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# Saxicolous lichens in the semi-arid Caatinga in Brazil show substratum shifts

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**ABSTRACT**
Saxicolous lichens were investigated for the first time in the southern reaches of the Caatinga biome in Sergipe, NE Brazil. Only 20 species could be identified, and three more are described as new to science: *Cresponea quinqueseptata* Aptroot & M.Cáceres, sp. nov. with 5-septate ascospores and yellow pruinose discs; *Fulgogasparrea intensa* Aptroot & M.Cáceres, sp. nov. with a cinnabar red, appressed thallus with marginally elongated lobes; and *Peltula nigrotestudinea* Aptroot & M. Cáceres, sp. nov. with flat, black, isolated areoles. A number of substrate shifts was observed: 1) the new species of *Peltula* Nyl. does not grow in places with run-off as usual, but on top of the boulders, where it is in the best position to catch the precipitation, which is the limiting factor here; 2) *Synalissa matogrossensis* (Malme) Henssen, which was previously known only from the type locality, where it grows on limestone, was found on granite; the apparently considerable width of its ecological amplitude is unusual. Its position inside the Lichinaceae was confirmed by sequence data; 3) *Xanthoparmelia succedans* Elix & J.Johnst. was found growing on bark, rather high on trees. The corticolous occurrence is attributed to high diaspores pressure; 4) the area and thus the tree bark is wet enough part of the year to sustain the growth of a corticolous Lichinaceae (one of only two compared to 340 saxicolous and terricolous species in the family) and other cyanophilic lichens; and 5) the new *Cresponea* Egea & Torrente is the first saxicolous species in the genus in the tropics, where the genus is most speciose; its thallus is deeply endolithic.

**KEY WORDS**
Roccellaceae, Teloschistaceae, Lichinaceae, Peltulaceae, Parmeliaceae, sequence, semi-arid, Sergipe, new species.

**RÉSUMÉ**
*Les lichens saxicoles de la Caatinga semi-aride au Brésil montrent des changements de substrat.*
Les lichens saxicoles ont été étudiés pour la première fois dans la partie méridionale du biome de la Caatinga à Sergipe, dans le nord-est du Brésil. Seules 20 espèces ont pu être identifiées, et trois autres sont décrites comme nouvelles pour la science : *Cresponea quinqueseptata* Aptroot & M.Cáceres, sp. nov.

avec des ascospores à 5-septate et des disques jaunes pruineux ; *Fulgogasparrea intensa* Aptroot & M.Cáceres, sp. nov. avec un thalle rouge cinabre, apposé avec des lobes marginalement allongés ; et *Peltula nigrotestudinea* Aptroot & M.Cáceres, sp. nov. avec des aréoles isolées, noires et plates. Un certain nombre de changements de substrat ont été observés : 1) la nouvelle espèce de *Peltula* Nyl. ne pousse pas dans les endroits où il y a du ruissellement comme d'habitude, mais au sommet de rochers, où elle est dans la meilleure position pour capter les précipitations, qui sont le facteur limitant ici ; 2) *Synalissa matogrossensis* (Malme) Henssen, qui n'était auparavant connu que de la localité type où il pousse sur du calcaire, a été trouvé sur du granit, la largeur apparemment considérable de son amplitude écologique est inhabituelle. Sa position au sein des Lichinaceae a été confirmée par les données de séquence ; 3) *Xanthoparmelia succedans* Elix & J.Johnst. a été trouvé poussant sur de l'écorce, plutôt haut sur les arbres. La présence corticale est attribuée à une forte pression des diaspores ; 4) la zone et donc l'écorce des arbres, est suffisamment humide une partie de l'année pour soutenir la croissance d'une Lichinaceae corticolore (l'une des deux seules espèces de la famille contre 340 saxicoles et terricoles) et d'autres lichens cyanophiles ; 5) la nouvelle espèce de *Cresponea* Egea & Torrente est la première saxicole du genre dans les tropiques, où le genre est le plus riche, son thalle est profondément endolithique.

**MOTS CLÉS**
Roccellaceae,
Teloschistaceae,
Lichinaceae,
Peltulaceae,
Parmeliaceae,
séquence,
semi-aride,
Sergipe,
espèces nouvelles.

