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Lichen Bioerosion on Fossil Vertebrates from the Cenozoic of Patagonia and Antarctica

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Different traces occur on fossil bones and teeth coming from the Early Miocene Gaiman Formation (Patagonia, Argentina). Most traces were attributed to the action of terrestrial and marine predators and scavengers. However, other traces on bones and teeth from this unit and one tooth from the Eocene La Meseta Formation (Antarctica) are attributed to chemical corrosion by lichens in recent times, that is, in a very late diagenetic time. The living lichens and calcium oxalate deposits occurring on the traces and their particular pattern indicates that they were not produced by vegetal roots. The lichens include reproductive structures which allowed a proper determination. A kind of corrosion pattern (Type 1) on bones and teeth from Patagonia is associated to *Sarcogyne orbicularis* Körber, *Verrucaria* sp. Schrad, and *Buellia* aff. *punctiformis* (Hoff.) Massal. The lichen *Aspicilia* aff. *aquatica* produced rounded holes on an Antarctic tooth (Type 2). On the same tooth, the epilithic lichen *Caloplaca* sp. Th. Fries did not leave any kind of mark on the enameloid.

Keywords   Bioerosion, Lichen, Taphonomy, Patagonia, Antarctica

INTRODUCTION

Ichnology, the discipline that deals with traces, includes the study of fossil (palaeoichnology) and modern ones (neoichnology). Both subdisciplines are strongly connected and frequently are inseparable. For example, traces generated by extant organisms have been sometimes misinterpreted as fossil structures. We believe that identifying the causal agent of these traces is as important as the determination of the timing between the trace and the fossilization process of the bones.

Bones and teeth are rather resistant to dissolution in comparison with carbonate shells (Acosta Hospitaleche, 2004; Cione et al., 2010) although they could eventually be destroyed by acidic media (Retallack, 1998). Frequently, the agent that produces the biogenic structure is not identified, although it is possible in some cases. One important agent of bioerosion on bones and pebbles are roots (Binford, 1981; Mikuláš and Žítt, 1999; Mikuláš, 2001). Roots involve anaerobic bacterial activity generating an acidic environment that could corrode bones and rocks (Simpson, 1975; Mikuláš, 2001). Several authors (Andrews, 1990; Lyman, 1994; Montalvo, 2002; Valli, 2004, and references cited therein) have interpreted these traces as fossils contemporary to the early diagenesis of the remains. We have observed frequently roots of living plant covering fossil bones in many archaeological sites and generating typical traces. Mikuláš (2001) described many traces on fossil bones as the result of roots, but he stressed that he had not seen them in action.

