



# Richness of lichens growing on Eocene fossil penguin remains from Antarctica

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## Abstract

Antarctica presents one of the most severe environmental conditions for life. Under these circumstances, cryptogams are the dominant photosynthetic organisms, among which we find a great richness of lichens. In Antarctic environments, lichens can grow on rocks or in this case on fossil remains, among the few available substrates. In the present contribution, we examined all fossil penguins of the Antarctic collection of the Museo de La Plata, as a significant sample of fossil vertebrates. The selected materials here described come from the Submeseta Formation (Eocene) on Seymour/Marambio Island, located northeast of the Antarctic Peninsula on the Weddell Sea. Given the scarcity of lichenological studies on this island, and the results presented here add significantly to our knowledge of the lichen species that occur there with the recognition of 11 taxa with a crustose morphology (epilithic and endolithic), the sampling of lichens growing on fossil bones acquired an evident importance.

**Keywords** Fossil penguin bones · Endolithic · Bioerosion · Taphonomy · Fungi systematic · Seymour/Marambio Island

## Introduction

The Antarctic regions present some of the most severe environmental conditions endured by plant life, involving habitats characterized by intense cold, physiological drought, and seasonal limitation of insolation. Antarctica presents a series of terrestrial ecosystems characterized by a greatly

reduced flora and fauna, which are isolated from other systems by extensive ocean barriers (Lee et al. 2017).

Terrestrial ecosystems are restricted to the 4% of ice-free lands during the summer months (Rudolph 1977, see also Lee et al. 2017). The severe weather conditions make Antarctica one of the harshest environments on Earth for the development of higher plants (Green et al. 2007). These Antarctic ecosystems are unique since cryptogamic plants and invertebrate animals are the most abundant groups; and among them, lichens (lichenized fungi) have a dominant role (Lindsay 1978; Øvstedal and Smith 2001). Crustose, squamulose, foliose, and fruticose thalli forms, are common and widespread, constituting communities included in two subformations: the crustose lichen subformation and the fruticose lichen and moss cushion subformation (Smith and Gimingham 1976).

In Antarctica, and many other places, fossil remains act as a substrate and are susceptible to lichen colonization. As a consequence, lichen activity damages the structure of fossils that lose material and become more fragile. In this context of biodeterioration, some remarkable studies have been carried out (Fernández-Jalvo et al. 2002; Thackeray et al. 2005; Acosta Hospitaleche et al. 2011; Gouric-Cavalli et al. 2018; Saitta et al. 2019). However, in a place, like Seymour Island, where only two lichen species are reported,

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*Gyalolechia desertorum* (Tomin) Søchting, Frödén & Arup and *Myriolecis mons-nivis* Darb. (Øvstedal and Smith 2001), a lot of work from a lichenological perspective is still necessary. In the present contribution, we examined all fossil penguins housed in the Antarctic collection of the Museo de La Plata, as a significant sample of fossil vertebrates of Seymour Island (Antarctica) looking for traces of lichens.

## Materials and methods

### Materials

Lichen species described here were obtained from Eocene penguin bones permanently housed in the collections of the División Paleontología Vertebrados (DPV) of the Museo de La Plata (MLP), La Plata (Argentina). From the approximately 10,000 bones examined, a total of 120 specimens were selected to sample.

### Methods

We examined 120 fossil remains looking for the better preserved lichen thalli. Lichens were observed under stereoscopic microscope Arcano Ztx and light Olympus BH2, and pictures were taken with a stereoscopic microscope ZEISS SteREO Discovery.V20.

