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**Standard Paper**

# Key to *Heterodermia* (*Physciaceae*, *Teloschistales*) in Brazil, with 15 new species

Maria Fernanda de Souza[1], André Aptroot[1] and Adriano Afonso Spielmann[1]

[1]Laboratório de Botânica/Liquenologia, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Avenida Costa e Silva s/n, Bairro Universitário, CEP 79070-900, Campo Grande, Mato Grosso do Sul, Brazil

## Abstract

The species of *Heterodermia* in Brazil have been revised based on literature reports, public databases and examination of 500 recent specimens from 15 states. So far, 43 species have been reported in the literature, two of which are not accepted here. We report 10 additional species from Brazil and describe 15 new to science, mostly from the Atlantic rainforest biome, raising the total number to 68, including two still undescribed species from Santa Catarina State. A key to all accepted species is given, keying out more species than represented in any previously published key of the genus. Based on new phylogenetic work, we do not accept the split genera that were recently proposed. We do informally recognize an additional group, the *H. dactyliza*-group. The following species are described as new: *Heterodermia amphilacinulata* M. F. N. Martins & M. P. Marcelli, *H. caneziae* M. F. Souza & Aptroot, *H. delicatula* M. P. Marcelli & M. F. N. Martins, *H. dissecticodiademata* M. F. Souza & Aptroot, *H. dissecticoflabellata* M. F. Souza & Aptroot, *H. flavodactyliza* M. F. Souza & Aptroot, *H. flavulifera* M. F. Souza & Aptroot, *H. labiata* M. P. Marcelli & M. F. N. Martins, *H. macrosoraliata* M. P. Marcelli & M. F. N. Martins, *H. minor* M. F. Souza & Aptroot, *H. neocrocea* M. F. Souza & Aptroot, *H. nigromarginata* M. F. Souza & Aptroot, *H. phyllalbicans* M. F. Souza & Aptroot, *H. spielmannii* M. F. Souza & Aptroot and *H. sublinearis* M. P. Marcelli & M. F. N. Martins. The following new combinations are also proposed: *Heterodermia africana* (Kurok.) M. F. Souza & Aptroot and *H. borphyllidiata* (Kalb & Meesim) M. F. Souza & Aptroot. Dissectic acid was found in species belonging to three different groups and was not restricted to (and characteristic of) one subgroup, as previously reported.

**Key words:** Atlantic rainforest, Cerrado, *Leucodermia*, lichens, phylogeny, *Polyblastidium*, taxonomy

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## Introduction

*Heterodermia* Trevis. is a genus of macrolichens in the *Physciaceae* (Jungbluth & Marcelli 2012) with *c.* 175 species worldwide (Lücking *et al.* 2017). The species are most common in tropical mountain regions, occurring mostly on tree bark or twigs but some species also, or even only, occur on rock or compacted soil.

The study of the genus started with Taylor (1847), who described the first species that would later be accepted in *Heterodermia*. Kurokawa (1962) made a monograph of the genus but still treated it as *Anaptychia* Körb. Later, Kurokawa (1998) and Trass (1992) provided lists of accepted species and valid combinations.

Although the difference between *Anaptychia* and *Heterodermia* was clear from the beginning, the distinction from *Physcia* (Schreb.) Michx. caused more problems. It was Swinscow & Krog (1976) who reported the distinguishing character, as well as providing a key to *Heterodermia* species for East Africa that has been used all over the tropics since. The common *Physcia* species that had been confused with *Heterodermia* for a long time was described as *Physcia atrostriata* Moberg and was treated in Moberg (1990). Several regional revisions are available: Aptroot (1988) treated the species from the Guianas; Scutari (1995) treated the species from a region in Argentina; Moberg & Nash (1999) treat the species known from a larger desert region on the border of Mexico and the USA; Chen & Wang (2001) made one of the first local treatments for China of part of the genus with a more refined species concept; Lendemer (2009) treated the species from the USA; Moberg (2011) treated the species of *Heterodermia* known from Central and South America, but applied a very wide species concept, accepting only 33 species which is less than currently known for even some states in Brazil; Rodriguez *et al.* (2012) treated the species from a different region in Argentina; Michlig *et al.* (2017) described several new species within the *H. comosa* (Eschw.) Follman & Redon group from Argentina, some of which also occur in Brazil. In their treatment for Thailand, Mongkolsuk *et al.* (2015) stressed the importance of terpenoid chemistry, the overall thallus appearance, and anatomy. In addition, they attempted to split the monophyletic genus *Heterodermia* into several groups, in which they formally described the genera *Leucodermia* Kalb and *Polyblastidium* Kalb. In their paper, *Heterodermia* s. str. are the species with a lower cortex present. They treated two further informally

**Author for correspondence:** Maria Fernanda de Souza. E-mail: mariaf.souza.bio@gmail.com

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named species groups, but the phylogenetic position of neither the named nor the unnamed groups as shown.

From Brazil, 41 species have so far been reported (see references below under the respective species), plus a small number of subspecific taxa. For instance, Eliasaro (1992) and Eliasaro & Fleig (1994) treated the species from Rio Grande do Sul. In addition, in an unpublished thesis dealing mostly with São Paulo specimens, Martins (2007) distinguished 17 additional, undescribed new species. Marcelli & Martins (2007) and Marcelli (2013) published some chapters from this work, but not the key or the new species. Two of the new species were described, one by Marcelli *et al.* (2007) and one by Benatti & Marcelli (2017). Both were not very distinct species and they are not accepted below. Reginaldo & Gumboski (2019) accepted some of these new species and reported them from Santa Catarina, also adding three new, so far undescribed species.

Here, we revised the species of the genus *Heterodermia* reported from Brazil based on literature references, public databases and the examination of over 500 specimens, mostly collected by ourselves and L. S. Canêz in 15 states all over the country. Fifteen species are described as new, partly based on our own material, partly by validating and describing some of the species distinguished by Martins (2007). Twelve further species are new reports for Brazil. We provide a key for all accepted species now known from Brazil.

## Material and Methods

We based our investigations on reports in the pertinent literature (e.g. Kurokawa 1962, 1998; Eliasaro 1992; Eliasaro & Fleig 1994; Martins 2007; Moberg 2011; Mongkolsuk *et al.* 2015), the observation of material and after consulting the databases of the herbaria B, CNHLH and UPS. Identification and descriptive work was carried out at the Universidade Federal de Mato Grosso do Sul using an Olympus SZX7 stereomicroscope and an Olympus BX50 compound microscope connected to a Nikon Coolpix digital camera. Sections were mounted in water, in which all measurements were also taken. The specimens from this study are mostly preserved in the herbarium CGMS.

Descriptions use and follow generally applied terms and patterns; arachnoid denotes a floccose hyphal layer at the lower surface. The algal layer is continuous, unless specifically mentioned as discontinuous.

The chemistry of all specimens was investigated by thin-layer chromatography (TLC) using solvent A (Orange *et al.* 2001). As reported by Mongkulsuk *et al.* (2015), this solvent gives the best results for the separation of the substances generally found in *Heterodermia*. For the identification of substances, we consulted Mongkolsuk *et al.* (2015) and Schumm & Elix (2015). Many specimens were tested with potassium hydroxide (K) on the upper lobe tips; in *Heterodermia* this is the best area for spot reactions since the medulla is often thin and testing the lower surface may give other results because there are often pigments present with separate reactions. The upper surface of the lobe tip reacts yellow when only atranorin and terpenoids (and sometimes dissectic acid) are present in the cortex and medulla, respectively, and the reaction becomes red when salazinic and/or norstictic acid are also present in the medulla; when a pigment was present on the lower surface, the pigment was also tested.