## INTRODUCTION

The natural vegetation of most of NE Brazil is a semi-arid biome called Caatinga (Castanho *et al.* 2020). It is one of the two most extensive contiguous areas of tropical dry forest in the world (Miles *et al.* 2006), and one of the most threatened of Brazil's six biomes (Castanho *et al.* 2020). The Caatinga vegetation is a semi-deciduous forest with many, usually locally endemic, *Cactaceae* (Taylor *et al.* 2014) generally on a Precambrian granite bedrock with little variation in altitude.

The Caatinga biome covers an area of 1.5 million square km (Sampaio *et al.* 1981), roughly 6 times the size of the United Kingdom. Lichens are present probably everywhere, but exploration has only started rather recently (Brako *et al.* 1985; Ahti *et al.* 1993; Cáceres 2007; Kalb 2008; Cáceres *et al.* 2008; Xavier-Leite *et al.* 2015) and focused on corticolous lichens. Saxicolous lichens have only been reported from a field trip through the northern part of the Caatinga, where a transect was made from coastal Rio Grande do Norte to continental southern Ceará (Aptroot & Cáceres 2016), and where the corticolous lichens in Chapada de Araripe were studied in detail, and from which area a few saxicolous lichens were reported (Menezes *et al.* 2013). The present paper reports the saxicolous lichens from an area in the southern Caatinga, from inland Sergipe state, close to the border with Alagoas and Bahia.

The saxicolous lichen vegetation occurs here on granite bedrock, which is here and there exposed, often in boulder-like formations, and more abundantly so in the vicinity of rivers, like here near the São Francisco river.

## MATERIAL AND METHODS

Identification and descriptive work were carried out in Itabaiana, Universidade Federal de Sergipe, using a Leica EZ4 stereo microscope and a Leica DM500 compound microscope, and in Campo Grande using an Olympus SZX7 stereo microscope and an Olympus BX50 compound microscope with interference contrast, connected to a Nikon Coolpix digital camera. Sections have been mounted in tap water, in which also all measurements were taken. Macrophotos were taken by a Nikon EOS. IKI reactions were seen by adding commercial undiluted Lugol (Merck 9261). The specimens from this study are preserved in ISE. The chemistry of most specimens has been investigated by thin layer chromatography (TLC) using solvent A (Orange *et al.* 2001).

Total DNA was extracted from dry specimens employing a modified protocol based on Murray & Thompson (1980). PCR amplification was performed with the primers ITS1F and ITS4 (White *et al.* 1990; Gardes & Bruns 1993) for the rDNA internal transcribed spacer 1, 5.8S and internal transcribed spacer 2 (collectively referred to as ITS). PCR reactions were performed under a program consisting of a hot start at 95 °C for 5 min, followed by 35 cycles at 94 °C, 54 °C and 72 °C (45, 30 and 45 s respectively) with a final 72 °C step 10 min. PCR products were checked in 1% agarose gels and positive reactions were sequenced with either one of the PCR primers ITS1F and ITS4 (White *et al.* 1990; Gardes & Bruns 1993).

BLAST of 5.8S-ITS2 sequences was used to select the most closely related taxa (Altschul *et al.* 1997). Phylogenetic trees with related taxa were constructed for confirmation of the phylogenetic position. No cladograms are presented here, as they were not very informative for the reasons mentioned below in the results section, under the discussion of the respective species.

## RESULTS

In total, only 20 saxicolous species were identified from this locality, viz. *Buellia sequax* (Nyl.) Zahlbr., *Caloplaca brachyloba* (Müll. Arg.) Zahlbr., *C. cupulifera* (Vain.) Zahlbr., *C. diplacia*

(Ach.) Riddle, *C. lecanorocarpa* Aptroot & M.Cáceres, *C. leptozona* (Nyl.) Zahlbr., *Collema texanum* Tuck., *Diploschistes actinostomus* (Paers.) Zahlbr., *Endocarpon pallidulum* (Nyl.) Nyl., *Lecanora subimmersa* (Fée) Vain., *Lichinella iodopulchra* (Couderc ex Croz.) P.P. Moreno & Egea, *Peltula euploca* (Ach.) Poelt ex Ozenda & Clauzade, *P. farinosa* Büdel, *P. patellata* (Bagl.) Swinscow & Krog, *P. placodizans* (Zahlbr.) Wetm., *Physcia convexa* Müll. Arg., *Rinodina oxydata* (A. Massal.) A. Massal., *Synalissa matogrossensis* (Malme) Henssen, *Xanthoparmelia neocumberlandica* T.H. Nash & Elix, and *X. succedans* Elix & J. Johnst.