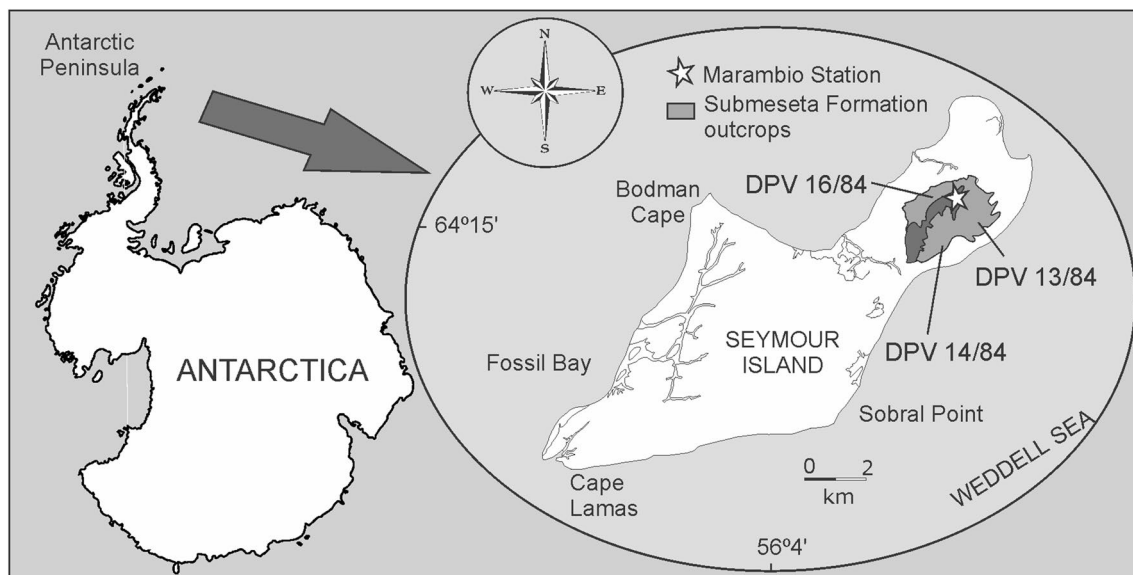
Morphological and anatomical studies include freehand cuts of the reproductive structures, in order to observe ascus and spores. The usual histochemical reactions were performed: K (KOH 10%), C (NaClO), and I (KI), which indicates the amyloid reactions of the asci and hamathecium.

For the identification of the species, the following bibliography was used: Castello and Nimis (1994), Seppelt et al. (1998), Øvstedal and Smith (2001), Ertz and Diederich (2004), Olech (2004), Sliwa (2007), Nash et al. (2007), and Arup (2009). The scientific names were updated according to the online databases of Index fungorum (<https://www.indexfungorum.org/>) and Mycobank (<https://www.mycobank.org/>).

### Study area

Materials come from Seymour/Marambio Island (Fig. 1), a small island located northeast of the Antarctic Peninsula on the Weddell Sea, West Antarctica. The entire island is a plateau of fourteen kilometers in length and eight kilometers in width, where the Argentinian Marambio Station has been established since 1969. The continued presence of this Station plus the weather conditions of the island, that is, ice free during the summer season, encouraged an intense scientific field work in the area. As a result, and after numerous and almost uninterrupted paleontological field works since 1977, the fossil vertebrate collection from Antarctica housed in the Museo de La Plata has become the largest in the whole world. It includes more than 20,000 fossil vertebrates; among them, bones were revised.

Penguin bones are very frequent among fossils from Seymour Island and constitute the most abundant vertebrates together with shark teeth. Bones examined here, all assigned to fossil penguins, come from different sites of the island located from 50 to 200 m.a.s.l. around the Marambio Station (Fig. 1). Most of the materials were collected in the



**Fig. 1** Map showing the collection sites in Seymour/Marambio Island, located at the east of the Antarctic Peninsula (West Antarctica)

locality (DPV) 13/84, a famous fossil site of Seymour Island initially explored by Otto Nordenskjöld (Wiman 1905), and subsequently by numerous paleontologists (see Acosta Hospitaleche et al. 2017, 2019). Bartonian levels of the Submeseta II Allomember of the Submeseta Formation crop out on this site and also in the equivalent locality DPV 14/84. In DPV 16/84, sediments are younger and correspond to the Priabonian Submeseta Allomember III of the Submeseta Formation.

## Results

In general terms, we observed that taphonomic damage reaches all the remains collected there. As a consequence, most of them are disarticulated and fragmented, with evidence of fish predation and scavenging, invertebrate feeding activity, encrusters, and bioerosion occasioned by lichen activity, among other traces.

After the examination of nearly 10,000 penguin bones, and given that our main objective was the systematic analysis of the lichens associated with these fossils, we selected the more complete and fertile lichen specimens, discarding those badly preserved and already sampled. A total of 10 species and a specimen that could only be identified at genus level were found. All species belong to the Division Ascomycota and Subdivision Pezizomycotina. A description of each species, the site of collection, distribution, and ecological data are provided below in the systematic section.

## Fungi systematics

Division Ascomycota R.H. Whittaker 1959

Subdivision Pezizomycotina O.E. Erikss. & Winka 1997

Class Lecanoromycetes O.E. Erikss. & Winka 1997

Subclass Lecanoromycetidae P.M. Kirk, P.F. Cannon, J.C.

David & Stalpers ex Miadl., Lutzoni & Lumbsch 2007

Order Caliciales Bessey 1907

Family Caliciaceae Chevall. 1826

Genus *Buellia* sp. De Not., 1846

*Observed material* MLP 78-X-26-134.

*Provenance* Locality DPV 13/84.

