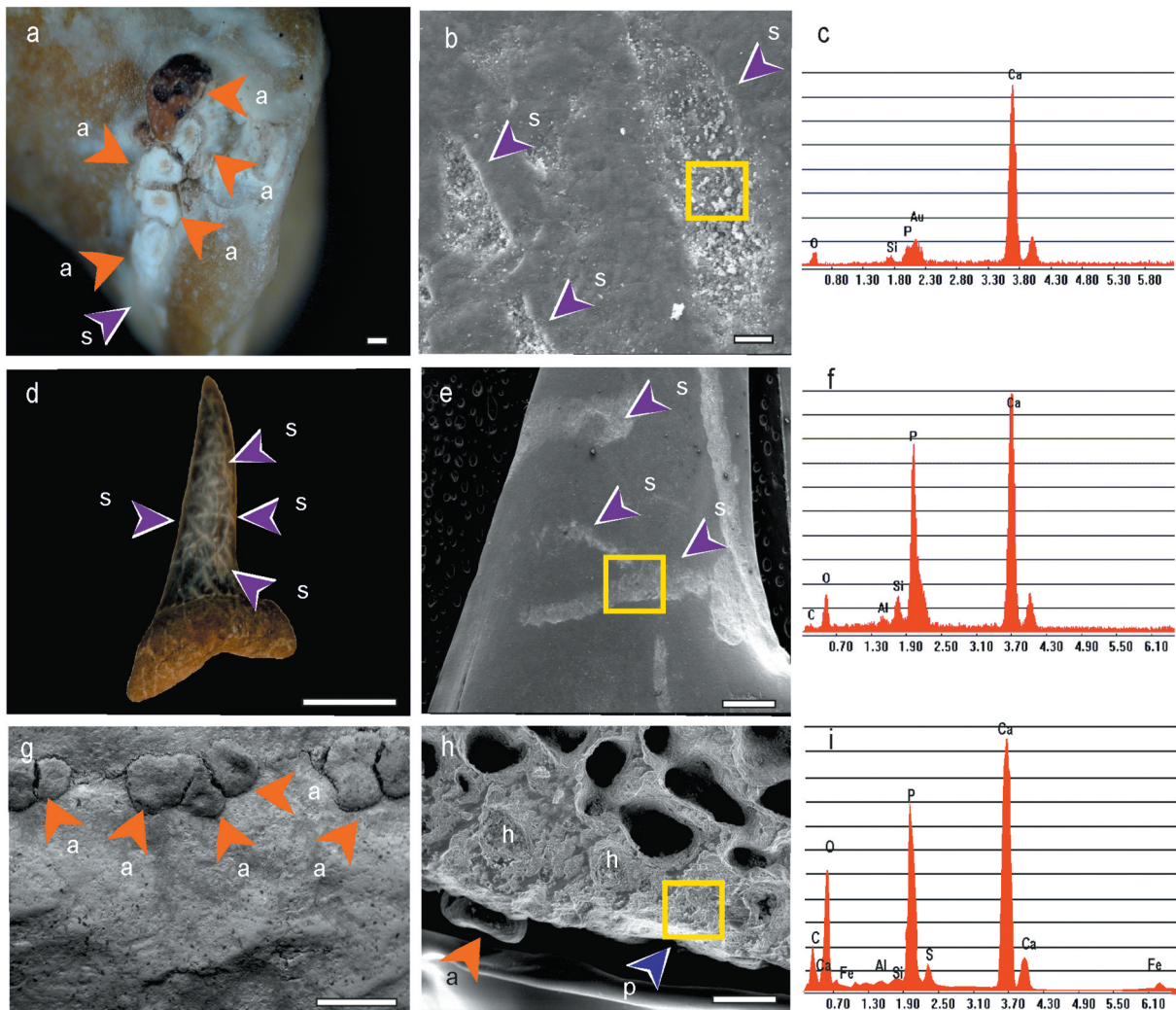


Figure 4. Lichen traces sulci and tip types. (a) Detail of penguin bone (MLP 20–407) showing the apothecia generating traces, (b) MEB image of a penguin bone (MLP 77-XII-22-43) with crystal deposits at the bottom of sulci, (c) EDAX analysis on the area indicated of the penguin fossil trace (b), (d) Shark teeth (MLP 86-II-29-1) with many sulci on the surface, (e) MEB picture showing some traces on the shark teeth, (f) EDAX analysis on the area indicated on the fossil shark teeth (e), (g) Penguin bone (MLP 12-1-20-34) showing many *Lecidea andersonii* apothecia emerging from inside of fracture in the fossil bone, (h) Penguin bone (MLP 08-XI-30-3-12) showing a transverse fracture on the near surface, with hyphae growing inside the fossil bone, (i) EDAX analysis of the area indicated on the fossil bone of (h). Abbreviations: a, apothecia; h, hyphae; p, pit; s, sulci. Scale bar = 20 mm (a), 50 μ m (b), 10 mm (d,e), 1 mm (g,h).