The more frequently used arrangement is the ethologic classification proposed by Seilacher (1953, 1964). This classification is based on the idea that each trace corresponds to a different type of behavior. In addition to the classic five categories of Seilacher, several other ethological trace groups have been recognized (Bromley, 1996). Some have a tentative status. More recently, Mikuláš (1999a, b) separated the traces created by metazoans from those of metaphytan origin and established three kinds of vegetal traces. Mikuláš (1999a, b) proposed the term "Cecidoichnia" for those generated by the interaction between a plant and another organism that can be also a plant, a fungus, a moneran, or an animal, leaving a gall on a xylic substrate. The other two classes are marks left by the putative action of roots: "Sphenoichnia" for the bioturbation that reflects root growth spreading down into a soft sediment and "Corrosichnia" for rhizocretions arising because of the corrosive action of plant roots (Mikuláš, 1999a, b). Although still in a tentative status, both terms began to be used by the
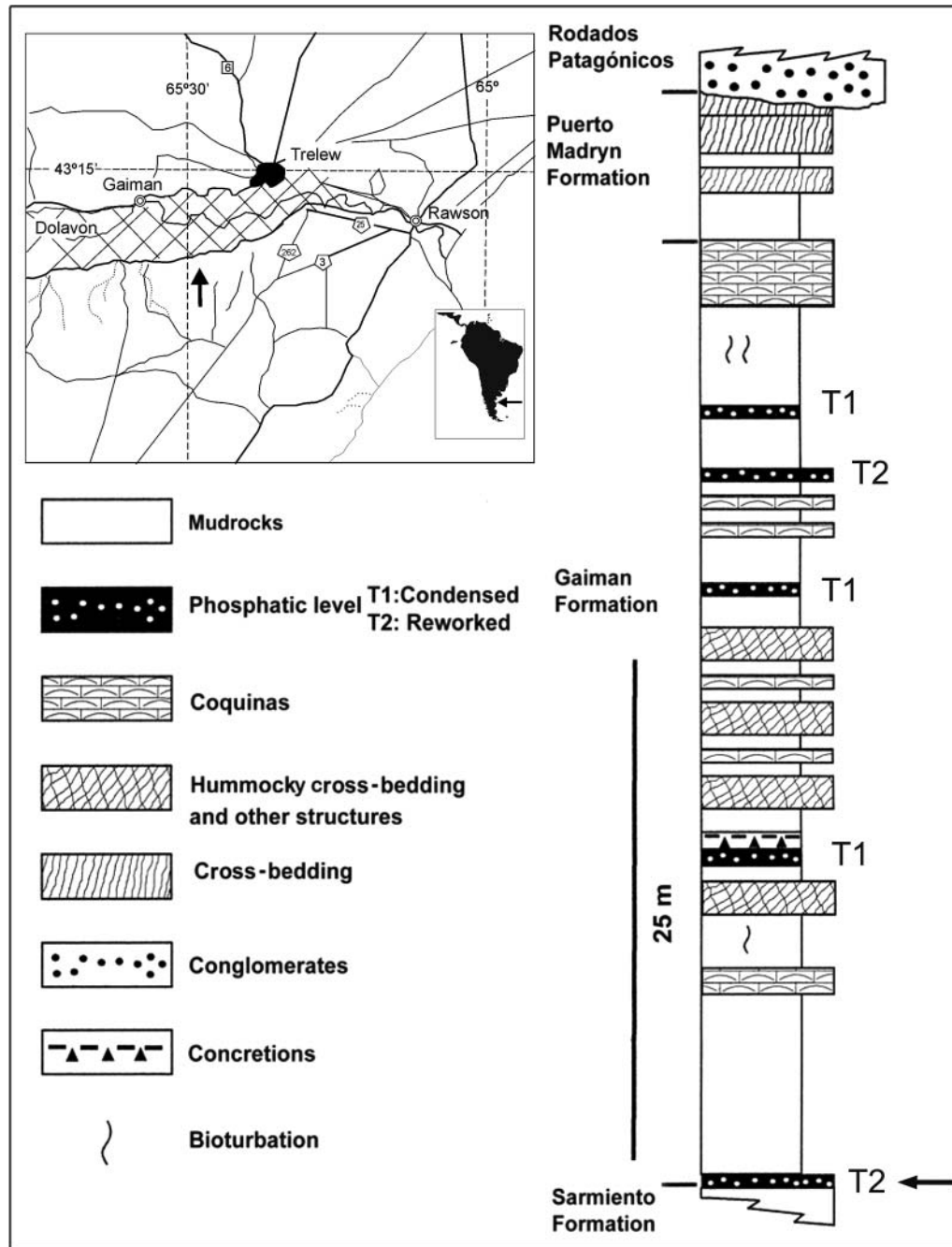
FIG. 1. Map and stratigraphic column of the Trelew-Gaiman area showing the fossil location. The arrow indicates the Bryn Gwyn fossil locality, material under study come from the lower levels.

scientific community not only for descriptive purposes but also as evidence of fossil plant communities.

During an investigation dealing with traces made by predators and scavengers on Miocene penguin bones of Patagonia, we observed other traces similar to those "root marks" described and figured by Mikuláš (2001). However, we found living lichens in these traces on penguin bones and shark teeth. The goal of this paper is to analyze the genesis of the marks of

Patagonia and some of Antarctica discussing their taphonomical context.