Total DNA was extracted from 18 selected dried specimens, all collected in Mato Grosso do Sul, Santa Catarina and Rio Grande do Sul in 2018 and 2019 (Supplementary Material Table S1, available online), employing a modification of Murray & Thompson's (1980) protocol. A portion was macerated with the aid of a micropestle in 600 µl CTAB buffer (CTAB 2%, NaCl 1.4 M, EDTA (pH 8.0) 20 mM, Tris-HCl (pH 8.0) 100 mM). The resulting mixture was incubated for 15 min at 65 °C. A similar volume of chloroform:isoamilalcohol (24:1) was added and carefully mixed with the samples until their emulsion. It was then centrifuged for 10 min at 13 000 g and the DNA in the supernatant was precipitated with isopropanol. After a new centrifugation of 15 min at the same speed, the pellet was washed in 70% cold ethanol, centrifuged again for 2 min and dried. It was finally resuspended in 200 µl of $ddH_2O$. PCR amplification was performed with the primers ITS1F and ITS4 (White *et al.* 1990; Gardes & Bruns 1993) for 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 (for 45, 30 and 45 s respectively) and a final 72 °C step for 10 min. PCR products were checked in 1% agarose gels and positive reactions were sequenced with the primer ITS4. Chromatograms were checked searching for putative reading errors, and these were then corrected. Sequences were downloaded and analyzed with Geneious. A full search for the best scoring maximum likelihood tree was performed in RAxML (Stamatakis 2006).

## Results

Based on an evaluation of literature reports and examination of materials, we accept 68 different species of *Heterodermia* known from Brazil, 15 of which are newly described below and 10 are new records.

We adopted, following Mongkolsuk *et al.* (2015), a species concept that does not allow variations in the presence or absence of major depsidones (the notable exception being *H. casarettiana* (A. Massal.) Trevis.). We pay special attention to the variation in phyllidia morphology. It appears that phyllidia can be used as a species character when no other secondary propagules are present. The shape of the phyllidia is different in every phyllidiate species. For example, the phyllidia in *H. squamulosa* (Degel.) W. L. Culb. and *H. phyllalbicans* M. F. Souza & Aptroot vary so much that they could be termed differently. Also, the isidia of *H. crocea* R. C. Harris and *H. neocrocea* M. F. Souza & Aptroot are quite dissimilar. The distribution of the pigments on the lower surface (in an arachnoid layer, spotted or absent) is a valuable character, as already reported by Lücking *et al.* (2008).

In *Heterodermia*, TLC is usually essential for a definite identification. However, with careful application of K most of the diagnostic substances can be detected. There have been many substances reported, and for several substances various different names or identifications are in use. For the identification of substances, we followed Schumm & Elix (2015) rather than Mongkolsuk *et al.* (2015) because of inconsistencies in the data shown in the latter reference. For instance, the $R_f$ value of even the major terpenoids as given in their tables 1 and 2 differ, and differ from their illustrated TLC plate, even in order of appearance. In addition, the nomenclature of the pigments differs between their text, table and plate, to the extent that identical substances may have been listed twice under different names.

In *Heterodermia*, atranorin and zeorin are always present and thus are not diagnostic. Norstictic acid (K+ yellow → orange-red), with or without connorstictic (or rarely only connorstictic), salazinic (K+ yellow → blood red), or dissectic acid (a green spot high in solvent A) are occasionally present, and their presence is

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effective at species level. Dissectic acid was found in species belonging to three different groups and was not restricted to (and characteristic of) one subgroup as mentioned by Mongkolsuk *et al.* (2015). Pigments are also diagnostic, even though the certain identification of the emodin derivatives is not always possible. The pigments are clustered in chemosyndromes and there are only three different main chemosyndromes that can be distinguished by colour and K reaction.

Usually, additional terpenoids are also present. In solvent A, they are well separated and from top to bottom of the plate they are: T1 (6α-acetoxyhopane-22-ol, above atranorin), zeorin, T2 (spathulene, 16β-acetoxyhopane-22-ol, below zeorin), T3 (6α,16β-diacetoxyhopane-22-ol), T4 (16β-acetoxyhopane-6α, 22-diol), T5 (6α-acetoxyhopane-16β, 22-diol, always a very narrow band), japonene and leucotylin (a usually vague round spot very low on the plate).

## Phylogeny

The focus of this paper is on species, not on deeper nodes in the phylogeny. However, species are classified in genera, and the generic division of the group is in flux and as yet unsettled. In order to test the validity of the split genera and to some extent our species concept, we sequenced 18 of our more recent specimens (see Supplementary Material Table S1 & Fig. S1, available online) and added these results to publicly available sequences. In the cladogram constructed from ITS only, four of the five groups found by Mongkolsuk *et al.* (2015) could be recognized (see Supplementary Material Fig. S1). In a concatenated tree based on ITS and mtSSU, the pattern is much less clear, and in fact none of the groups, and none of the split genera are monophyletic. It is not a good sign when the more information that is added, the more confused the pattern becomes, and in any case *Heterodermia* s. str. is paraphyletic. Therefore, we do not accept the split genera introduced by Mongkolsuk *et al.* (2015), who also did not present any cladograms supporting their division. We do informally recognize an additional group, the *H. dactyliza*-group, which is morphologically and ecologically well characterized, and has been a source of confusion to some previous authors: sometimes specimens belonging to this group are included inside the *H. obscurata*-group, sometimes they belong to *Leucodermia*.

A problem with the current phylogeny of *Heterodermia* s. lat. is that the identification or even the concept of many species varies among authors. All our specimens with the same identification clustered together but, for example, specimens called *H. microphylla* (Kurok.) Skorepa from other parts of the world identified as such do not cluster with them, suggesting that different but similar species are involved.

## Key to the species of *Heterodermia* in Brazil

### *Key to the groups*

1 Thallus with lower cortex . . . . . 1. **Heterodermia** sensu stricto
Thallus without lower cortex, or lower cortex along the margins only . . . . . 2

2(1) Cilia commonly white, lobes either linear and rarely branched or short and pulvinate . . . . . 3
Cilia commonly black, thallus usually sympodially branched . . . . . 4

3(2) Lobes linear and little branched . . . . . 2. **Heterodermia leucomelos** group (*Leucodermia*)
Lobes canaliculate, thallus almost pulvinate . . . . . 3. **Heterodermia comosa** group

4(2) Lobes dichotomously branched, remaining discrete, tips incurved, lower surface with marginal cortex, upper cortex generally over 200 µm thick . . . . . 4. **Heterodermia dactyliza** group
Lobes generally sympodially branched, often confluent, tips not incurved, lower surface without cortex, upper cortex generally under 150 µm thick . . . . . 5. **Heterodermia japonica/obscurata** group (including *Polyblastidium*)

### *1. Key to* Heterodermia *s. str.*

1 Thallus with isidia or phyllidia . . . . . 2
Thallus with soredia or without vegetative propagules . . . . . 6

2(1) Thallus with isidia . . . . . 3
Thallus with phyllidia . . . . . 4

3(2) Thallus K+ yellow → red, with salazinic acid . . . . . **H. antillarum** (Vain.) Swinscow & Krog
Thallus K+ yellow, without salazinic acid . . . . . **H. isidiophora** (Vain.) D. D. Awasthi

4(2) Thallus K+ yellow, without depsidones . . . . . **H. lepidota** Swinscow & Krog
Thallus K+ yellow → orange-red or red, with depsidones . . . . . 5

5(4) Thallus K+ yellow → red, with salazinic acid . . . . . **H. phyllalbicans** M. F. Souza & Aptroot
Thallus K+ yellow → orange-red, with norstictic and dissectic acid . . . . . **H. dissecta** (Kurok.) D. D. Awasthi

6(1) Thallus with soredia . . . . . 7
Thallus without soredia . . . . . 10

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7(6) Thallus K+ yellow → orange-red or red, with depsidones . . . . . 8
Thallus K+ yellow, without depsidones . . . . . 9

8(7) Thallus K+ yellow → orange-red, with norstictic acid . . . . . **H. pseudospeciosa** Kurok.
Thallus K+ yellow → red, with salazinic acid . . . . . **H. albicans** (Pers.) Swinscow & Krog

9(7) Lobes elongated, spores over 30 µm long . . . . . **H. speciosa** (Wulf.) Trevis.
Lobes short, spores under 30 µm long . . . . . **H. tremulans** (Müll. Arg.) Culb.

10(6) Medulla with yellow pigment . . . . . **H. rugulosa** (Kurok.) Wetmore
Thallus without yellow pigment . . . . . 11

11(10) Thallus with pseudocyphellae . . . . . **H. diademata** (Taylor) D. D. Awasthi
Thallus without pseudocyphellae . . . . . 12

12(11) Thallus with dissectic acid . . . . . **H. dissecticodiademata** M. F. Souza & Aptroot
Thallus without dissectic acid . . . . . **H. major** (Nyl.) Trevis.