Family Roccellaceae Chevall.
Genus *Cresponea* Egea & Torrente

***Cresponea quinqueseptata*** Aptroot & M. Cáceres, sp. nov.
(Fig. 1C, D)

Saxicolous *Cresponea* with apothecia yellow pruinose, ascospores broadly fusiform, consistently (4-)5-septate, 30-37 × 5-7 µm.

Mycobank No. — MB 839714.

Type. — **Brazil**, Sergipe, Poço Redondo, Cajueiros, Trilha Ecoparque, 09°39'43"S, 43°40'18"W, on exposed granite, 15.XI.2018, *M. Cáceres & A. Aptroot* (holo-, ISE[ISE48046]; iso-, ABL).

Description
*Thallus*
Endolithic, up to 3 mm immersed into the rock in between rock crystals, not visible from above, extending in fissures between rock granules, only visible when rock fragments are removed, with trentepohlioid algae.

*Apothecia*
Sessile, rather evenly dispersed to crowded, angular to somewhat sinuous in outline, 0.5-2.0 mm diam.; disc black, thinly yellow pruinose; margin higher than the disc, shiny, black, crenulate to fissured, *c*. 0.2 mm wide.

*Epihymenium*
Dark brown, *c.* 30 µm high, with superficial yellow crystals.

*Hymenium*
Hyaline to somewhat greyish brown, *c.* 150 µm high, filaments anastomosing. *Hymenium* and *excipulum* black and continuous, *c*. 100 µm thick.

*Asci*
Cylindrical, *c.* 70-75 × 13-16 µm, wall *c.* 2-3 µm thick, with small apical chamber.

*Ascospores*
8/ascus, hyaline, broadly fusiform, consistently (4-)5-septate, 30-37 × 5-7 µm, constricted at some septa, ends rounded, wall *c.* 0.5 µm thick.

*Pycnidia*
Not observed.

Chemistry. — Apothecia disc pigment KOH+ yellow exuding (no TLC performed).

Ecology and distribution. — On exposed granite in Caatinga. Known only from Brazil.

Discussion
The genus *Cresponea* (Egea & Torrente 1993) contains 20 species and is in the tropics as far as known strictly corticolous, usually occurring on overhanging bark of old trees. This species is the first saxicolous one in the tropics outside the tropics, *C. premnea* (Ach.) Egea & Torrente is rarely found saxicolous, and is being recognized as a separate variety, var. saxicola (Leight.) Egea & Torrente. The new species differs from all other known species by the asymmetrically broadly fusiform, consistently (4-)5-septate ascospores. The endolithic thallus is remarkable: No thallus is visible unless rock fragments are removed. *Cresponea* specimens are usually impossible to sequence and the current species concept dates back to the last century (Egea & Torrente 1993) has not been recently tested. Especially, the variation in ascospore septation and the colour of the pruina were not given much attention in that treatment, but that might well be useful characters to distinguish species. In our experience, *Cresponea* species are not variable in pruina colour; pruina can be absent, especially in older specimens, but we are not aware of any species that is variable in pruina colour. Indeed, the present new species is characterized by quite invariably 5-septate ascospores, and yellow pruina on the disc. The corticolous species that is closest in characters, *C. proximata* (Nyl.) Egea & Torrente, is quite variable in ascospore septation, even within one specimen, e.g. the type specimen has (3-)5-6(-8)-septate ascospores.

Family Teloschistaceae Zahlbr.
Genus *Fulgogasparrea*
S.Y.Kondr., M.H.Jeong, Kärnefelt, Elix, A.Thell & Hur

***Fulgogasparrea intensa*** Aptroot & M. Cáceres, sp. nov.
(Fig. 2A, B)

Saxicolous *Fulgogasparrea* with thallus and apothecia intensely cinnaber red, thallus margins elongated, lobate, apothecia primordial.

Mycobank No. — MB 839715.

Genbank. — MZ198742.

Type. — **Brazil**, Sergipe, Poço Redondo, Cajueiros, Trilha Ecoparque, 09°39'43"S, 43°40'18"W, on exposed granite, 15.XI.2018, *M. Cáceres & A. Aptroot* (holo-, ISE[ISE48030]; iso-, ABL).