*Description* Thallus inconspicuous. Apothecia to 1 mm diameter, disc black, pruinose. Thalline excipulum grey. Asci 8-spored. Spores brown septate ellipsoid  $10 \times 3 \mu\text{m}$ . Spot tests: all negative. The scarcity of the collected material prevents the species identification.

Order Lecideales Vain. 1934

Family Lecideaceae Chevall. 1826

Genus *Lecidea* Ach. 1803

*Lecidea andersonii* Filson 1974 (Fig. 2a)

*Observed material* MLP 08-XI-30-28, MLP 13-XI-28-140, and MLP 13-XI-28-410.

*Provenance* MLP 13-XI-28-140 from DPV 13/84, MLP 08-XI-30-28, and MLP 13-XI-28-410 from Locality DPV 14/84.

*Description* Thallus endolithic or as small grey areole, to 1 cm diam. Hyphae of endolithic thallus with scabrous surface, c. 2 cm. Black apothecia, often grouped cauliflower-like together, to 1.5 mm diameter, proper margin thin, distinct, often crenulated. Hymenium 40–50  $\mu\text{m}$  height, colourless, except by the uppermost part which is blue-green to brownish-green, composed short, rectangular, radiating hyphae 2–3  $\mu\text{m}$  across, with undulating walls. Exiple and epithecium N + red. Paraphyses end cell only slightly enlarged to 2.5  $\mu\text{m}$  diam. Spores ellipsoid, hyaline to  $9\text{--}10 \times 3\text{--}5 \mu\text{m}$ .

*Ecology and distribution* bipolar species. In Antarctica: distributed in Southern Antarctic Peninsula and continental Antarctica. On rocks.

Order Teloschistales D. Hawksw. & O.E. Erikss. 1986

Family Teloschistaceae Zahlbr. 1898

Genus *Athallia* Arup, Frödén & Søchting 2013

*Athallia holocarpa* (Hoffm.) Arup, Frödén and Søchting 2013 (Fig. 2b)

*Observed material* MLP 08-XI-30-28, MLP 12-I-20-30, MLP 92-II-2-194, MLP 13-XI-28-140, MLP 78-X-26-106, MLP 13-XI-28-472, and MLP 14-I-10-170.

*Provenance* MLP 12-I-20-30, and MLP 92-II-2-194 from Locality DPV 16/84; MLP 78-X-26-106 and MLP 08-XI-30-28 from Locality DPV 14/84; MLP 13-XI-28-140, MLP 13-XI-28-472, and MLP 14-I-10-170 from Locality DPV 13/84.

*Description* Thallus inconspicuous or forming thin, effuse, pale grey crust. Apothecia of 0.3–0.5(1) mm in diameter, usually very crowded. Disc orange or yellowish orange, margin concolourous with disc or slightly paler. Thalline excipulum broad, cortex composed of paraplectenchymatous tissue. True excipulum fan-shaped. Hypothecium without oil droplets. Hymenium c. 60  $\mu\text{m}$  high, with medium coarse epipsamma. Paraphyses branched, apically slightly enlarged to 2.5  $\mu\text{m}$ . Asci 8-spored. Spores (13)  $14\text{--}20 \times 10\text{--}14 \mu\text{m}$ . Septum 4–6  $\mu\text{m}$ . Thallus K-, apothecia K + violet-red.

*Ecology and distribution* Cosmopolitan species. In Antarctica: distributed in South Orkney Islands, South Shetland Islands, and Antarctic Peninsula. Grows mainly on various enriched siliceous rocks, boulders, and pebbles, but occurs also on lime-rich stone, slate, mortar, and concrete.