***Buellia* aff. *punctiformis* (DC.) A. Massal.**

Class Eurotiomycetes Erikas and Winka

Order Verrucariales Mattick ex D. Hawksw. and O.E.Erikss.

Family Verrucariaceae Zenker

Genus *Verrucaria* Shrad.

***Verrucaria* sp.**

The environment and climatic conditions

Sulci-type lichen traces were observed in fossils collected in outcrops of the Patagonian region (Argentina). The penguin bones and shark teeth mentioned in the text come from the early Miocene

Gaiman Formation, exposed in the Chubut Province (Patagonia, Argentina), whereas the lungfish tooth plates come from the Late Cretaceous Los Alamitos Formation in the Río Negro Province (Patagonia, Argentina). This area, Patagonia, is a plateau characterised by a climate mainly arid, with a great thermal amplitude and marked seasonality. Although with local variations according to the area and the proximity to the sea; frosts are frequent even sometimes in the summer, rainfalls are scarce, and winds can be very strong. The temperature drops to approximately 12°C, while in summer temperatures of more than 38°C are frequently recorded (<https://www.smn.gob.ar/estadisticas>). Thus, the surficial sediments, and the fossils contained therein, are exposed to hostile conditions.

Pits type lichen traces (Fig. 3)

This pattern consists of isolated holes distributed in the fossil surface of the fossil (Figure 3). Due to the absence of surficial sulci, these traces use to be more unnoticed among other visible traces. These pits (Figure 4h) can be confused with perforations made by many organisms, like vertebrate teeth, worms, sea urchins and

dermestids. However, the presence of apothecia into the pits (Figures 3a,c-f, 4g) and, in some cases, also hyphae extending towards the interior of the fossil remains (Figures 3e-f, 4h), allows the accurate identification of the agent causing the trace and the mechanism of action by which it occurs. In this case, mineral deposits produced by the lichens associated with the traces were not found, and the results of the chemical analysis correspond to the bone composition (Figure 4h-i).

The substrate

Differences in the substrate composition, hardness and/or density could be related with the kind and magnitude of the traces left by the lichen. The following bones, preserved as calcium phosphate, and attacked by endolithic lichens were examined. A penguin pedal phalanx (MLP 13-XI-28-520) presents strong signs of weathering, with longitudinal eyelet fractures subparallel to each other on both surfaces. The presence of lichen is closely related to the fractures, within which the apothecia grow following the lines of fissures and fractures. Another penguin pedal phalanx (MLP 12-XI-1-39-44), strongly deteriorated by the weathering action present cracking and peeling of the periosteal bone. The apothecia are distributed along the entire surface and constitute isolated circular accumulations. The rougher portions, like those within cracks or the eroded surface are the surfaces preferred for lichens growing.

Something similar happens with the penguin coracoid MLP 84-11-1-48 that presents two sets of fractures. The first one, longitudinally developed, corresponds to biostratinomy and is caused by weathering. The second set belongs to the fossil diagenesis and perpendicularly cuts the first set. Apothecia are located within a wedge fracture that reaches the trabecular bone on one of the surfaces.

A fragment of penguin pelvis (MLP 13-XI-28-521) more strongly eroded and without the periosteal bone presents diagenetic fractures perpendicular to the bone tissue fibres. Associated to these fractures, numerous but isolated lichen apothecia are observed. Finally, the coracoid MLP 13-XI-28-522 presents abundant longitudinal fractures, parallel to the bone fibres on one of the surfaces and with apothecia within. On the opposite face, the incipient detachment of the periosteal bone leaves the trabecular tissue partially exposed and colonised by apothecia.

The causal agent

The lichen species found associated with the Pits type are detailed below in a Fungi taxonomy.

Division Ascomycota (Berk.) Caval.-Sm.