### *2. Key to the* H. leucomelos *group*

1 Thallus with phyllidia . . . . . **H. borphyllidiata** (Kalb & Meesim) M. F. Souza & Aptroot
Thallus without phyllidia . . . . . 2

2(1) Lower surface with brown to brick red colour . . . . . 3
Lower surface without pigment or with yellow or pink colour . . . . . 4

3(2) Lower surface brown, K− . . . . . **H. fertilis** Moberg
Lower surface brick red, K+ red . . . . . **H. vulgaris** (Vain.) Follm. & Redón

4(2) Lower surface without pigment or with pink pigment . . . . . 5
Lower surface with yellow, K+ greenish yellow pigment . . . . . 8

5(4) Lobes ending in curls . . . . . **H. circinalis** (Zahlbr.) W. A. Weber
Lobes remaining flattened . . . . . 6

6(5) Thallus K+ yellow → red, with salazinic acid . . . . . **H. leucomelos** (L.) Poelt
Thallus K+ yellow, without depsidones . . . . . 7

7(6) Thallus with tubercles . . . . . **H. sublinearis** M. P. Marcelli & M. F. N. Martins
Thallus without tubercles . . . . . **H. boryi** (Fée) Kr. P. Singh & S. R. Singh

8(4) Thallus K+ yellow → red, with salazinic acid . . . . . **H. caneziae** M. F. Souza & Aptroot
Thallus K+ yellow, without depsidones . . . . . **H. lutescens** (Kurok.) Follm.

### *3. Key to the* H. comosa *group*

1 Upper surface with cilia . . . . . 2
Upper surface without cilia . . . . . 10

2(1) Lower surface with soredia . . . . . 3
Lower surface without soredia . . . . . 5

3(2) Soralia lip-shaped . . . . . **H. macrosoraliata** M. P. Marcelli & M. F. N. Martins
Soralia not lip-shaped . . . . . 4

4(3) Lower surface with pigment . . . . . **H. sorediosa** Michlig *et al.*
Lower surface without pigment . . . . . **H. namaquana** Brusse

5(2) Lower surface with orange pigment . . . . . **H. neocomosa** M. P. Rodríguez *et al.*
Lower surface without pigment . . . . . 6

6(5) Lower surface veined . . . . . **H. mobergiana** Michlig *et al.*
Lower surface not veined . . . . . 7

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7(6) Thallus with helmet-shaped lobes . . . **H. comosa** (Eschw.) Follm. & Redon
Thallus without helmet-shaped lobes . . . 8

8(7) Thallus K+ yellow → red, with norstictic and salazinic acid . . . **H. cubensis** (Kurok.) Trass
Thallus K+ yellow, without norstictic and/or salazinic acid . . . 9

9(8) Cilia partly with black tips . . . **H. stellata** (Vain.) W. A. Weber
Cilia white . . . **H. spinigera** (Kurok.) Moberg

10(1) Thallus with lip-shaped soralia . . . 11
Thallus without soralia . . . 13

11(10) Thallus with norstictic acid . . . **H. allardii** (Kurok.) Trass
Thallus without norstictic acid . . . 12

12(11) Thallus closely appressed, without cilia . . . **Heterodermia** sp. 1
Thallus pulvinate to ascending, with marginal cilia . . . **H. galactophylla** (Tuck.) W. Culb.

13(10) Lower surface with pigment . . . **H. hypochracea** (Vain.) Swinscow & Krog
Lower surface without pigment . . . 14

14(13) Thallus K+ yellow → orange-red, with norstictic acid, marginal cilia forming a dense mat . . . **H. barbifera** (Nyl.) Kr. P. Singh
Thallus K+ yellow, without norstictic acid . . . 15

15(14) Apothecia with cilia . . . **H. trichophora** (Kurok.) Trass
Apothecia without cilia . . . 16

16(15) Apothecia laminal . . . **H. palpebrata** (Tayl.) Trass
Apothecia terminal . . . **H. podocarpa** (Bél.) D. D. Awasthi

### *4. Key to the* H. dactyliza *group*

1 Lower surface with yellow pigment . . . **H. flavodactyliza** M. F. Souza & Aptroot
Lower surface without yellow pigment . . . 2

2(1) Thallus K+ yellow, without depsidones . . . **H. dactyliza** (Nyl.) Swinscow & Krog
Thallus K+ yellow → orange-red or red, with depsidones . . . 3

3(2) Thallus K+ yellow → orange-red, with norstictic acid . . . **H. nigromarginata** M. F. Souza & Aptroot
Thallus K+ yellow → red, with salazinic acid . . . **Heterodermia** sp. 2

### *5. Key to the* H. japonica/obscurata *group*

1 Thallus with isidia or phyllidia . . . 2
Thallus with soredia or without vegetative propagules . . . 9

2(1) Thallus with isidia . . . 3
Thallus with phyllidia . . . 5

3(2) Lower surface without pigment . . . **H. corallophora** (Tayl.) Skorepa
Lower surface with pigment . . . 4

4(3) Isidia partly decorticate . . . **H. neocrocea** M. F. Souza & Aptroot
Isidia corticate . . . **H. crocea** R. C. Harris

5(2) Lower surface with yellow pigment . . . 6
Lower surface without pigment . . . 7

6(5) Yellow pigment present as tiny spots . . . **H. flavulifera** M. F. Souza & Aptroot
Yellow or orange pigment present in an arachnoid layer . . . **H. flavosquamosa** Aptroot & Sipman

7(5) Thallus K+ yellow → orange-red, with norstictic acid . . . **H. appendiculata** (Kurok.) Swinscow & Krog
Thallus K+ yellow, without norstictic acid . . . 8

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8(7) Phyllidia partly ecorticate, partly granular . . . . . **H. microphylla** (Kurok.) Skorepa
Phyllidia corticate, dorsiventral . . . . . **H. squamulosa** (Degel.) W. L. Culb

9(1) Thallus with soredia . . . . . 10
Thallus without soredia . . . . . 18

10(9) Lower surface with yellow or orange pigment . . . . . 11
Lower surface without yellow or orange pigment . . . . . 14

11(10) Yellow pigment K+ green . . . . . **H. casarettiana** (A. Massal.) Trevis.
Yellow or orange pigment K+ red to purple . . . . . 12

12(11) Yellow pigment present as tiny spots . . . . . **H. delicatula** M. P. Marcelli & M. F. N. Martins
Yellow or orange pigment present in arachnoid layer . . . . . 13

13(12) Lower pigment bright yellow . . . . . **H. subcitrina** Moberg
Lower pigment ochraceous to orange . . . . . **H. obscurata** (Nyl.) Trevis.

14(10) Thallus K+ yellow, without depsidones . . . . . 15
Thallus K+ yellow → orange-red or red, with depsidones . . . . . 16

15(14) Lower cortex absent . . . . . **H. japonica** (Sâto) Swinscow & Krog
Lower surface with a thin false cortex without rhizines . . . . . **H. spathulifera** Moberg

16(14) Thallus K+ yellow → red, with salazinic acid . . . . . **H. hypocaesia** (Yasuda ex Räsänen) D. D. Awasthi
Thallus K+ yellow → orange-red, with norstictic acid . . . . . 17

17(16) Soralia labriform . . . . . **H. labiata** M. P. Marcelli & M. F. N. Martins
Soralia irregular . . . . . **H. propagulifera** (Vain.) Dey

18(9) Lower surface with yellow to orange pigment . . . . . 19
Lower surface without pigment . . . . . 25

19(18) Thallus with depsidones, K+ yellow → orange-red or red, rarely only yellow . . . . . 20
Thallus without depsidones, always K+ yellow . . . . . 23

20(19) Yellow or orange pigment K+ red to purple . . . . . 21
Yellow pigment K+ green . . . . . **H. amphilacinulata** M. F. N. Martins & M. P. Marcelli

21(20) Thallus K+ yellow, with dissectic acid . . . . . **H. dissecticoflabellata** M. F. Souza & Aptroot
Thallus K+ yellow → orange-red, with norstictic acid . . . . . 22