Description
*Thallus*
Spreading, covering an area of up to 5 cm diam., *c*. 0.2 mm thick, continuous, closely appressed, rimose, cinnabar red; areoles angular, *c*. 0.5 mm diam., marginal areoles elongated, up to 1 mm long; some central areoles raised and somewhat


Fig. 1. — **A**, **B**, *Leprocollema nova-caledoniarum* A.L. Sm., ISE 48008: **A**, habitus (all the brownish black), with a turtle; **B**, detail with apothecium. **C**, **D**, *Cresponea quinqueseptata* Aptroot & M. Cáceres, sp. nov., holotype: **C**, apothecia (note that the thallus is immersed in the rock); **D**, ascospore. Scale: B, 0.5 mm; C, 2 mm; D, 20 µm.

warty, up to 0.4 mm high, with some punctiform dark depressions without differentiated structures.

*Apothecia and pycnidia*
Not observed.

Chemistry. — Thallus KOH+ blood red. TLC: An anthraquinone.

Ecology and distribution. — On exposed granite in Caatinga. Known only from Brazil.

## Discussion

The genus *Fulgogasparrea* S.Y. Kondr. so far comprises three American species (Kondratyuk *et al.* 2015) and one Asian species. Sequence data (not shown here but submitted to Genbank) place this species phylogenetically close to *F. brouardii* (B. de Lesd.) S.Y. Kondr. from which it markedly differs by the appressed, cinnaber red thallus with elongated marginal lobes. The other two American species, *F. appressa* (Wetmore & Kärnefelt) S.Y. Kondr., Elix, Kärnefelt & A. Thell and *F. decipioides* (Arup) S.Y. Kondr., M.H. Jeong,