Order Lecanorales Nannf. 1932

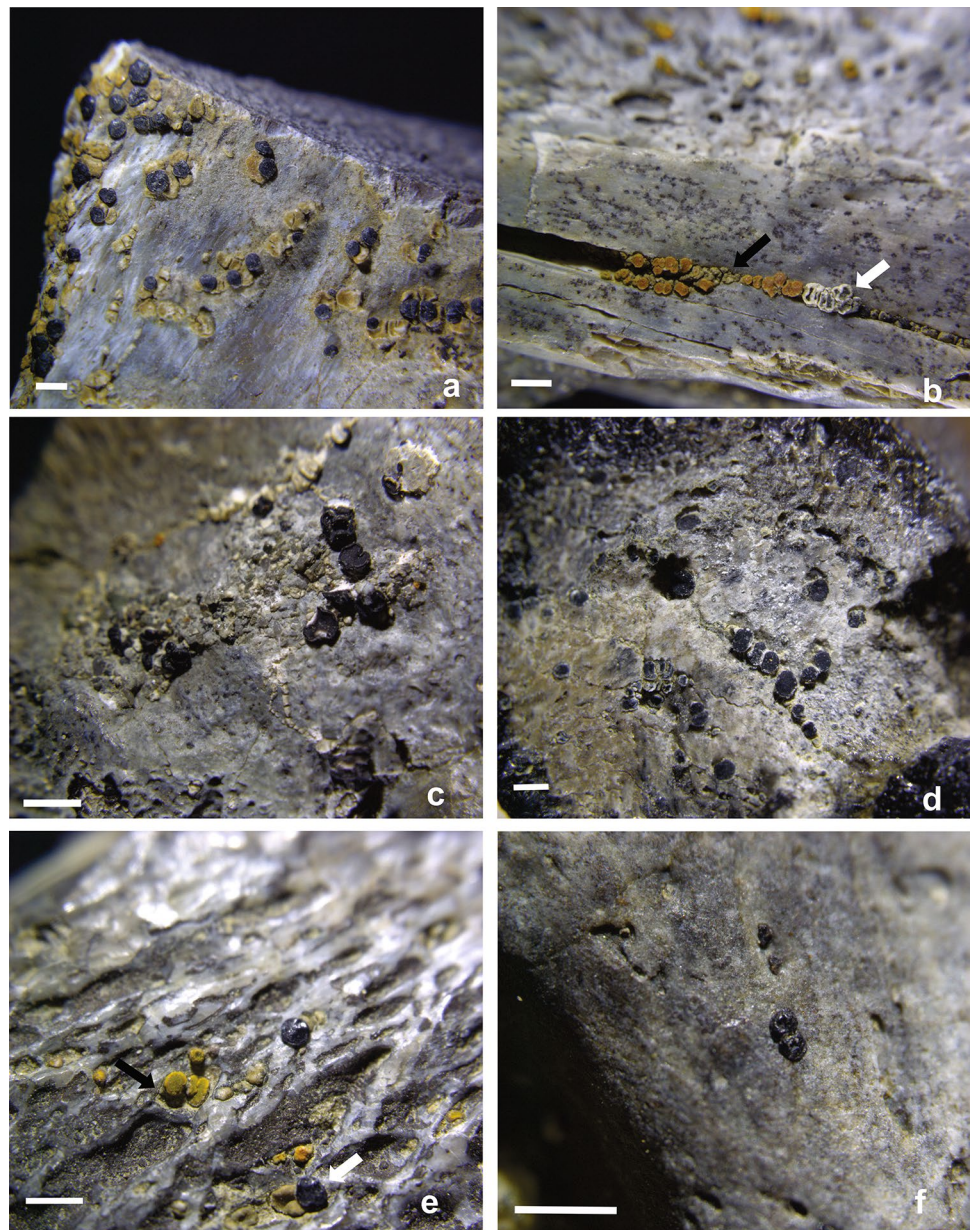
Family Lecanoraceae Körb. 1855

Genus *Carbonea* (Hertel) Hertel 1983

*Carbonea vorticosa* (Flörke) Hertel 1983 (Fig. 2c)



**Fig. 2** Details of the lichen found in fossil penguin bones: **a** *Lecidea andersonii*; **b** *Athallia holocarpa* (black arrow) and *Lecanora flotowiana* (white arrow); **c** *Carbonea vorticosa*; **d** *Myriolecis mons-nivis*; **e** *Candelariella aurella* (black arrow) and *Lecidea andersonii* (white arrow); **f** *Sarcogyne privigna*. Variations in tone and colour correspond to differences in the maturation or dehydration degree of the apothecia. Scale bars represent 1 mm



*Observed material* MLP 13-XI-28-459, MLP 08-XI-30-3/12, and MLP 96-I-6-40

*Provenance* Locality DPV 13/84

*Description* Thallus is usually lacking or very thin, greyish. Apothecia numerous, sessile, O.I-D.7 mm broad, often with constricted base. Disc flat or slightly convex, black, shining. True excipulum slightly raised, brown-black. Hypothecium 70–110  $\mu\text{m}$  brown-black. Hymenium 40–50  $\mu\text{m}$ , epihymenium blue-green. Paraphyses conglutinate, sometimes branched, with tips scarcely thickened. Asci cylindrical-clavate, of *Lecanora*-type. Spores ellipsoid, hyaline to 10–13  $\times$  4.5–5  $\mu\text{m}$ . Thallus K-, C-, and Pd-

*Ecology and distribution* Cosmopolitan species. In Antarctica: distributed in South Orkney Islands, South Shetland

Islands, Antarctic Peninsula, and continental Antarctica. On rocks in inland hills.