22(21) Yellow pigment present as tiny spots . . . . . **H. dendritica** (Pers.) Poelt
Yellow or orange pigment present in an arachnoid layer . . . . . **H. corcovadensis** (Kurok.) Elix

23(19) Yellow or orange pigment K+ red to purple . . . . . 24
Yellow pigment K+ green . . . . . **H. lamelligera** (Taylor) Trass

24(23) Secondary lobes without pseudocyphellae; main lobes over 1 mm wide . . . . . **H. flabellata** (Fée) D. D. Awasthi
Secondary lobes with pseudocyphellae; main lobes under 1 mm wide . . . . . **H. minor** M. F. Souza & Aptroot

25(18) Thallus K+ yellow → orange-red or red, with depsidones . . . . . 26
Thallus K+ yellow, without depsidones . . . . . 27

26(25) Thallus K+ yellow → red, with salazinic acid . . . . . **H. spielmannii** M. F. Souza & Aptroot
Thallus K+ yellow → orange-red, with norstictic acid . . . . . **H. africana** (Kurok.) M. F. Souza & Aptroot

27(25) Ascospores over 35 µm . . . . . **H. magellanica** (Zahlbr.) Swinscow & Krog
Ascospores under 35 µm . . . . . **H. hypoleuca** (Ach.) Trevis.

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## Taxonomy

### New species

### *Heterodermia amphilacinulata* M. F. N. Martins & M. P. Marcelli sp. nov.

MycoBank No.: MB 839878

Similar to *H. flabellata* but with the yellow pigment K+ green.

Type: Brazil, São Paulo State, municipality of São Bento do Sapucaí, corticolous, 15 July 1998, *Marcelli* 28792, *Gugliotta* & *Maziero* (SP—holotype).

(Fig. 1A)

*Thallus* greyish white, loosely adnate, up to 15 cm in width, 225–450 µm thick; upper cortex 225–250 µm thick, lower cortex lacking. *Lobes* with anisotomic dichotomous ramifications, 3.0–6.0 × 0.7–1.2 mm, flat to slightly convex. *Soredia*, *phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate with yellow arachnoid pigment. *Cilia* 1.0–3.0 × 0.1–0.2 mm, mostly black, simple when young, soon becoming squarrosely branched, projecting outwards and forming a mat.

*Apothecia* 1.0–4.5 mm diam., laminal to submarginal; margin lacinulate with lower side of the lacinules having yellow pigment; disc concave, epruinose, brown; *ascospores* ellipsoid, 39–50 × 19–24 µm, sporoblastidia 1 to 4.

*Chemistry.* Atranorin, zeorin, 6α,16β-diacetoxyhopane-22-ol (T3), 6α-acetoxyhopane-16β, 22-diol (T5), hybocarpone, demethylhybocarpone. Thallus K+ yellow; yellow pigment K+ green.

*Etymology.* Named after the lacinulae that are present on the amphithecium.

*Distribution and ecology.* Known only from São Paulo State, in Atlantic rainforest and the Cerrado.

*Discussion.* This is similar to *H. flabellata*, but with the yellow pigment K+ green. It has the same chemistry as *H. casarettiana* (A. Massal.) Trevis. and they can be considered a species pair.

*Additional specimen examined.* **Brazil:** *São Paulo State*: Mogi-Guaçu Municipality, corticolous, 1995, *Marcelli* 29373, *Marbach, Ribeiro* & *Luchi* (SP).

### *Heterodermia caneziae* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839879

Similar to *H. lutescens* but with salazinic acid.

Type: Brazil, Rio Grande do Sul State, Vacaria, Fazenda da Estrela, corticolous, 12 January 2004, *Canêz* 988 & *Spielmann* (CGMS—holotype).

(Fig. 1B)

*Thallus* pale ochraceous grey, rather loosely hanging to subfruticose, up to 6.5 cm wide, 150–200 µm thick; upper cortex 50–75 µm thick, lower cortex lacking. *Lobes* with dichotomous ramifications, leaving large interspaces, not laterally overlapping, 3.0–6.0 × 0.8–1.2 mm, flat to slightly concave. *Soredia*, *phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate, but with a broad corticate margin, with K+ greenish yellow pigment. *Cilia* rather abundant, black, 0.2 × 2–5 mm, mostly simple, some sparingly dichotomously branched.

*Apothecia* unknown.

*Chemistry.* Atranorin, zeorin, salazinic acid, and the unknown lutescens pigment. Thallus K+ yellow; pigment K+ greenish yellow.

*Etymology.* Named after our colleague and esteemed teacher Luciana da Silva Canêz.

*Distribution and ecology.* Known only from Rio Grande do Sul, in Atlantic rainforest.

*Discussion.* This species is similar to *H. lutescens* (Kurok.) Follmann but with salazinic acid.

### *Heterodermia delicatula* M. P. Marcelli & M. F. N. Martins sp. nov.

MycoBank No.: MB 839888

Similar to *H. obscurata* but the pigment on the lower surface is restricted to tiny spots.

Type: Brazil, São Paulo, Ubatuba, Parque Estadual da Serra do Mar, corticolous, 17 March 2006, *Martins* 578 & *Jungbluth* (SP—holotype).

(Fig. 1C & D)

*Thallus* greenish to whitish grey, loosely adnate to elevated, up to 7.5 cm in width, 110–135 µm thick; upper cortex 10–60 µm thick, algal layer subcontinuous, 20–60 µm, lower cortex lacking. *Lobes* with sympodial to irregular ramifications, leaving large interspaces to laterally overlapping, 1.5–3.0 × 1.0–2.0 mm, flat to slightly convex. *Soredia* farinose, in labriform soralia at the end of secondary lobes, whitish grey. *Phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate with yellow arachnoid pigment in tiny spots. *Cilia* 1.0–3.0 × 0.1–0.2 mm, mostly black, simple when young, soon becoming squarrosely branched, projecting outwards.

*Apothecia* unknown.

*Chemistry.* Atranorin, zeorin, 6α-acetoxyhopane-22-ol (T1), 6α,16β-diacetoxyhopane-22-ol (T3), leucotylin, 7-chloroemodin, and other emodin derivatives. Thallus K+ yellow; pigment K+ violet.

*Etymology.* Named after the fragile thallus.

*Distribution and ecology.* Known only from the states of Paraná, São Paulo and Santa Catarina, in Atlantic rainforest and the Cerrado.

*Discussion.* This species is similar to *H. obscurata* (Nyl.) Trevis. but the pigment on the lower surface is restricted to tiny spots.