Class: Lecanoromycetes O. E. Erikss. and Winka

Order Pertusariales M. Choisy ex D. Hawksw. and O.E. Erikss.

Family Megasporaceae Lumbsch, Feige and K. Schmitz

Genus *Aspicilia* A.Massal.

***Aspicilia* aff. *aquatica* (Fr.) Körb.**

Order Acarosporales Zahlbr.

Family Acarosporaceae Zahlbr.

Genus *Sarcogyne* Flot.

***Sarcogyne privigna* (Ach.) A. Massal.**

Order Teloschistales D. Hawksw. and O.E. Erikss.

Family Teloschistaceae Zahlbr.

Genus *Catenarina* Søchting, Søgaard, Arup, Elvebakk and Elix

***Catenarina iomma* (Olech and Søchting) Søchting and Søgaard**

Genus *Athallia* Arup, Frödén and Søchting

***Athallia holocarpa* (Hoffm.) Arup, Frödén and Søchting**

Order Caliciales Bessey

Family Caliciaceae Chevall.

Genus *Buellia* De Not

***Buellia* sp.**

Order Lecideales Vain.

Family Lecideaceae Chevall.

Genus *Lecidea* Ach.

***Lecidea andersonii* Filson**

Order Lecanorales Nannf.

Family Lecanoraceae Körb.

Genus *Carbonea* (Hertel) Hertel***Carbonea vorticosa* (Flörke) Hertel****Genus *Polyozosia* A. Massal.*****Polyozosia dispersa* (Pers.) S.Y. Kondr., Lökös and Farkas*****Polyozosia mons-nivis* (Darb.) S.Y. Kondr., Lökös and Farkas****Genus *Lecanora* Körb.*****Lecanora flotowiana* Spreng.****Class: Candelariomycetes Voglmayr and Jaklitsch****Order Candelariales Miadl., Lutzoni and Lumbsch****Family Candelariaceae Hakul.****Genus *Candelariella* Müll.Arg.*****Candelariella aurella* (Hoffm.) Zahlbr.****Class Eurotiomycetes Erikas and Winka****Order Verrucariales Mattick ex D.Hawksw. and O.E.Erikss.****Family Verrucariaceae Zenker****Genus *Staurothele* Norman*****Staurothele* aff. *frustulenta* Vain.****Class, order and family *incertae sedis*****Genus *Oevstedalia* Ertz and Diederich*****Oevstedalia antarctica* Ertz and Diederich*****The environment and climatic conditions***

The materials described and figured in this contribution come from the Eocene Submeseta Formation, in Marambio/Seymour Island (West Antarctica). This area has an extreme cold snowy climate, which is characterised by permanent frost and strong winds. Particularly from the sector from which the Pit type lichen traces come, some ice-free areas occur during summer, and some days with extremely high temperatures that exceed the 10°C were recorded. The greatest limitation for the growth of lichens in this area are the winter temperature frequently lower than -30°C and the blizzard (<https://www.smn.gov.ar/estadisticas>).

Discussion and conclusions

After a decade of the first discoveries of the traces certainly generated by lichens on fossil bones and teeth surfaces, two patterns can be clearly distinguished, we named them Sulci and Pits types. The first traces doubtlessly assigned to lichens were identified on early Miocene fossil penguin bones from Patagonia (Argentina) and are characterised by the presence of lines clearer than the rest of the bone surface along which some pits are located. These traces, assigned to the Sulci type, were historically confused with root traces, and even sometimes assigned to Sphenoichnia or Corrossichnia.

Sphenoichnia is characterised by superficial dendritic traces that constitute U-shaped channels with main branches and bifurcations of 0.15 mm to 1 mm width (Andrews 1990; Lyman and Lyman 1994). These traces are produced by rootlets developing on the fossil/sediment interfase after burial and indicate the development of an herbaceous cover during the soil formation (Montalvo 2002: fig 4a,b; Bastourre and Salazar Siciliano 2012). Although the size of Sphenoichnia could be comparable with the smaller lichen traces described here, the patterns left of the surface by roots and hyphae are quite different. Whereas the lichen traces left a pattern with interconnected lines that extend and cover a large area of the fossil surface, Sphenoichnia is characterised by a pattern of more 'crowded' lines that anastomose and overlap each other (Figure 2d). On the contrary, Corrossichnia represents larger traces of irregular outlines and a high degree of corrosion. These traces, produced also by roots, are wider than 1.5 mm width and present scarce or nule bifurcations (Retallack 1983, 1990). Remains of modern roots were found in association (Montalvo 2002) like in the bones we used for comparisons (Figure 2d).