Genus *Myriolecis* Clem. 1909

*Myriolecis dispersa* (Pers.) Śliwa, Zhao Xin and Lumbsch 2015

*Observed material* MLP 12-I-20-30

*Provenance* Locality DPV 16/84

*Description* Thallus endolithic or superficial and then visible as a very thin membranaceous layer. Apothecia variable in size (0.3–0.7 mm in diameter), shape, margin structure, and disc colour. Margin thin, corticate, and in some way dentate or thick and  $\pm$  powdery, usually white but in some localities dark to blackened. Disc pale, greenish-grey, brownish,

or blackish. Thalline excipulum variable in thickness and abundance of algae, cortex not well delimited. Epithecium granulose. Epithymenium brownish or olive, hymenium 50  $\mu\text{m}$ . Paraphyses thin, septate, branched, and anastomosed. Spores ellipsoid, hyaline 8–12  $\times$  5–6  $\mu\text{m}$ . Thallus and apothecial margin K-, C-, P-, or P+ orange.

**Ecology and distribution** Cosmopolitan species. Distribution in Antarctica: due to taxonomic confusion, the distribution of this taxon is uncertain. On boulders and stones of recent glacier moraines or on introduced wood. Main component of epilithic communities in newly deglaciated moraines and one of the most important pioneer taxa of lichens. On a wide range of substrata, including calcareous and siliceous rock, concrete and mortar, dusty bark, and many man-made substrates, including metal, also communally on other lichens.

*Myriolecis mons-nivis* (Darb.) Śliwa, Zhao Xin and Lumbsch 2015 (Fig. 2d)

**Observed material** MLP 08-XI-30-3/12, MLP 92-II-2-194, MLP 14-I-10-170, and MLP 12-XI-1-27/28.

**Provenance** MLP 08-XI-30-3/12, MLP 12-XI-1-27/28, and MLP 14-I-10-170 from Locality DPV 13/84; MLP 92-II-2-194 from Locality DPV 16/84.

**Description.** Thallus present only under and near apothecia, yellowish. Apothecia 0.5–1.3 mm in diameter, few compressed together. Thalline margin very thin to almost excluded, yellowish. Disc black. Thalline excipulum with abundant algae, cortex not well delimited, uniform. True excipulum distinct, thin. Epithecium granulose. Hymenium 60  $\mu\text{m}$ , epithymenium bluish-green (N + red). Hypothecium distinct. Paraphyses slightly branched, thin. Asci 8-spored. Spores ellipsoid, hyaline to 10–11  $\times$  5–5.5  $\mu\text{m}$ . Thallus and apothecial margin K-, C-, and P-.

**Ecology and distribution** Endemic from Antarctica, distributed in Antarctic Peninsula and South Shetland Islands. In snow bed communities.

Genus *Lecanora* Ach. 1809

*Lecanora flotowiana* Spreng. 1820 (Fig. 2b)

**Observed material** MLP 08-XI-30-28, MLP 13-XI-28-472, and MLP 14-I-10-170.

**Provenance** MLP 08-XI-30-28 from Locality DVP 14/84; MLP 13-XI-28-472 from Locality DPV 13/84.

**Description.** Thallus endolithic or very poorly developed, as a very thin film without a cortex. Apothecia variable in size, up to 2.5(3) mm in diameter, often clustered, cauliflower-like,  $\pm$  stalked. Disc dark brown, flat to  $\pm$  convex,  $\pm$  pruinose. Thalline margin thin or thick, pale grey, sometimes crenulate. True margin up to 20  $\mu\text{m}$  thick, composed of elongated cells running parallel to the paraphyses. Hymenium colourless, epithecium brown. Hypothecium 5–0  $\mu\text{m}$  high, hyaline, composed of irregular to isodiametric, short, agglutinated cells. Small crystals occur in cortex

in lower parts of the apothecia. Spores ellipsoid, hyaline 10–15  $\times$  5–7  $\mu\text{m}$ . Paraphyses thick, straight. Thallus and apothecial K-, C-. **Ecology and distribution** Cosmopolitan species. Distribution in Antarctica comprises Bouveteya, South Sandwich Islands, South Orkney Islands, South Shetland Islands, and Antarctic Peninsula. On rock walls and stones, prefers drier rather, close to bird nests.