MATERIALS AND METHODS

The material under analysis came from the Early Miocene Gaiman Formation (Scasso and Castro, 1999; Cione and Azpelicueta, 2002; Cione and Báez, 2007), cropping out in the
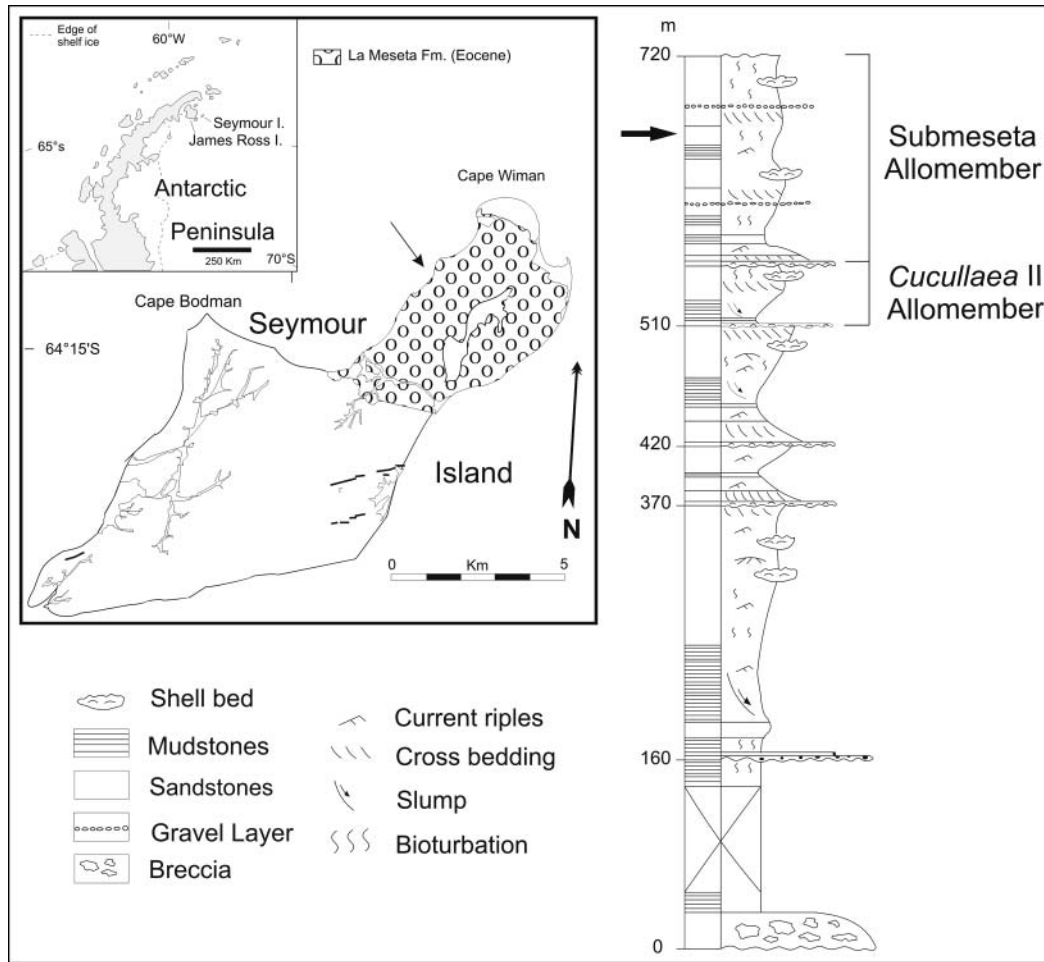
FIG. 2. Map and stratigraphic column of Seymour Island (Peninsula Antarctica). The arrow indicates the fossil locality.

southern bluff of the lower Río Chubut River, Chubut, Argentina (Fig. 1) and the Middle-Late Eocene La Meseta Formation (Marenssi et al., 1998), Seymour Island, Peninsula Antarctica (Fig. 2). All the remains are housed in the División Paleontología de Vertebrados, Museo de La Plata (MLP), Ciudad de La Plata, Argentina.

The material was studied with a stereoscopic microscope Arcano ZTX Zoom (10-40X), and those remains with traces were analyzed with SEM Jeol JS M-6360 LV and Philips SEM 505. A chemical microanalysis with electron probe EDAX DX Prime 10 was done to compare the composition of the materials found on the traces and that of the unaltered surface of bones and teeth.

The reproductive structures were mounted in glycerine gelatine. The asci and ascosporis were measured (25 spores for each sample) using an optic microscope Nikon Eclipse E 200 (1000X) and a camera Nikon Coolpix S10.

Lichens were identified using the systematics classification of Calvelo and Liberatore (2002).