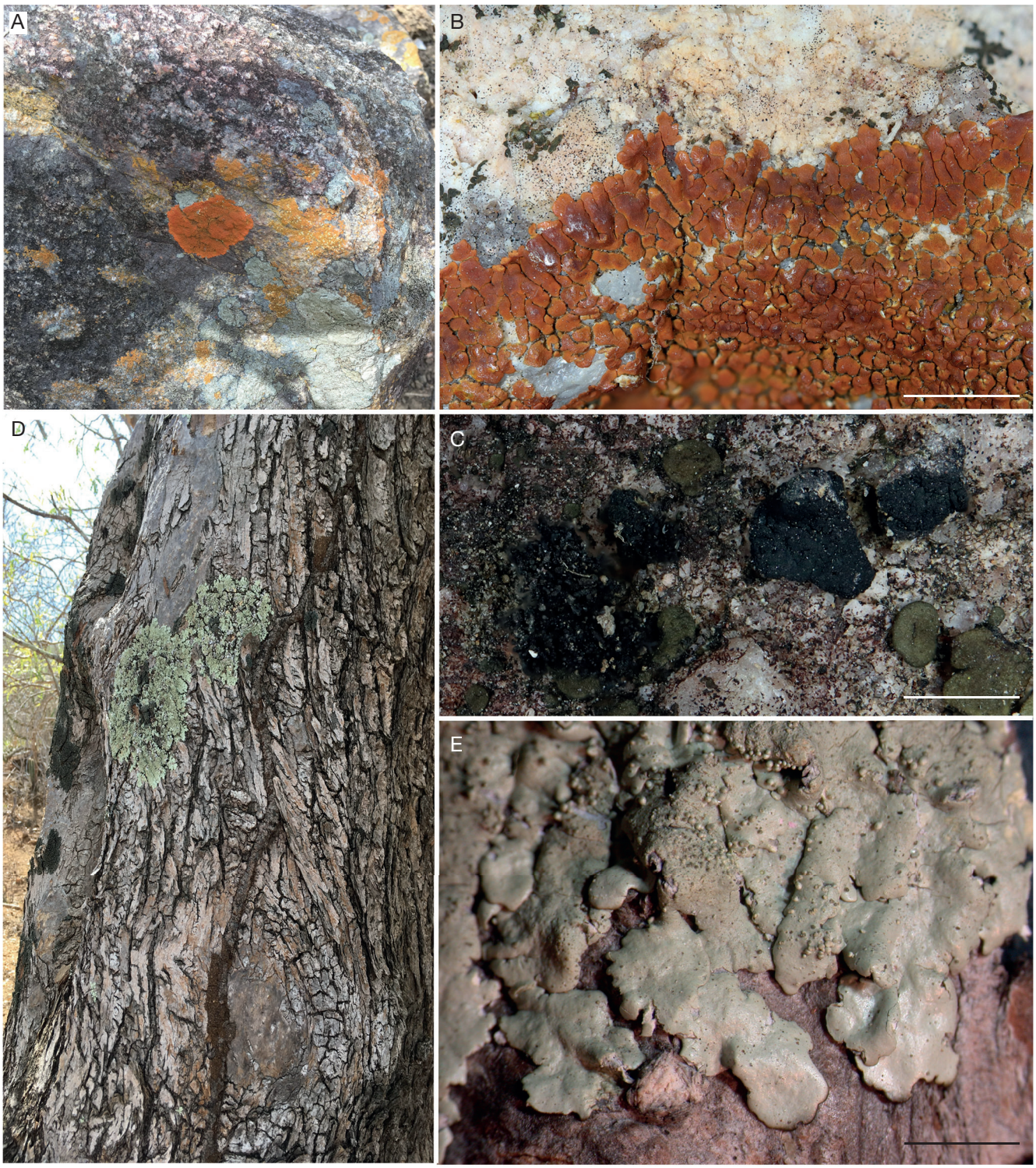


Fig. 2. — **A**, **B**, *Fulgogasparrea intensa* Aptroot & M. Cáceres, sp. nov., holotype: **A**, habitus; **B**, detail with elongated marginal lobes; **C** *Lichinella iodopulchra* (Couderc ex Croz.) P.P. Moreno & Egea (right) and *Synalissa matogrossensis* (Malme) Henssen (left); both black (the brown squamules are *Peltula euploca* (Ach.) Poelt ex Ozenda & Clauzade), ISE 48050; **D**, **E**, corticolous *Xanthoparmelia succedans* Elix & J.Johnst., ISE 48020; **D**, habitus; **E**, detail. Scale bars: 2 mm.

Kärnefelt, Elix, A. Thell & Hur, are both yellow; the latter is also sorediate. Presenting a phylogeny of the group would be premature at the moment. It would key out in the world key to *Caloplaca* s. lat. (Schumm & Aptroot 2019) in Group B at 17a. The species is not very similar to other species of *Caloplaca* s. lat. that we know of; the thalli are quite conspicuous and rather thick, and the colour is very intense. In the field, it reminds more of *Rusavskia elegans* (Link) S.Y. Kondr. & Kärnefelt than of a *Caloplaca*, but it is closely appressed and placodioid.

Family Lichinaceae Nyl.
Genus *Leprocollema* Vain.

***Leprocollema nova-caledoniarum*** A.L. Sm.
[often as *novae-caledoniarum*]
(Fig. 1A, B)

Specimen examined. — **Brazil**. *Sergipe*: Poço Redondo, Cajueiros, Trilha Ecoparque, on tree base, 15.XI.2018, *M. Cáceres & A. Aptroot* (ISE[ISE48008], ABL).

Genus *Lichinella* Nyl.

***Lichinella iodopulchra*** (Couderc ex Croz.)
P.P. Moreno & Egea
(Fig. 2C)

Selected specimen examined. — **Brazil**. *Sergipe*: Poço Redondo, Cajueiros, Trilha Ecoparque, on exposed granite, 15.XI.2018, *M. Cáceres & A. Aptroot* (ISE[ISE48031], ABL).

Genus *Synalissa* Fr.

***Synalissa matogrossensis*** (Malme) Henssen
[often as *mattogrossensis*]
(Fig. 2C)

Genbank. — MZ198740.

Selected specimen examined. — **Brazil**. *Sergipe*: Poço Redondo, Cajueiros, Trilha Ecoparque, on exposed granite, 15.XI.2018, *M. Cáceres & A. Aptroot* (ISE[ISE48050], ABL).

Comments
The sequence falls inside the Lichinaceae, close to *Lichina* C.Agardh (data not shown). The position of this species inside the family is thus confirmed. As long as the type species of *Synalissa*, *S. ramulosa* (Hoffm. ex Berh.) Fr. has not yet been successfully sequenced (our recent attempts with fresh material from Belgium failed), this does not give additional information about the generic placement of *S. mattogrossensis*. The two species may or may not be closely related.

Family Peltulaceae Büdel
Genus *Peltula* Nyl.

***Peltula nigrotestudinea*** Aptroot & M. Cáceres, sp. nov.
(Fig. 3A, B)

Saxicolous *Peltula* with thallus almost black, consisting of angular, flattened, thick areoles with large interspaces between them.