Class Candelariomycetes Voglmayr & Jaklitsch 2018

Subclass Candelariomycetidae Miqdl. et al. ex Timdal & M. Westb. 2016

Order Candelariales Miqdl., Lutzoni & Lumbsch 2007

Family Candelariaceae Hakul. 1954

Genus *Candelariella* Müll. Arg. 1894

*Candelariella aurella* (Hoffm.) Zahlbr. 1928 (Fig. 2e)

**Observed material** MLP 12-I-20-30, MLP 13-XI-28-442, MLP 13-XI-28-140, and MLP 13-XI-28-410.

**Provenance** MLP 13-XI-28-140 and MLP 13-XI-28-442 from Locality DPV 13/84; MLP 13-XI-28-410 from Locality DPV 14/84; and MLP 12-I-20-30 from Locality DPV 16/84.

**Description** Thallus crustose, granulose,  $\pm$  dispersed, usually lacking, yellow, lemon-yellow to greenish-yellow. Apothecia frequent 0.2–1.2 mm in diameter. Thalline margin entire to slightly crenulate, thin to disappearing. Disc flat to slightly convex, darker thin margin, often greenish-yellow. Asci 8-spored. Paraphyses unbranched. Spores oblong, ellipsoid, straight or slightly curved, usually unicellular, 12–25  $\times$  5–7.5  $\mu\text{m}$ .

**Ecology and distribution** Cosmopolitan species. In Antarctica: South Orkney Islands and South Shetland Islands. Mostly on calcium-rich rocks, on rocks in ornitocoprophilous communities one of the main components of epilithic communities on recent glacier moraines, sometimes on bark or wood.

Subclass Acarosporomycetidae V. Reeb, Lutzoni & Cl. Roux 2004

Order Acarosporales V. Reeb, Lutzoni & Cl. Roux 2007

Family Acarosporaceae Zahlbr. 1906

Genus *Sarcogyne* Flot. 1851

*Sarcogyne privigna* (Ach.) A. Massal 1854 (Fig. 2f)

**Observed material** MLP 84-II-1-214, MLP 13-XI-28-410, MLP 78-X-26-134/140, and MLP 12-I-20-30.

**Provenance** MLP 13-XI-28-140 and MLP 84-II-1-214 from DPV 13/84; MLP 13-XI-28-410 from DPV 14/84; and MLP 12-I-20-30 from DPV 16/84.

**Description** Thallus endolithic. Apothecia usually irregular, 1–3 mm wide, disc black to blackish red, plane; margin black, often very prominent, sometimes flexuous, often undulate; epithymenium pale brown-orange, not carbonaceous, 8–10(– 12)  $\mu\text{m}$  thick hymenium, orange to pale yellow, 60–85(– 110)  $\mu\text{m}$  tall; paraphyses simple, hypothecium hyaline to pale yellow or very pale brown, 15–35  $\mu\text{m}$



thick; asci clavate,  $45\text{--}55 \times 10\text{--}12 \mu\text{m}$ ,  $100 +$ -spored; ascospores hyaline, simple, cylindrical, or rarely ellipsoid,  $3\text{--}5(-5.5) \times 1\text{--}2 \mu\text{m}$ . Spot tests: all negative.

**Ecology and distribution** Cosmopolitan species. On wet rocks; on acidic and carbonaceous rocks, often in washes, drainages, the flood plains of rivers or on surfaces where it is inundated during storms.

Class Eurotiomycetes O.E. Erikss. & Winka 1997

Subclass Chaetothyriomycetidae Doweld 2001

Order Verrucariales Mattick ex D. Hawksw. & O.E.

Erikss. 1986

Family Verrucariaceae Eschw. 1824

Genus *Staurothele* Norman 1852

*Staurothele* aff. *frustulenta* Vain 1921 (Fig. 3a)

**Observed material** MLP 96-I-6-40

**Provenance** Locality DPV 13/84

**Description** Thallus crustose, verrucose to  $\pm$  areolate, thin, black or blackish-brown. Perithecial warts, c. 0.5 mm in diameter. Involucrellum continuous, black-brown. Asci 1-spored. Spores muriform with many cells, when mature dark brown,  $50\text{--}60 \times 16\text{--}20 \mu\text{m}$ . Hymenial algae cells  $5\text{--}6 \times 4 \mu\text{m}$ . Spot tests: all negative.

**Ecology and distribution** Bipolar species. In Antarctica only known from Alexander Island (Antarctic Peninsula) and Livingston Island (South Shetland Islands). On rocks and stones in moist sites, mainly in melt channels.