RESULTS

Two different kinds of marks produced by endolithic lichens were identified. Type 1 was recognized on penguin bones (Fig. 3A) and shark teeth (Fig. 3B) from the Gaiman Formation (Early Miocene). Individual marks are grooves lighter than surrounding bone or enameloid surfaces. Marks are unbranched, linear, more or less straight, different in length, intercrossed at random, and without an anastomosing pattern. The hyporelief is constant in width and depth along the trace. In some remains, due to a large concentration, the individualization of each trace is not possible. Small pits are distributed along the traces (Fig. 3C) corresponding to the position of the apothecia (Fig. 3D).

The profiles of EDAX from the bottom of traces on shark teeth (Fig. 4A) revealed high peaks of calcium, phosphorus, and oxygen and minor peaks of carbon, silicium, and aluminium (Fig. 4C). The EDAX profiles from the rest of the enameloid showed high peaks of calcium, phosphorus, and oxygen only (Fig. 4E).
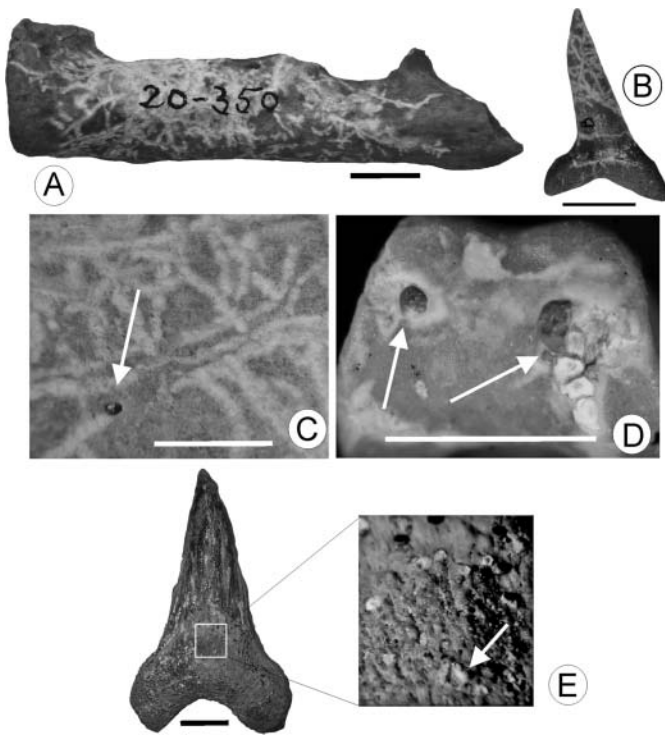
FIG. 3. Type 1 lichen mark from Gaiman Formation (Early Miocene), Argentina: (A) Fossil penguin bone (MLP 20-350), (B) Shark teeth (MLP MLP 86-II-29-2), (C) Fossil penguin bone (MLP 77-XII-22-2) in detail with small pits corresponding to the location of the apothecia, (D) Penguin bone (MLP 20-407) in detail showing the apothecia generating the mark. Type 2 lichen mark: (E) Shark teeth from La Meseta Formation (Late Eocene), Peninsula Antartica, with a detail showing the isolated holes corresponding to the apothecia. Bar: 10 mm in A, B and E; 5 mm in C and D.

The profiles of EDAX from the bottom of traces on bone (Fig. 4B) revealed high peaks of calcium and minor of oxygen, silicium, and phosphorus (Fig. 4D). The EDAX profiles from the rest of the periostial bone showed high peaks of calcium and phosphorus and minor of oxygen, silicium, magnesium, sodium, and aluminum (Fig. 4F).

The occurrence of carbon and the high rate of calcium and oxygen on the trace should indicate the presence of calcium oxalate attributed to the lichen action. The rest of the chemical elements detected on the unaltered surfaces of the enameloid and the periostial bone should correspond to the original calcium phosphate. Other elements correspond to the sedimentary matrix.

Type 2 was recognized only on Antarctic shark teeth. Isolated pits (Fig. 3E) belonging to the apothecia are distributed on the enameloid. Holes are small, subspherical, and slightly concave. No linear traces are developed.

DISCUSSION

Structures studied herein differ from the mechanical predation and scavenging marks that are common on the penguin bones from Gaiman Formation and that were caused by fishes

and mammals (see Cione et al., 2010) and appear clearly of biochemical origin. These predation traces do not occur in the fossil remains of La Meseta Formation.