Mycobank No. — MB 839716.

Genbank. — MZ198741.

Type. — **Brazil**, Sergipe, Poço Redondo, Cajueiros, Trilha Ecoparque, 09°39'43"S, 43°40'18"W, on exposed granite, 15.XI.2018, *M. Cáceres & A. Aptroot* (holo-, ISE[ISE48066]; iso-, ABL).

Description
*Thallus*
Spreading, covering an area of up to 5 cm diam., *c*. 0.4 mm thick, containing of areoles with large interspaces between them, closely appressed, almost black; areoles angular, rather irregularly shaped, *c*. 0.6-1.2 mm diam., flat, marginal areoles not elongated; sides somewhat rounded; attachment area roughly of similar size as upper surface; not distinctly pulvinate or turbinate.

*Apothecia and pycnidia*
Not observed.

Chemistry. — No secondary substances detected.

Ecology and distribution. — On exposed granite in Caatinga. Known only from Brazil.

Discussion
The genus *Peltula* comprises *c.* 50 species (Kauff *et al.* 2018). This species differs morphologically and phylogenetically (data not shown but sequence submitted to genbank) from all described, respectively sequenced species. Kauff *et al.* 2018 give a discussion of the various different thallus types known within the genus, and illustrate many examples. This new species differs from all the discussed and illustrated types by the flat, thick squamules with broad (not turbinate) attachment areas. The very dark, almost black, colour is also quite typical. An exepetnded phylogeny is not presented here as it would add little to the one presented by the relatively recent one by Kauff *et al.* (2018). It may be a local endemic, especially as it occupies an ecological niche (exposed granite) that is not usually inhabited by *Peltula* species. It is thus very different from any described species in the genus.

Family Parmeliaceae Zenker
Genus *Xanthoparmelia* (Vain.) Hale

***Xanthoparmelia succedans*** Elix & J.Johnst.
(Fig. 2D, E)

Genbank. — MZ198743 (corticolous) and MZ198744 (saxicolous).

Selected specimens examined. — **Brazil**. *Sergipe*: Poço Redondo, Cajueiros, Trilha Ecoparque, on tree bark, 15.XI.2018, *M. Cáceres & A. Aptroot* (ISE 48020, ABL); same data, on exposed granite, *M. Cáceres & A. Aptroot* (ISE[ISE48062], ABL).

Comments
The sequences are almost identical, and they fall well inside the genus *Xanthoparmelia* (data not shown).

## DISCUSSION

The saxicolous lichen vegetation of the southern Caatinga contains some surprizes as to substrate. To summarize them: 1) a *Peltula* grows on top of the boulders, without


Fig. 3. — *Peltula nigrotestudinea* Aptroot & M. Cáceres, sp. nov., holotype: **A**, habitus on top of granite boulder, with a *Xanthoparmelia*; **B**, detail showing thallus areoles. Scale bars: 1 mm.

any apparent source of water, while *Peltula* species usually grow close to streams or on places with run-off; 2) *Synalissa mattogrossensis,* which was known only from limestone, was found on siliceous rock, not on obviously dusty or eutrophicated places; 3) a *Xanthoparmelia* is found high up the trees on bark also not obviously dusty; with 820 known species it is the largest lichen genus, and they are invariably saxicolous or terricolous elsewhere; 4) a Lichinaceae is present on trees as well; it might be one of the two out of 340 known species of Lichinaceae which are corticolous, but the habitat is still vastly different, not wet tropical; and 5) an endolithic species of *Cresponea* was

found on rock. The genus was in the tropics restricted to old, overhanging trees.

In order to find an explanation for these substrate shifts, which affect a relatively large percentage (20%) of the saxicolous biodiversity found, one could start looking at all kind of ecological explanations. However, there seems to be nothing special about e.g. the rock type, the bark (varying from smooth to fissured) and the vegetation (rather low, open forest with succulents not unlike those present in e.g. Baja California, Arizona, Madagascar, South Africa, Australia or the Galapagos, Castanho *et al.* 2020, all areas where the above substrate shifts have not been observed).