Pezizomycotina O.E. Erikss. & Winka 1997

Incertae sedis

Genus *Oevstedalia* Ertz & Diederich. 2004

*Oevstedalia antarctica* (C. W. Dodge) Ertz & Diederich., 2004 (Fig. 3b)

**Observed material** MLP 13-XI-28-410.

**Provenance** Locality DPV 14/84.

**Description.** Thallus crustose, composed of colonies or coalescing, brown. Algae chlorococcoid in clusters. Perithecia immersed in thallus. Perithecial wall pale reddish brown in the upper side, exposed part, almost hyaline below, basally and laterally  $40\text{--}80 \mu\text{m}$  thick, apically up to

$110 \mu\text{m}$ . Pseudoparaphyses up to  $35 \mu\text{m}$  long,  $0.8\text{--}1 \mu\text{m}$  diam. Asci subcylindrical, variable in length, when mature up to  $250 \mu\text{m}$  in length and  $20\text{--}33 \mu\text{m}$  in diam.; living asci with 8 conidial 'balls' filled with ascoconidia. Ascoconidia  $3.7\text{--}4.5 \times 2\text{--}2.5 \mu\text{m}$ . (Ertz and Diederich 2004).

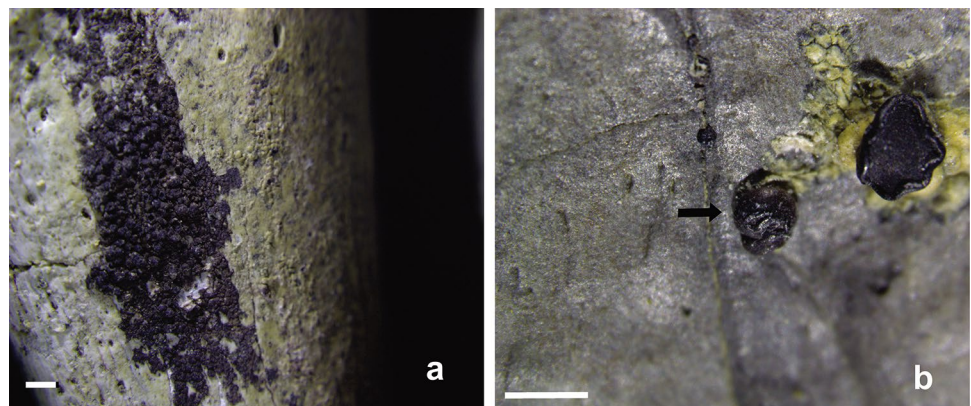
**Ecology and distribution** Endemic from Antarctica, distributed in South Shetland Islands, Antarctic Peninsula, and continental Antarctica. Collected on wood, rocks, detritus, and whale bones, and seems to be not rare, and widespread.

## Discussion and conclusions

The substrate where lichen grew corresponds to fossil penguin bones that lived in Antarctica between the Ypresian and Bartonian ages (Eocene). After transportation and unburial, these fossils suffer a series of taphonomic processes, among which the lichen attack is included. The unconsolidated sediments carrying these fossils are mostly sands and lutites, while vertebrate remains, such as the penguin bones examined here, are commonly preserved as calcium phosphate. All reported lichens in this contribution presented a crustose growth both (epilithic and endolithic), which are expected for this area (Øvstedal and Smith 2001). Excepting *Myriolecis mons-nivis*, which was previously reported for Seymour Island (Øvstedal and Smith 2001), the other species here described were previously found only in the Antarctic Peninsula (Øvstedal and Smith 2001, 2004; Ertz and Diederich 2004; Olech 2004) and constitute new reports for this island.

The lichens assemblage examined here comprises two species endemic from Antarctica, two with a bipolar distribution and others cosmopolitan. The Antarctic species *Oevstedalia antarctica* and *Myriolecis mons-nivis* have been cited growing on different kinds of surfaces, probing their generalist condition regarding the substrate preferences. On the other hand, *Lecidea andersonii*, the bipolar species, is also found in Norway and Iceland (Ruprecht et al. 2010), and *Staurothele* aff. *frustulenta*, previously considered as a bipolar taxon, and cited for Antarctica and Scandinavia (Øvstedal

**Fig. 3** Details of the lichen found in fossil penguin bones: **a** *Staurothele* aff. *frustulenta*; **b** *Oevstedalia antarctica*, and a vertical fissure on the bone surface filled by small apothecia. Variations in tone and colour correspond to differences in the maturation or dehydration degree of the apothecia. Scale bars represent 1 mm



and Smith 2001), has been recently found in Italy (Nimis and Martellos 2017), South Korea, and Argentina, showing a wider distribution than previously thought. In both last countries, *Staurothele* aff. *frustulenta* was growing in concrete (Rosato 2006; Kondratyuk et al. 2017), a substrate completely different than fossil bones. The cosmopolitan species, *Myriolecis dispersa* and *Candelariella aurella* do not seem to have a preference in the substrate on which they grow, since they have been found growing on concrete in urban environments (Sliwa 2007; García 2018) and also on fossil bones, like the cases presented here.