Formerly, traces similar to Type 1 had been interpreted as to the action of vascular plants roots (e.g., Simpson, 1975; Mikuláš, 2001). The *Sphenoichnia* type was previously interpreted as the marks produced by rootlets growing on the fossil-sediment interface after burial and were interpreted as indicators of an herbaceous cover on the soil. These traces were supposed to have been generated in the early stages of the burial process and were used as a helpful tool in the identification of paleosols (see Montalvo, 2002). *Corrosichnia* traces were recognized by the corrosion produced in the exposed surface of the periostial bone which produces clearly defined lines. According to Montalvo (2002), this dissolution suggests that root growth has affected the bones only in recent times, during late burial stages.

Previous authors working with fossils (Simpson, 1975; Mikuláš, 2001; Montalvo, 2002) did not observe the actual association of roots with the marked substrate. From a morphological point of view, the initial pattern of root damage is usually a reticulate network of shallow grooves. Our observations of actual root marking bones in archaeological sites show that they are not only reticulated but also branched and more sinuous than our Patagonian material (see also Lyman, 1994; Valli, 2004; White and Folkens, 2005). Traces of the Type 2 were also described on rocks (Chen and Blume, 2002).

Lichens are one of the main biodegradators of rocks and bones along with fungi and bacteria. They contribute with secondary minerals to substrate (Arocena et al., 2007). Among the most frequent minerals of such origin are whewellite ($CaC_2O_4 + H_2O$), weddellite ($CaC_2O_4 + 2H_2O$), and calcium oxalate (CaC_2O_4). These compounds are the product of the neutralization of the oxalic acid secreted by the fungal part of the lichen with the Ca^{++} liberated from the substrate (Arocena et al., 2007), in this case fossil bones and teeth.

The presence of apothecia inside the structures suggests a bioerosive process generated by the thallus of lichen in the surface. The analyses of the traces with SEM and EDAX confirmed the chemical action and the absence of it on the nearby bone (Fig. 4B, MLP 77-XII-22-43) and tooth surface (Fig. 4A, MLP 86-II-29-1).

We identified the lichen species *Caloplaca* sp. and *Aspicilia* aff. *aquatica* associated to the Antarctic material, and *Sarcogyne orbicularis*, *Verrucaria*, and *Buellia* aff. *punctiformis* to the Patagonian material (see Appendix 1 for systematic details). These taxa inhabit the study areas. We found that the epilithic *Caloplaca* does not produce any trace, while *Aspicilia* aff. *aquatica* generates rounded holes (see Type 2 above). The endolithic *Sarcogyne orbicularis*, *Verrucaria* and *Buellia* aff. *punctiformis* produce clear lines on the surface (see Type 1 above).
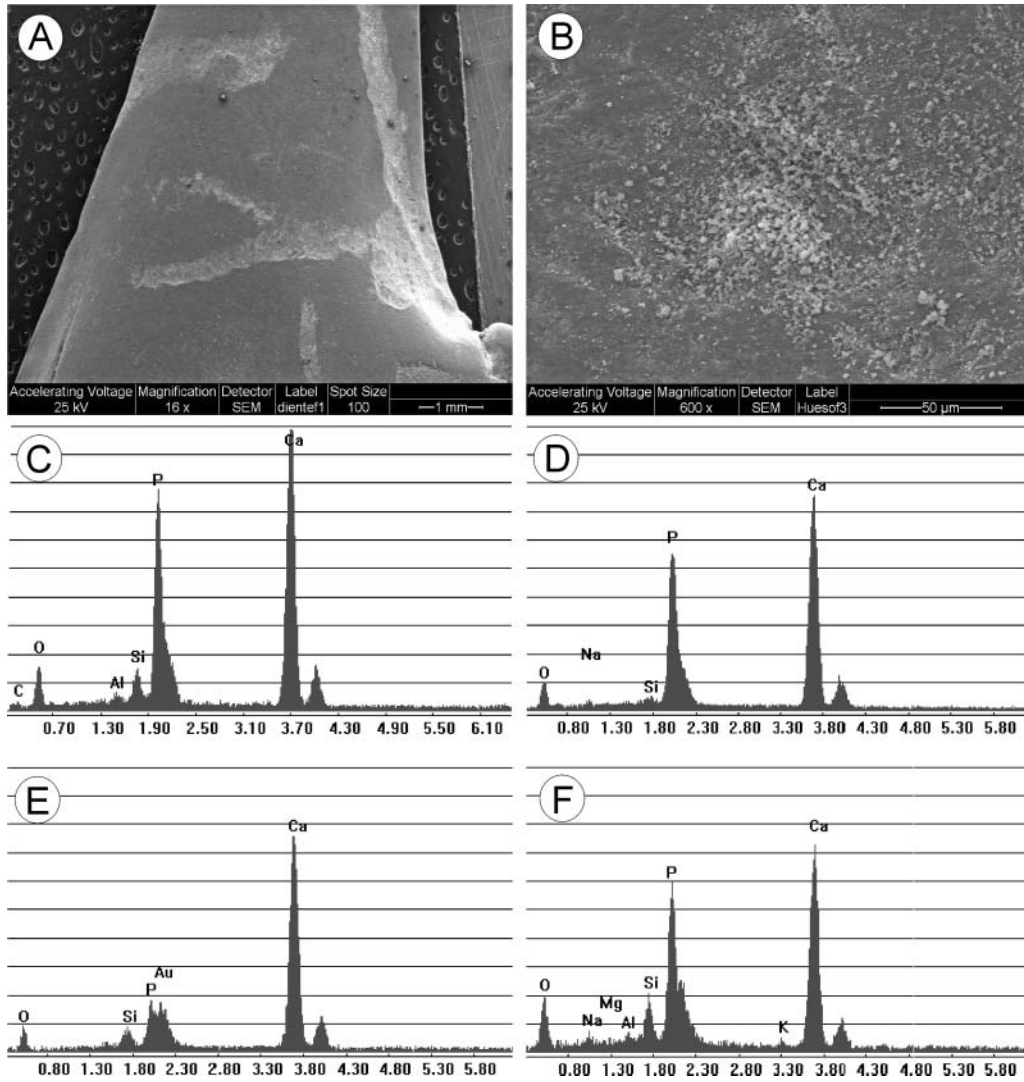
FIG. 4. Profiles of the Edax analysis of fossils coming from Gaiman Formation (Early Miocene), Argentina: (A) Shark teeth (MLP MLP 86-II-29-1), (C) from the bottom of the trace, (E) from the rest of the enameloid; (B) Penguin bone (MLP 77-XII-22-43), (D) from the bottom of the trace, (F) from the rest of the surface.