Despite the superficial similarities, the closer examination of our samples reveals unique features like the small pits where the apothecia occur, allowing the correct identification of the lichens as causal agents.

Lichen traces assigned to the Sulci type are easier to observe due to the decolouration of the substrate surface, whether it is periosteal bone, enamel or enameloid, although the differences in the substrate (hardness, density, resistance) would determine the abundance and density of endolithic lichen under the same conditions. It means that the materials easier to degrade would be preferred by lichens that grow and spread on the surface and within the fossil, although it is not a restrictive parameter.

Pits-type lichen traces, only found in Antarctic materials, are more difficult to recognise, and easily misinterpreted as holes generated by boring invertebrates or pits caused by teeth. The dermestid action and even the sea urchin traces are characterised by the presence of a central hole with a moderate depth and radial scratches (Irazoqui and Acosta Hospitaleche 2021) Figures 2 and 3 show fossil traces observed in Antarctic materials from the same localities). When these traces are obscured by weathering, they can be easily confused with the endolithic lichen activity. Something similar happens with the Gastrochaenolitidae *Clavichnus ionasi*, attributed to the feeding activity of annelids or sipunculid worms (Muñiz et al. 2010) and observed in modern whale carcasses (Higgs et al. 2011), but also in Oligocene marine birds (Kiel et al. 2011). Likewise, *Nihilichnus* isp. (Figure 3b) consists of holes produced by vertebrates exclusively on cortical bones (Mikuláš et al. 2006; Rasser et al. 2016) and can be confused with the lichen activity.

However, in our specimens, the presence of apothecia within the pits and the recognition with an appropriate magnification of the clusters of hyphae connected to them (and extending deeper), dispels all doubts and allows its accurate assignment to traces generated by lichens. The morphology of the pits is variable

according to the species, and usually retains small portions of fresh or dehydrated lichens inside. After the evaluation of the taphonomic attributes of the fossils, it is also worth noting that the Pits type constitutes a completely different pattern, and it is not the result of the weathering action on the Sulci type lichen traces. Differences in the weathering degree observed in the periosteal bone and the enamel/enameloid of the specimens here described, support it.

To understand why the identified lichens cause these two different patterns of damage, three variables are discussed here. The lichens specificity, the kind of substratum, and the climate/environmental conditions are considered below.

Three species belonging to three families were found in association with the sulci-type lichen trace, whereas 13 species contained in eight families (plus an *incertae sedis* taxa) were found in relation with the pits type lichen traces (see Table 1). The Acarosporaceae *Sarcogyne*, the Caliciaceae *Buellia*, and a Verrucariaceae *Verrucaria* species are all associated with the sulci-type trace. Besides, the Teloschistaceae (*Caloplaca* and *Catenarina*) develops two endolithic species associated with the pits type trace, but also an epilithic species harmless to fossils in terms of biodeterioration. In fact, saxicolous lichens could modify their locations when the environmental parameters change, and thus the endolithic condition could parallelly appear in different clades.

The substrate, considered in our descriptions, is mainly composed of calcium phosphate and the same for both lichen traces. Although differences in the magnitude and density of the traces were identified according to the resistance of the substrate (bones, teeth, and tooth plates), the architecture of the lichen trace remains invariable.

Finally, and not less important, are the extreme differences in the climatic conditions between Antarctica and Patagonia, given that lichens are climatic sensitive organisms. The extreme conditions of the Antarctic continent, where the temperature usually drops to -30°C represent a strong constraint for different organisms. Although during the austral summer the temperature of Seymour Island or the Antarctic Peninsula reaches could be comparable to those recorded in Southern South America during winter, the low temperatures of the Antarctic winter are unique. Added to this is the absence of sunlight for prolonged periods of time, which also impacts the photosynthetic organism's metabolism. Some authors suggest that the endolithic condition is an adaptation to extreme climates (Friedmann 1982; Kappen et al. 1981; Omelon et al. 2006a, b; Bell 1993; Kidron 2000; Walker and Pace 2007a, 2007b; Wierzchos et al. 2012), so we could think that in extreme climates such as the Antarctic ones, the lichen thallus could be immersed deeper in the bone, while in Patagonia the thallus would be closer to the surface, where the clearer lines are observed.