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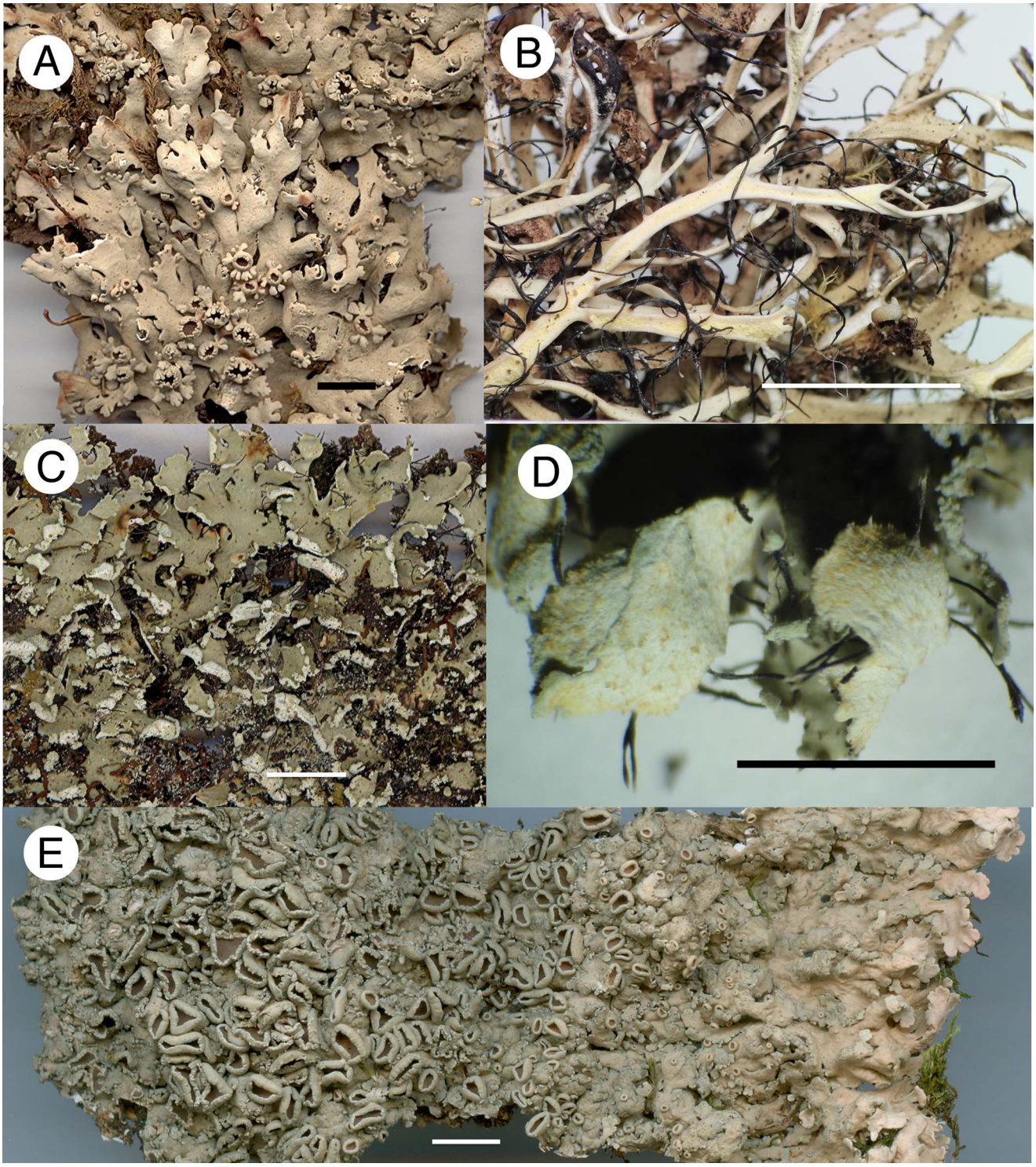


**Fig. 1.** Holotypes of new species of *Heterodermia*. A, *H. amphilacinulata*. B, *H. caneziae*. C & D, *H. delicatula* (D, lower surface showing the pigment in spots). E, *H. dissecticodiademata*. Scales = 5 mm. In colour online.

*Additional specimens examined.* **Brazil:** *São Paulo State*: same details as the type, *Martins* & *Jungbluth* 576, 583, 584; Parque Estadual da Cantareira, vi 2000, *Benatti* s. n.; Ilha Comprida, 2004, *Canêz* et al. 1267; Botucatu, 2006, *Martins* et al. 1245 (all in SP herbarium). *Paraná*: 2020, *Aptroot* & *Souza* 82129 (on leaves), 82178 & 82187 (all CGMS). Also reported from Santa Catarina State by Reginaldo & Gumboski (2019).

### *Heterodermia dissecticodiademata* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839889

Similar to *H. diademata* but with dissectic acid.

Type: Brazil, Rio Grande do Sul, Porto Alegre, near the Laguna Guaíba lake, corticolous, 27 September 2014, *Cáceres* 22247 & *Aptroot* (CGMS—holotype; ABL—isotype).

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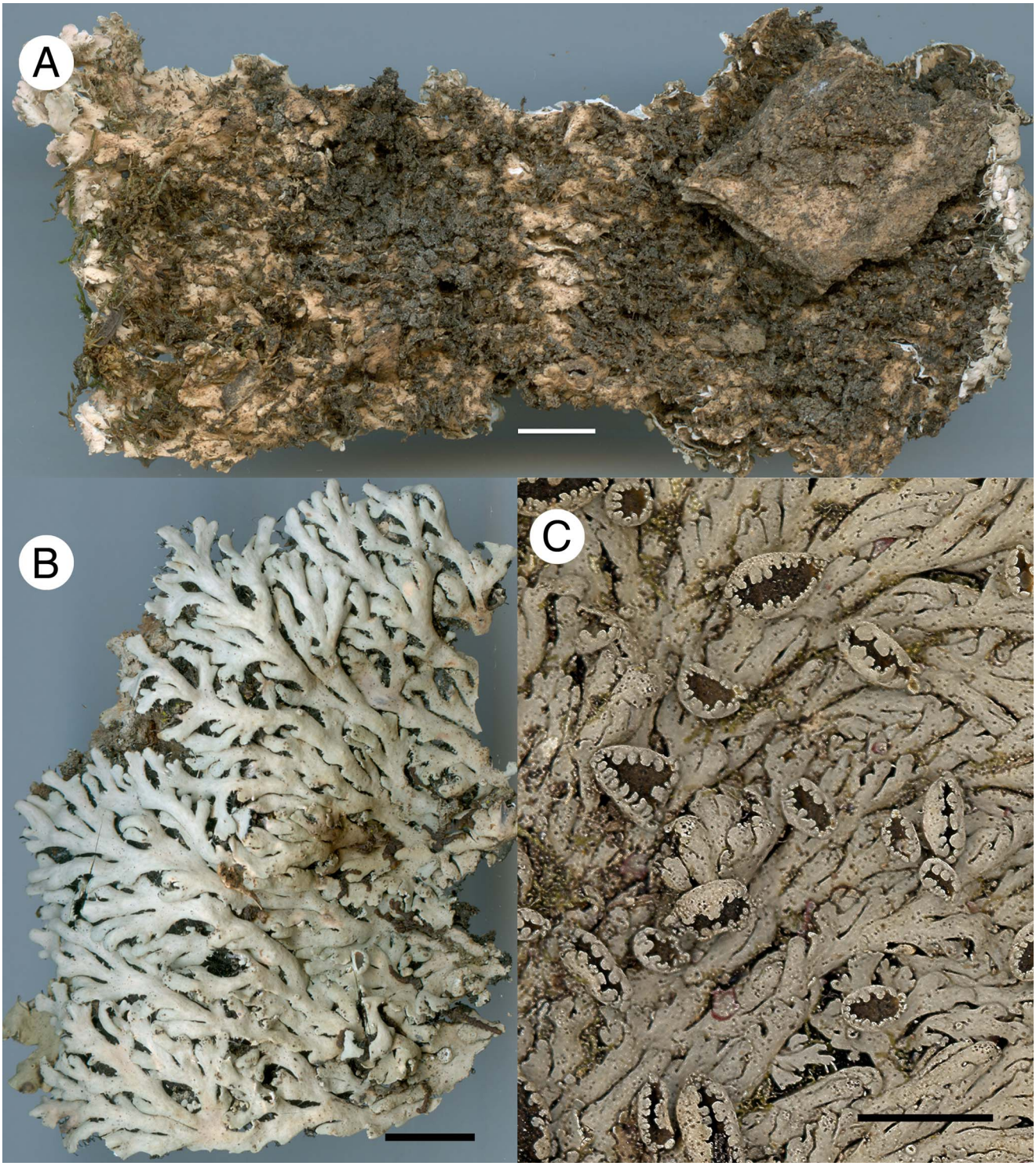


**Fig. 2.** Holotypes of new species of *Heterodermia*. A, *H. dissecticodiademata* (lower surface). B, *H. dissecticoflabellata*. C, *H. flavodactyliza*. Scales = 5 mm. In colour online.

(Fig. 1E, 2A)

*Thallus* mineral grey with pink coloration towards the lobe tips, loosely adnate, up to 8.5 cm in width, 250–350 µm thick; upper cortex *c.* 35 µm thick, lower cortex *c.* 35 µm thick. *Lobes* with a sympodial ramification, laterally overlapping, leaving almost no open spaces, in most parts of the thallus completely confluent, up to 1.5 cm long, 2.0–3.5 mm wide, flat to slightly concave or convex, tips crenulate, without pseudocyphellae. *Soredia*, *phyllidia* and *isidia* absent, but central part of the thallus with minute secondary lobules that occasionally extend to the apothecium margins. *Medulla* white. *Lower surface* pale ochraceous, some lobe tips pinkish. *Rhizines* abundant, whitish to pale ochraceous or partly grey, on the marginal lobes simple, *c.* 0.50 × 0.05 mm, on

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the central part of the thallus becoming sparsely branched and up to 2 mm long, not projecting outwards.