All the species described here prefer well-lit places (Øvstedal and Smith 2001; Arup 2009), which is expected since in the absence of vascular plants, lichens must be adapted to receive direct solar radiation. Their endolithic condition could be an important advantageous to withstand the extreme cold, since most of the thallus would be protected inside the rocks (Pointing and Belnap 2012; Wierzchos et al. 2013; de los Ríos et al. 2014; Wierzchos et al. 2015), or bones in these cases.

In the summer season, the rock surface prevents the thallus from suffering sudden changes in temperature due to the action of the wind, which can be very windy in Antarctica (Friedmann 1982). However, endolithic growth can also be interpreted as a successful strategy to avoid high light intensities which may damage photosynthesis (Tretiach 1995), or as a strategy to avoid competition. Endolithic growth provides access to an otherwise sparsely inhabited habitat, not sharing the space with epilithic species (Bungartz et al. 2004).

Although bones do not provide a continuous and stable substrate for lichens, they frequently grow on the surface of fossil bones, and many species are particularly found within them. Independently of fossil size, we found lichen in small bone fragments (e.g. broken phalanges) and also in larger elements, such as femora and coracoids that belonged to giant penguins. However, we noticed that weathered surfaces with exposed trabecular tissues, surficial fissures, and fractures (see for example Fig. 2b) are the preferred substrate, providing probably a more protected place against the extreme environmental conditions dominated by snow and strong winds.

Crustaceous morphologies (epilithic and endolithic) could be more resistant to mechanical action, contrary to morphologies with greater thallus development (foliose and fruticose), which are more affected. The predominance of endolithic over epilithic lichen species is also explained by the mechanical damage produced by the action of the wind and snow plus the transport. However, it could be also a strategy to avoid competition in reduced substrate surfaces. Endolithic lichens are characterized by lower biomass than epilithic ones, and maximum hydration of the thallus is reached at levels five times lower (Tretiach

1995). Therefore, the optimal content of thallus water for photosynthesis and respiration is lower in endolithic than that in epilithic lichens (Tretiach and Pecchiari 1995), and also the endolithic growth structure increases porosity and probably allows more moisture to accumulate (Bungartz et al. 2004).

Whereas weather conditions are similar in the whole James Ross Basin, it means, in the Seymour/Marambio, Cockburn, Snow Hill, Vega, and James Ross islands, the topography and presence of glaciers in some areas determine strong differences in the substrate. Some of the lichen species were described from bones collected in Seymour Island, also grow in the nearby Cockburn Island, an even smaller island also without glaciers and snow during summer. However, given the presence of a more consolidated substrate in the surficial deposits (rocks, not bones) of the latter, we observed that lichens are extremely more abundant in Cockburn Island. The unconsolidated condition of the sediments exposed in Seymour Island attempts against the settlement of extended lichen communities.

In this context, fossil bones are an important source for the study of lichens richness, providing a suitable substrate for growing and protecting them from extreme conditions. Besides, considering that most of the biological studies, including lichenological sampling, are developed on the west side on the Antarctic Peninsula (e.g. Pannewitz et al. 2003; Olech 2004; Rodriguez et al. 2018), fossils already housed in collections became even more important, providing a unique possibility to study them in their original substrate.

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**Data availability** Materials reviewed in this work are housed in the collection of the División Paleontología Vertebrados (DPV) of the Museo de La Plata (MLP), La Plata (Argentina): MLP 78-X-26-134; MLP 08-XI-30-28; MLP 13-XI-28-140; MLP 13-XI-28-410; MLP 12-I-20-30; MLP 92-II-2-194; MLP 78-X-26-106; MLP 13-XI-28-472; MLP 14-I-10-170; MLP 13-XI-28-459; MLP 08-XI-30-3/12; MLP 96-I-6-40; MLP 12-I-20-30; MLP 08-XI-30-3/12; MLP 14-I-10-170; MLP 12-XI-1-27/28; MLP 13-XI-28-442; MLP 84-II-1-214; and MLP 78-X-26-134/140.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** The senior Curator of the División Paleontología Vertebrados (Museo de La Plata) from La Plata city (Argentina) allowed the authors the access to the penguin bones used in the present analysis, and the permission for the results publication, all according to the Argentinian laws and requirements, in consonance with the Antarctic Treaty.

**Consent to participate** All the authors declare having consented to the participation of this manuscript.

**Consent for publication** All the authors declare their consent to the publication of this manuscript.

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