To conclude, both types of lichen traces occur in bones and teeth and contribute with the fossil deterioration and eventually its destruction. For that reason, lichens must be considered as important destructive agents acting during the taphonomic history of the remains. Because we could not find any evidence of the fossil condition of these traces, a modern age is here assumed in all the examined cases. However, lichens appear in the Neoproterozoic-early Palaeozoic (Nelsen et al. 2020) and the origin of the macrolichen clades has been estimated in 65–35 Mya. These traces may potentially have developed at any time in the taphonomic history of these remains. So far, the Sulci Type was observed in Cretaceous lungfish tooth plates (this work), and in Miocene penguin bones and shark teeth (Acosta Hospitaleche et al. 2011, and this work), whereas the Pits Type was found in Jurassic fish (Gouiric-Cavalli et al. 2019), and Eocene penguin bones (García et al. 2020b; 2021, and this work). The correct interpretation of these traces, and their

differentiation from other structures caused by plants, invertebrates, and vertebrates, establishes the bases for the recognition of these same traces but as fossilised elements, that is, caused by lichens in the geological past.

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Disclosure statement

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Author statements

CAH conceived the idea and all the authors participated in the design of the contribution and the interpretation of the results. CAH, RG and LMP wrote the text, CAH, RG and GM prepared the figures. All the authors approved the final version of the manuscript.

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Appendix 1. Examined specimens

Fossil element	Repository number	Reference
Fossil penguin bones	MLP 20–350, MLP 20–407, MLP 77-XII-22-2, MLP 77-XII-22-43/48 MLP 08-XI-30-3-12, MLP 08-XI-30-28, MLP 12-I-20-30, MLP 12-XI-1-27/28, MLP 13-XI-28-140, MLP 13-XI-28-410, MLP 13-XI-28-442, MLP 13-XI-28-459, MLP 13-XI-28-472, MLP 14-I-10-170, MLP 78-X-26-106, MLP 78-X-26-134/140, MLP 84-II-1-214, MLP 92-II-2-194 MLP 96-I-6-40 MLP 08-XI-30-3-12A, MLP 08-XI-302-3-12B, MLP 12-I-20-34	Acosta Hospitaleche et al. 2011; this paper García et al. 2020a; this paper García et al. 2021; this paper
Fossil shark teeth	MLP 69-II-29-4, MLP 09-X-15-2, MLP 13-XI-28-520, MLP 12-XI-1-39-44, MLP 84–11-1-48, MLP 13-XI-28-521, MLP 11-II-20-21/25, MLP 11-II-20-39, MLP 11-II-20-46, MLP 11-II-20-49, MLP 12-I-20-110, MLP 12-I-20-118, MLP 12-I-20-174, MLP 12-I-20-38, MLP 12-I-2074/72, MLP 12-I-20-113, MLP 12-I-20-28, MLP 12-I-20-58, MLP 12-XI-28-27, MLP 13-XI-28-175, MLP 13-XI-28-243, MLP 13-XI-28-277, MLP 13-XI-28-310, MLP 13-XI-28-438, MLP 14-XI-27-238, MLP 14-XI-27-25, MLP 144 (DVP 13/84), MLP 17 falanges, MLP 28-I-19, MLP 78-X-26-126, MLP 78-X-26-134, MLP 84-II-1-588, MLP 84-II-1-48, MLP 84-II-1-78, MLP 91-II-1-276, MLP 92-II-2_194, MLP 94-III-15-386/388, MLP 94-III-15-478, MLP D8-MTI, MLP IAA 4/94, MLP YAC B, MLP 20–540, MLP 20–545, MLP 20–524, MLP 69-III-29-28, MLP 97-VI-8-1, MLP 20–371, MLP 20–377, MLP 77-XII-22-24, MLP 77-XI-22-28, MLP 77-VII-14-1/14, MLP 69-III-29-23, MLP 20–350, MLP 77-XI-22-30, CNP. PV.1989.10, MLP 71-VII-14-3, MLP 77-XII-22-22/29, MLP 69-III-29-7/26, MLP 20–256, MLP 77-XII-22-6, MLP 77-XII-22-10, MLP 77-XII-22-13, MLP 77-XII-22-17/21.	Acosta Hospitaleche et al. 2011; this paper
Fossil shark teeth	MLP 09-X-15-1	This paper
Fish bones	IAA-Pv 330	Gouiric-Cavalli et al. 2019
Lungfish tooth plates	MACN RN 157; MACN RN 158	This paper