*Apothecia* common, covering most of the thallus, cupulate, often almost closed and elongate in outline, up to 3.5 mm diam., laminal; margin grey, *c.* 1 mm wide, incurved, crenulate; disc deeply concave, epruinose, pale brown; *ascospores* 8 per ascus, fusiform to citriform, brown, 1-septate, thick-walled, 25–29 × 11–13 µm, without sporoblastidia.

*Chemistry.* Atranorin, dissectic acid, zeorin, 6α,16β-diacetoxyhopane-22-ol (T3), 6α-acetoxyhopane-16β, 22-diol (T5), japonene. Thallus K+ yellow.

*Etymology.* A fertile species with dissectic acid.

*Distribution and ecology.* Known only from Rio Grande do Sul State, in urban areas, and Santa Catarina State, in the Atlantic rainforest biome.

*Discussion.* This species is similar to *H. diademata*, but with dissectic acid. *Heterodermia verdonii* Elix is also similar and has the same chemistry but has copious pseudocyphellae. The decomposition of dissectic acid may cause the pinkish colour on the lobe tips.

*Additional specimen examined.* **Brazil:** *Santa Catarina*: Riqueza Municipality, *Spielmann* s. n. (CGMS).

### *Heterodermia dissecticoflabellata* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839890

Similar to *H. flabellata*, but contains dissectic acid.

Type: Brazil, Mato Grosso do Sul, Bonito, Fazenda Marambaia, corticolous on *Myrsine,* 30 October 2018, *Aptroot* 77031 & *Souza* (CGMS—holotype; ABL—isotype). GenBank Nos: OK058284 (ITS) and OK058302 (mtSSU).

(Fig. 2B)

*Thallus* mineral grey, rather tightly adnate, up to 6.5 cm wide, 180–250 µm thick; upper cortex 100–125 µm thick, lower cortex lacking. *Lobes* with anisotomic ramifications, leaving large interspaces, not laterally overlapping, 3.5–4.0 × 1.5–2.5 mm, flat to slightly convex. *Soredia*, *phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate with yellow arachnoid pigment. *Cilia* 0.5–0.9 × 0.1–0.2 mm, mostly black but often with whitish base, simple, projecting outwards.

*Apothecia* 1.7–2.0 mm, laminal to submarginal; margin dentate; disc concave, epruinose, brown; *ascospores* 8 per ascus, ellipsoid, distinctly curved, 1-septate, thick-walled, 25–30 × 13–15 µm, without sporoblastidia, lumina angular.

*Chemistry.* Atranorin, dissectic acid, zeorin, 6α,16β-diacetoxyhopane-22-ol (T3), 16β-acetoxyhopane-6α, 22-diol (T4), leucotylin, 7-chloroemodin, and probably chloroskyrin. Thallus K+ yellow; pigment K+ purple.

*Etymology.* The name refers to the similarity with *H. flabellata* but containing dissectic acid.

*Distribution and ecology.* Known only from Mato Grosso do Sul and Minas Gerais, in Atlantic rainforest.

*Discussion.* This species is very similar to *H. flabellata* but it contains dissectic acid.

*Additional specimens.* **Brazil:** *Mato Grosso do Sul*: Jardim, 2018, *Aptroot* 77474; Campo Grande, 2019, *Aptroot* 79034. *Minas Gerais*: Itatiaia, 2009, *Spielmann* 7651 (all CGMS).

### *Heterodermia flavodactyliza* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839891

Similar to *H. dactyliza* but with orange, K+ violet pigment on the lower surface.

Type: Brazil, Minas Gerais, Caraça, corticolous, 2 April 2006, *Spielmann* 2925 (SP—holotype).

(Fig. 2C)

*Thallus* mineral grey, tightly adnate, more than 6.5 cm wide, 325–400 µm thick; upper cortex 100–165 µm thick, lower cortex lacking. *Lobes* with anisotomic ramifications, contiguous but not confluent, without interspaces, not laterally overlapping, 3.0–6.0 × 1.0–1.7 mm, flat to slightly convex. *Soredia*, *phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* mostly ecorticate with yellow arachnoid pigment, with corticate margins of 0.2 mm wide. *Cilia* black, projecting outwards, rather sparse, simple, 0.5–1.2 × 0.2 mm.

*Apothecia* 4.0–6.0 mm, laminal to submarginal; margin dentate; disc concave, epruinose, brown; *ascospores* 8 per ascus, ellipsoid, distinctly curved, 1-septate, thick-walled, 30–37 × 13–16 µm, with 2–4 sporoblastidia.

*Chemistry.* Atranorin, zeorin, emodin and 5,7-dichloroemodin. Thallus K+ yellow; pigment K+ purple.

*Etymology.* The name refers to the similarity with *H. dactyliza*, but with a yellow-orange pigment on the lower surface.

*Distribution.* Known only from Minas Gerais, in the Atlantic rainforest biome.

*Discussion.* This species is similar to *H. dactyliza* (Nyl.) Swinscow & Krog but with an orange, K+ violet pigment on the lower surface.

### *Heterodermia flavulifera* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839892

Similar to *H. flavosquamosa* but with spotted pigment.

Type: Brazil, Rio Grande do Sul, Vacaria, Fazenda da Estrela, saxicolous, 10 January 2004, *Canêz* 1056 (CGMS—holotype).

(Fig. 3A)

*Thallus* greenish to whitish grey, loosely adnate to elevated, up to 7.0 cm in width, 200–250 µm thick; upper cortex 30–60 µm thick, lower cortex lacking. *Lobes* with sympodial to irregular ramifications, leaving interspaces, laterally overlapping, 4.0–6.0 × 1.0–1.5

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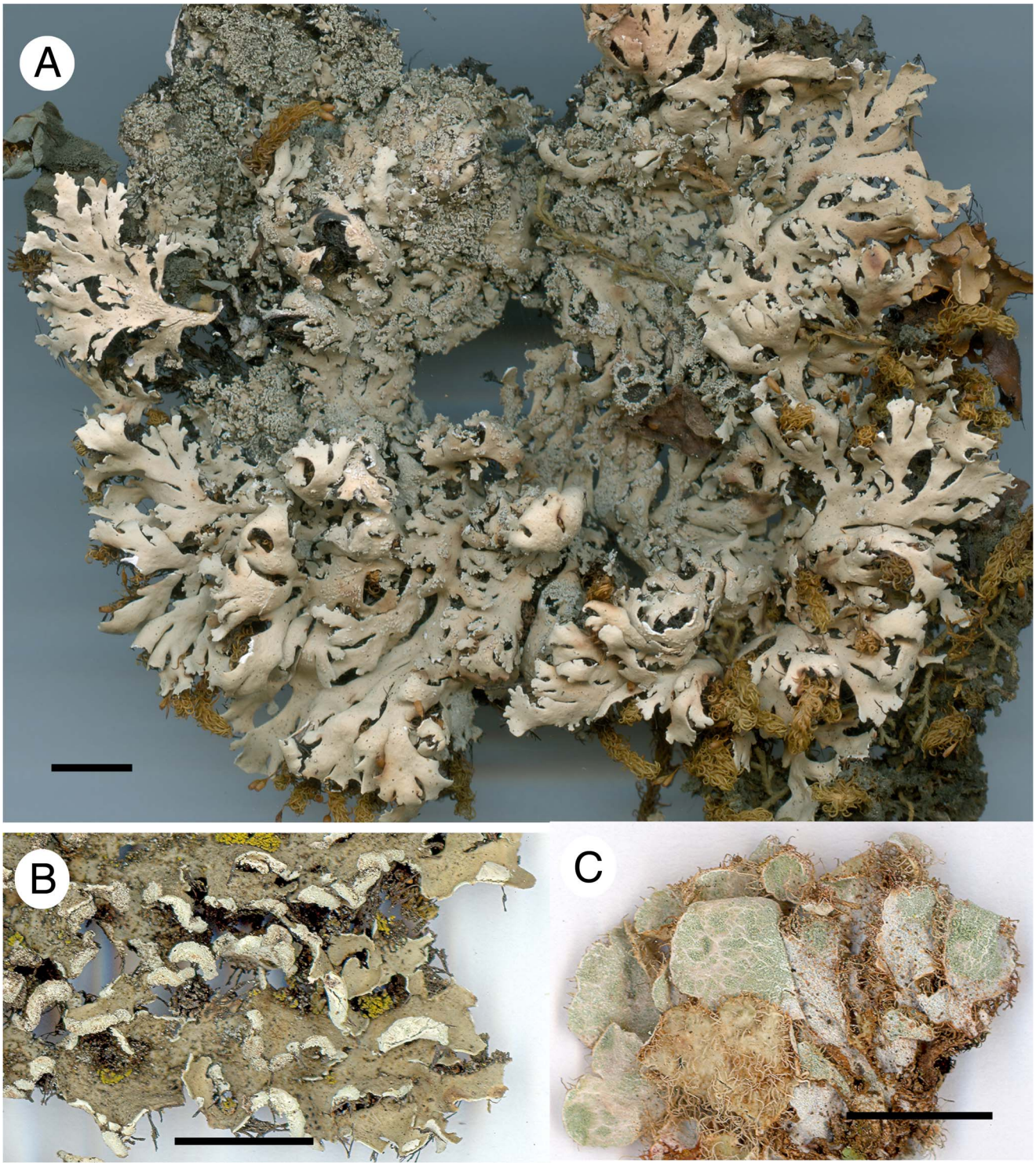