The real specialty of this Caatinga area is the climate: The temperature is high all around the year (on many days above 30° C and it almost never falls below 15° C), but there is considerable precipitation, in the order of 300-600 mm/year, but with a long dry and a shorter wet season. The mean annual evaporation is in the same order of magnitude as the precipitation. What does this all mean for the saxicolous lichens? Exposed rock surfaces can warm up in the sun to temperatures far above the ambient temperature, and rock surface temperatures in the order of 60° C have been reported. In desert areas (Lange 1969), lichens are only metabolically active during a short period at dawn, but on most days in the year, as situations are not much different over the year. In this semi-arid Caatinga, lichens are probably only active during and shortly after rain, so in practice only seasonally. This may well explain the position of the *Peltula* on top of the boulders, where it will catch more and more often rain than at the sides.

Interactions of lichens with their substrate have been studied both experimentally and by observing and comparing lichen occurrences. The ability to attach to a certain substrate is a prerequisite for the occurrence of the respective species. It has repeatedly been reported that the smoothness of the substrate is of more relevance in this aspect than the actual nature of the substrate. For instance, in tropical rain forest situations, plastic, with its smooth surface, is colonized by foliicolous lichens, while rubber tyres are colonized by corticolous lichens. Generally, foliicolous lichens are also regularly found on smooth, hard rock surfaces. In general, lichens can attach either to limestone, or to siliceous rock. Apparently, different acids/strategies are involved; this, strangely, seems to have never been investigated in any detail though.

Lichens can be widespread and can actually distribute over long distances. Although in the past decade some widespread species have turned out to be genetically diverse, there are also clear examples of species that are cosmopolitan, including very unexpected ones like *Geisleria sychnogonoides* Nitschke (Aptroot *et al.* 2014). Intercontinental travel of diaspores occurs every year if not every day; for instance, everybody in NW Europe can regularly see Sahara sand on his car or bicycle. Diaspore pressure is however still an important influence: When a certain species is common in an environment, it can extend beyond its usual range of substrate. For example, the lichen vegetation of polyester boxes is in general determined by the lichen vegetation in the vicinity, but mostly so by the lichen vegetation on the tree above it. This may actually account for the freak occurrence of a *Xanthoparmelia* on bark in the Caatinga. The morphology, chemistry and sequence of the corticolous material was identical to some of the saxicolous material. *Xanthoparmelia* is the most abundant lichen on the surrounding rocks, and this is clearly the source of the diaspores. Similarly, *Xanthoparmelia* species were observed occasionally (by the first author in The Netherlands and in Tasmania) on asphalt roads close to huge populations on siliceous rock. The real enigma here is why *Xanthoparmelia* is not found more often on trees, in areas where they are common on rock. We postulate that *Synalissa mattogrossensis* which was described from limestone but occurs on granite in the Caatinga is simply not very substrate-specific; it was only reported once before, and the extent of its ecological amplitude was simply unknown. Although many lichens, including Lichinaceae, are reported to be restricted to either limestone or siliceous rock, there are a few species that have been reported from both (Schultz 2005), and *Lichinella iodopulchra*, which accompanies the *Synalissa* in the Caatinga, is one of them. This observation should however be kept in mind when identifying (and describing) lichens; Quite often the substrate is used as identification character, in keys and descriptions, and this clearly can be misleading.

As to the occurrence of the Lichinaceae on tree, We noted that one of the other species on the same trees is the cyanophilic lichen *Coccocarpia palmicola*, which was originally described from the same habitat as *Leprocollema nova-caledoniarum*. Apparently, this bark, although seemingly very dry, is at least part of the year wet enough to sustain the growth of cyanophilic lichens, and not supporting competing organisms that could outcompete the cyanophilic lichens in dry periods.

The saxicolous *Cresponea* is lichenized with a trentepohlioid algae. Trentepohlioid algae are not abundantly present on exposed granite, but apparently, the occasional periods with precipitation allow its occurrence in this habitat in the Caatinga, enabling the occurrence of lichens lichenized with them.

In summary, we observed five different substrate shifts in the Caatinga, and instead of coining one theory, we come up with four different explanations: 1) the new *Peltula* grows on top of the boulders, where it is in the best position to catch the precipitation, which is the limiting factor; 2) *Synalissa matogrossensis* was only seemingly restricted to limestone, as it was known from the type locality only and the apparently considerable width of its ecological amplitude hence unknown; 3) *Xanthoparmelia* can only grow on bark when diaspores are abundant; 4) The area and thus the tree bark is wet enough part of the year to sustain the growth of a corticolous Lichinaceae and other cyanophilic lichens; and 5) the same applies to the trentepohlioid algae on granite, allowing the occurrence of a *Cresponea* lichenized with a trentepohlioid photobiont.

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