The effects of lichens on their mineral substrates can be attributed to both physical and chemical processes. The physical effects are reflected by the mechanical disruption of rocks caused by hyphal penetration, expansion, and contraction of lichen thallus, swelling action of the organic and inorganic salts originating from lichen activity. The secretion of carbon dioxide (product of the thallus) which mixed with water forms carbonic acid that allows the corrosive effect of fungal hyphae of lichens penetrating the rock (e.g., Syers and Iskander, 1973). In addition, lichens can also damage the substrate with their acid secretions: carbon dioxide, lichenic acids, and oxalic acid (Lisci et al., 2003) can effectively dissolve minerals and chelate metallic cations. The oxalic acid reacts with the mineral substrate forming different oxalates, particularly calcium oxalate, which is by far the most common (Adamo and Violante, 2000; Lisci et al., 2003). The oxalates tend to accumulate in the thallus or the lichen-rock interface due to its low solubility, forming a patina, or a crystalline surface (Jackson, 1981).

As a result of the weathering induced by lichens, many rock-forming minerals exhibit extensive surface corrosion. The precipitation of iron oxides and amorphous alumino-silica gels, the neoformation of crystalline metal oxalates, and secondary clay minerals have been frequently identified in a variety of rocks colonized by lichens in nature (Chen et al., 2000). Studies include granite (Prieto et al., 1999) and marble substrates (Videla et al., 2003; Guidobaldi et al., 1984).
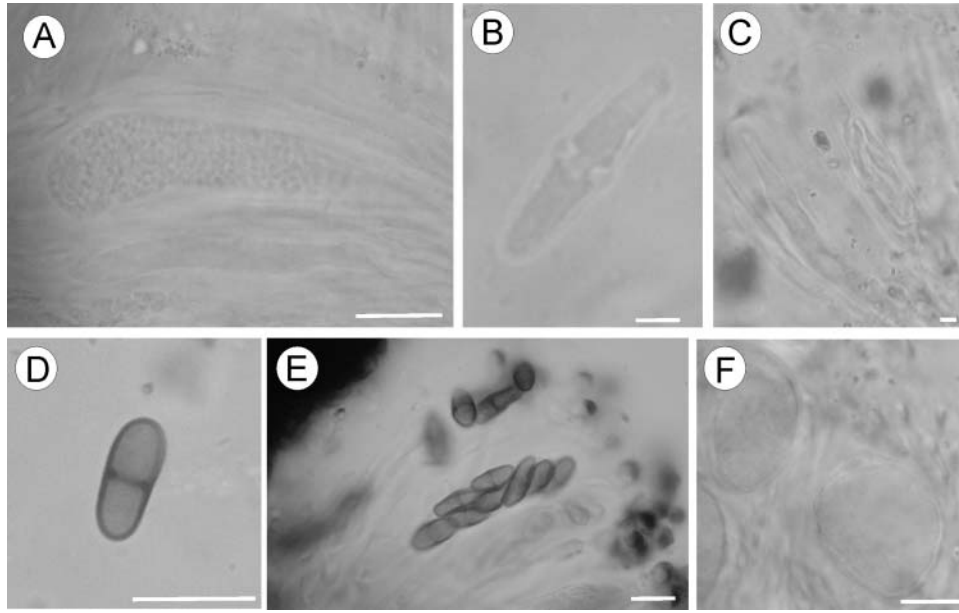
FIG. 5.   Lichen identified on the fossil under study: (A) Asci with spores of *Sarcogyne orbicularis* (Bar: 5 μm); (B–C) *Caloplaca* sp: (B) Spores, (C) Asci with spores (Bar: 12 μm); (D–E) *Buellia* aff. *punctiformis*: (D) Spores, (E) Asci with spores (Bar: 5 μm); (F) Spores of *Verrucaria* sp. (Bar: 5 μm).

CONCLUSIONS

As far as we know, this is the first description of lichen traces on bones and teeth. Herein we deal with extant environments when endolithic lichens are corroding bones. We found that living lichens presently form linear traces and pits on bones and teeth. Consequently, traces were generated after the exhumation of fossil material, acting as a bioclast during a time long enough to enable the colonization. It implies an exposition period of the remains equivalent at least to the necessary time to erode the substrate, plus the times required for the development of the populations of endolithic lichens. Moreover, if these remains were reburied for a new depositional event, the time span would be reflected by the presence of the lichen marks.

The thorough analysis on penguin bones and shark teeth, and the results obtained by EDAX allowed us to reach the following conclusions. Two kinds of structures occurred during late diagenesis and are not related to the presence of roots. Each type was occasioned by different lichen genera.

Type 1 is represented by clear and unbranched lines with small pits along them, generated by the lichen species *Sarcogyne orbicularis*, *Verrucaria*, and *Buellia* aff. *punctiformis.* Type 2 corresponds to isolated and subrounded holes made by *Aspicilia* aff. *aquatica*, lacking any linear traces.

The presence of these biogenic structures is related to taphonomical processes involving bones and teeth. The settlement of the endolithic lichen communities here identified is related to the availability of calcium resulting from the weathering of bioclastic calcium phosphate.

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APPENDIX 1

Fungi Systematics

Lichens are fungi (Ascomycetes or seldom Basidiomycetes) living in symbiosis with photosynthesizing organisms (cyanobacteria or green algae) (Hale, 1974). The fungus (mycobiont) and the alga (phycobiont) form the thallus which grows where the alga and fungus could not survive alone successfully. In this way, lichens successfully colonize a wide spectrum of substrates, such as plants, soils, and even glass (Richardson, 2001; Lisci et al., 2003). The reproductive structures are dispersed in the atmosphere and fall into any cavities that retain water, and where new growth may arise (Garty, 1992). On porous surfaces, the lichens establishment is favored, colonization is easier, and the endolithic and epilithic forms transform the substrates causing biocorrosion.

Division Ascomycota
Class Lecanoromycetes
Subclass Acarosporomycetidae
Order Acarosporales
Family Acarosporaceae
Genus *Sarcogyne* Flotow
Species *Sarcogyne orbicularis* Körber
(Fig. 5A)

Referred materials: On the penguin bones: MLP 20-348, MLP 20-377, MLP 20-387, MLP 77-XII-22-7, MLP 77-XII-22-10, MLP 20-281, coracoids distal end MLP 71-VII-14-2, , MLP 20-350, MLP 77-XII-22-50, MLP 77-XII-22-6.