**Fig. 3.** Holotypes of new species of *Heterodermia*. A, *H. flavulifera*. B, *H. labiata*. C, *H. macrosoraliata*. Scales = 5 mm. In colour online.

mm, flat to slightly convex. *Soredia* and *isidia* absent. *Phyllidia* copious in the centre of the thallus, flat to upright, dissected, *c.* 0.2–0.5 mm. *Medulla* brown. *Lower surface* ecorticate with yellow spotted pigment. *Cilia* 1.5–2.0 × 0.1–0.2mm, mostly black, simple when young, soon becoming dichotomously branched, projecting outwards.

*Apothecia* 2.0–5.0 mm, laminal to submarginal; margin with phyllidia; disc concave, epruinose, black; *ascospores* ellipsoid, 1-septate, thick-walled, 37–42 × 18–21 µm, without sporoblastidia, lumina spade-shaped.

*Chemistry.* Atranorin, zeorin, 16β-acetoxyhopane-6α, 22-diol (T4), emodin and 5,7-dichloroemodin. Thallus K+ yellow; pigment K+ purple.

*Etymology.* Bearing yellow spots.

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*Distribution and ecology.* Known only from Rio Grande do Sul, in Atlantic rainforest.

*Discussion.* This species is similar to *H. flavosquamosa* but with a spotted pigment.

*Additional specimen examined.* **Brazil:** *Rio Grande do Sul*: same locality and date as the type, corticolous, *Canêz* 1028 (CGMS).

### *Heterodermia labiata* M. P. Marcelli & M. F. N. Martins sp. nov.

MycoBank No.: MB 839893

Similar to *H. japonica* but with norstictic acid and labriform soralia.

Type: Brazil, São Paulo, Parque Estadual das Fontes do Ipiranga, corticolous, 24 August 2000, *Marcelli* 34718 & *Andrade* (SP—holotype).

(Fig. 3B)

*Thallus* greenish grey, loosely adnate to elevated, up to 5.5 cm in width, 175–200 µm thick; upper cortex 10–60 µm thick, algal layer subcontinuous, 25–45 µm thick, lower cortex lacking. *Lobes* with sympodial to irregular ramifications, leaving large interspaces to laterally overlapping, 1.5–3.0 × 1.0–2.0 mm, flat to slightly convex. *Soredia* farinose, in labriform soralia at the ends of secondary lobes, whitish grey. *Phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate without pigment. *Cilia* 1.0–3.0 × 0.1–0.2 mm, mostly black, simple when young, soon becoming squarrosely branched, projecting outwards.

*Apothecia* unknown.

*Chemistry.* Atranorin, norstictic acid, zeorin and 6α,16β-diacetoxyhopane-22-ol (T3). Thallus K+ yellow → orange-red.

*Etymology.* Named after the labiate soralia.

*Distribution and ecology.* Known only from São Paulo, in urban areas and Atlantic rainforest.

*Discussion.* This species is similar to *H. japonica* but with norstictic acid and labriform soralia.

*Additional specimens examined.* **Brazil:** *São Paulo*: same locality and date as the type, *Marcelli* & *Andrade* 34694; *ibid*., 2006, *Martins* 375 & 376; Ubatuba, Parque Estadual da Serra do Mar, 2006, *Martins* & *Jungbluth* 556 (all in SP).

### *Heterodermia macrosoraliata* M. P. Marcelli & M. F. N. Martins sp. nov.

MycoBank No.: MB 839894

Similar to *H. galactophylla* but with cilia on the upper surface, and with norstictic acid.

Type: Brazil, São Paulo, Pratânia, Fazenda Palmeira da Serra, corticolous, 7 May 2006, *Martins* 1134 & *Kitaura* (SP—holotype).

(Fig. 3C)

*Thallus* greenish to whitish grey, pulvinate to loosely adnate, up to 2.5 cm in width, 110–250 µm thick; upper cortex 35–110 µm thick, lower cortex lacking, algal layer discontinuous. *Lobes* spathulate, with few irregular ramifications, laterally overlapping, 2.0–3.5 mm wide, flat to convex, ending in large soralia on the lower surface becoming up to 2.0 mm. *Soredia* granular, in large and well-developed soralia with greenish coloration, which dominate the thallus aspect. *Phyllidia* and *isidia* absent. *Medulla* white. *Upper surface* with white cilia. *Lower surface* ecorticate, white, without corticate margin. *Cilia* 0.1–1.2 × 0.1 mm, mostly whitish, simple.

*Apothecia* unknown.

*Chemistry.* Atranorin, norstictic acid and zeorin. Thallus K+ yellow → orange-red.

*Etymology.* Named after the large soralia.

*Distribution and ecology.* Known only from São Paulo and Santa Catarina, in the Cerrado and Atlantic rainforest.

*Discussion.* This species is similar to *H. galactophylla* but with cilia on the upper surface, and norstictic acid present. It was described as '*Heterodermia manuelensis*' by Martins (2007).

*Additional specimens examined.* **Brazil:** *São Paulo*: same locality and date as the type, *Martins* & *Kitaura* 1131, 1132 & 1174 (all in SP). Also reported from Santa Catarina State by Reginaldo & Gumboski (2019).

### *Heterodermia minor* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839895

Similar to *H. flabellata* but main lobes less than 1 mm wide and secondary lobes with pseudocyphellae.

Type: Brazil, Mato Grosso, Cuiabá, Chapada dos Guimarães, corticolous, 12–19 September 2020, *Aptroot* 81780 & *Souza* (CGMS—holotype; ABL—isotype).

(Fig. 4A)

*Thallus* mineral grey, rather tightly adnate, up to 5 cm wide, 200–250 µm thick; upper cortex 100–125 µm thick, lower cortex lacking. *Lobes* with anisotomic ramifications, leaving interspaces, barely laterally overlapping, 1.5–2.5 × 0.7–0.9 mm, flat to slightly convex. Secondary lobes (lobes in the central part of the thallus) divergent (curved outwards), mostly ending in a white pseudocyphella. *Soredia*, *phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate with yellow-orange arachnoid pigment. *Cilia* 0.3–0.6 × 0.1 mm, mostly black, simple, projecting outwards.

*Apothecia* unknown.

*Chemistry.* Atranorin, zeorin, 6α,16β-diacetoxyhopane-22-ol (T3) and 7-chloroemodin. Thallus K+ yellow; pigment K+ purple.

*Etymology.* The name refers to the small size, compared to the only other *Heterodermia* species with pseudocyphellae, the large *H. major*.

*Distribution and ecology.* Known only from Mato Grosso State, in Cerrado forest.