Description: The thallus is endolithic, white-grayish. Apothecia are superficial, black and pruinose, with margin lecideine. The asci are clavate, 73-81 $\times$ 10-18 μm. The ascospores are numerous, unicellular, colorless, rounded-elliptic, small and 4 $\times$ 2 μm.

Remarks: Widely distributed, cosmopolitan genus with only a few species. The species *S. orbicularis* is the only one known in Argentina (Calvelo and Liberatore, 2002) which grows on calcareous rock but also artificial substrates such as cement

mortars. It prefers vertical-subvertical surfaces, exposed to the sun and rain.

Subclass Lecanoromycetidae
Order Lecanoralesterv
Family Physciaceae
Genus *Buellia* De Notaris
Buellia aff. *punctiformis* (Hoff.) Massal.
(Figs. 5 D–E)

Referred material: Penguin bone MLP 20-524.

Description: Endolithic thallus, immersed into the lamellar bone. Apothecia erumpent, disciform, black, lecidein margin. Subhymenium brown. Hymenium = 120 mm, Paraphysises unbranched, brown with flared ends. The ascospores are 11–13 × 4–6 μm. The apothecia leave circular marks on the substrate.

Remarks: This species was mentioned in Argentina by Cengia Sambo (1930) as *B. myriocarpa* (D.C.) Mudd., and found in Rawson (Chubut Province, Argentina) on bushes and on weathered vertebrate bones.

Subclass Ostropomycetidae
Order Pertusariales
Family Megasporaceae
Genus Aspicilia Masal
Aspicilia aff. *aquatica* (Fr.) Körb

Referred material: Shark tooth MLP 88-I-1-192.

Description: Thallus crustose areolate, whitish grey; geometrical areolaof 1 mm. diam. Apothecia half immerse in the center of the areolae, with a polygona shape, disc flat, dark epithecium. Asci claviform, spores colorless, subspheric to spheric, 10–12 μm diam. TLC: no substances detected.

Remarks: This lichen grow on wet schistose rocks. Its distribution is bipolar, including North America, north of Europe, and Antarctica, where it is found on the Shetland Islands and Orcadas del Sur (Ovstedal and Lewis Smith, 2001).

Subclass Lecanoromycetidae
Order Teloschistales
Family Teloschistaceae
Genus *Caloplaca* Fries
(Figs. 5 B–C)

Referred material: On the penguin bone MLP 96-I-6-13 (penguin synsacrum and thoracic vertebrae) from the late Eocene of Antarctica) and the shark tooth MLP 88-I-1-192.

Description: The thallus is not visible, endolithic. The apothecial are superficial, yellow orange, with margin lecanorine. Disc yellow orange are flat to slightly convex. The asci are clavate, apical apparatous J+, octosporous, 46–60 × 8–14 μm. Ascospores are ellipsoid, polardiblastic, colorless, 18–24 × 4–8 μm.

Remarks: Caloplaca is a widespread, cosmopolitan genus with 450 species and 56 present in Argentina (Calvelo and Liberatore, 2002). Their requirements vary greatly, and among them are nitrophilous species, photophilous species, but also sciophilous forms; some are xerophitic while others depend more on rain and humidity.

Twenty-two species are listed from the Antarctic region, but about ten more, probably undescribed species, are present there. About one-third of the species in the Antarctic region are bipolar or widespread in cold regions; these include mainly terricolous and muscicolous species, and none is marine (SøChting and Olech, 1995).

Class Eurotiomycetes
Order Verrucariales
Family Verrucariaceae
Genus *Verrucaria Schrader*
Verrucaria sp. Schrader
(Fig. 5F)

Referred material: Penguin bone MLP 97-VI-3-1.

Description: Thallus crustose areolate 1 mm. de thick; grey; areolae geometric up to 1 mm wide; perithecia emerging, wide ostíolus; light colored involucrellum, poorly developed, perithecial wall and subhymenium colorless. Paraphyses simple; without endohymenial algae, claviforme asci, 4–8 globose ascospores 10–12 μm in diameter.

Remarks: Some especies of *Verrucaria* grow in lake and sea environments, but others live on continental rocks (Nimis et al., 1987; Nimis et al., 1996). In Argentina there are 12 species (Grassi, 1950; Calvelo and Liberatore, 1987).