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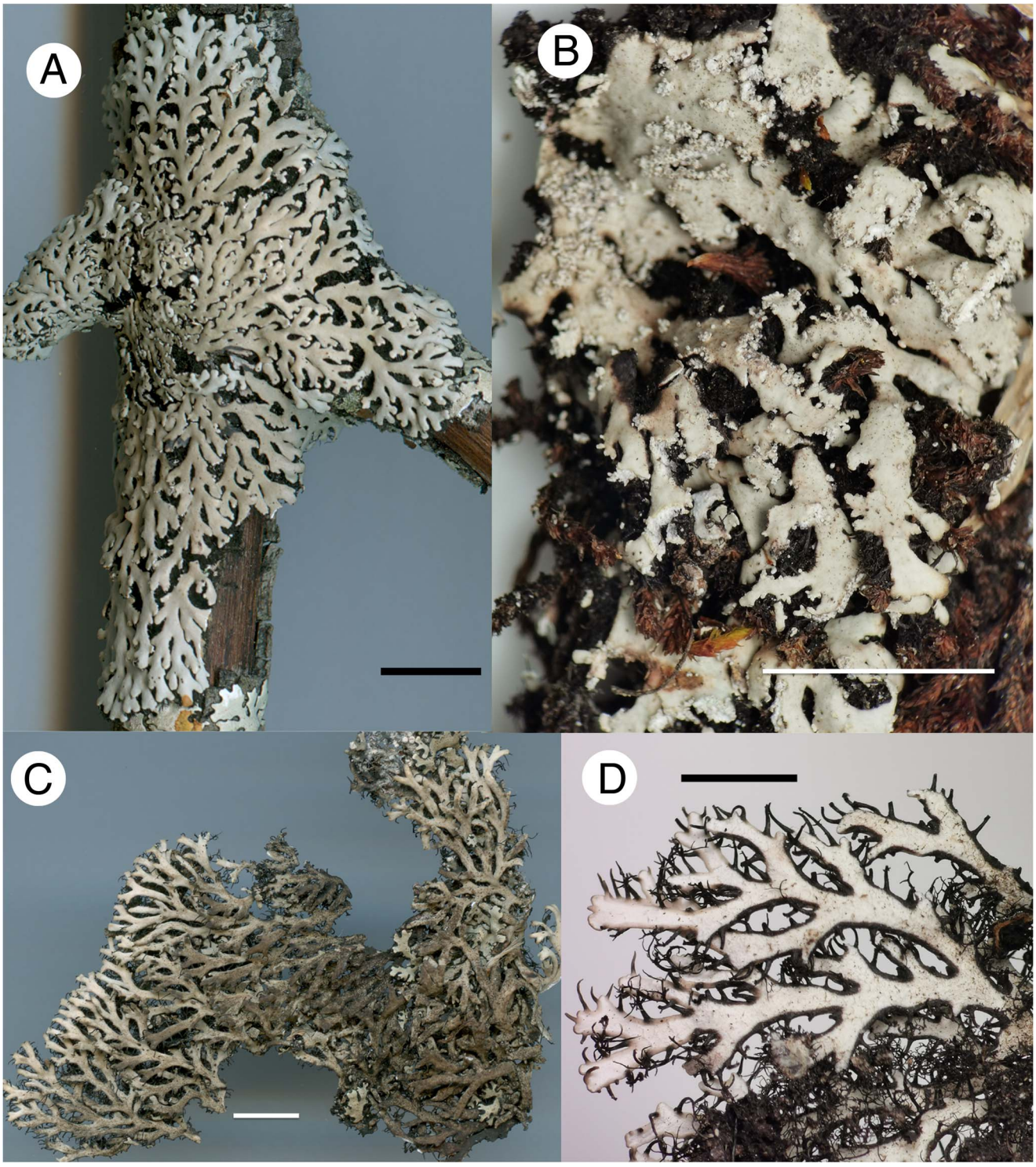


**Fig. 4.** Holotypes of new species of *Heterodermia*. A, *H. minor*. B, *H. neocrocea*. C & D, *H. nigromarginata* (D, lower surface showing the black margins). Scales = 5 mm. In colour online.

*Discussion.* This species is similar to *H. flabellata* but the main lobes are less than 1 mm wide and the secondary lobes end in pseudocyphellae.

*Additional specimen examined.* **Brazil:** *Mato Grosso*: same locality and date as the type, *Souza* & *Aptroot* 88 (CGMS).

### *Heterodermia neocrocea* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839896

Similar to *H. crocea* but with granular, partly decorticate isidia.

Type: Brazil, Santa Catarina, Urubici, saxicolous, 19 July 2019, *Aptroot* 79672 (CGMS—holotype; ABL—isotype).

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(Fig. 4B)

*Thallus* mineral grey, loosely adnate, up to 3.0 cm in width, 150–200 µm thick; upper cortex 25–50 µm thick, lower cortex lacking. *Lobes* with sympodial to irregular ramifications, leaving large interspaces, 1.5–2.5 × 0.8–1.2 mm, flat to slightly convex. *Isidia* simple to mostly branched, mostly marginal, partly decorticate, resembling polysidiangia, whitish grey, 0.1–0.2 mm wide and high. *Soredia* and *phyllidia* absent. *Medulla* white. *Lower surface* ecorticate with yellow arachnoid pigment. *Cilia* 0.7–2.0 × 0.1 mm, sparse, black, mostly simple, rarely sparingly squarrosely branched, projecting outwards.

*Apothecia* unknown.

*Chemistry.* Atranorin, zeorin, 16β-acetoxyhopane-6α-22-diol (T4), emodin and 5,7-dichloroemodin. Thallus K+ yellow; pigment K+ purple.

*Distribution and ecology.* Known only from Santa Catarina, in Atlantic rainforest.

*Etymology.* A new species similar to *H. crocea*.

*Discussion.* This is similar to *H. crocea* but with smaller, granular, partly decorticate isidia.

### *Heterodermia nigromarginata* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839897

Similar to *H. dactyliza* but with norstictic acid and black margins on the lower surface.

Type: Brazil, Minas Gerais, Caraça, saxicolous, 5 April 2006, *Canêz* 1975 (CGMS—holotype).

(Fig. 4C & D)

*Thallus* ochraceous grey, loosely adnate, up to 9.0 cm wide, 250–300 µm thick; upper cortex 100–165 µm thick, lower cortex lacking. *Lobes* with irregularly dichotomic ramifications, leaving large interspaces, occasionally laterally overlapping, 1.5–2.5 × 0.6–0.9 mm, convex. *Soredia*, *phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate, without yellow pigment, with black corticate margins of 0.2 mm wide. *Cilia* 0.5–1.2 × 0.1–0.2 mm, black, mostly simple or irregularly branched, projecting outwards.

*Apothecia* unknown.

*Chemistry.* Atranorin, norstictic acid, 6α-acetoxyhopane-22-ol (T1), zeorin, 6α,16β-diacetoxyhopane-22-ol (T3) and japonene. Thallus K+ yellow → orange-red.

*Etymology.* Named after the black margins on the lower surface.

*Distribution and ecology.* Known only from the states of Minas Gerais and Bahia, in the Atlantic rainforest biome.

*Discussion.* This species is very similar to *H. dactyliza* but it contains norstictic acid and the lower surface has black margins.

*Additional specimen examined.* **Brazil:** *Bahia State*: Chapada Diamantina, Palmeiras Municipality, saxicolous, 2017, *Cáceres* 40911 & *Aptroot* (ISE, ABL).

### *Heterodermia phyllalbicans* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839898

Similar to *H. albicans* but with phyllidia instead of soredia.

Type: Brazil, Mato Grosso do Sul, Campo Grande, corticolous, 20 November 2019, *Aptroot* 80466 & *Souza* (CGMS—holotype; ABL—isotype).

(Fig. 5A)

*Thallus* mineral grey, tightly to loosely adnate, up to 10.0 cm in width, 100–150 µm thick; upper cortex 25–50 µm thick, lower cortex 25–50 µm thick. *Lobes* with sympodial to irregular ramifications, often laterally overlapping, 1.5–2.5 × 0.8–1.2 mm, flat to slightly concave. *Phyllidia* mostly marginal, whitish grey, becoming granular. *Soredia* and *isidia* absent. *Medulla* white. *Lower surface* corticate, pale ochraceous in colour. *Rhizines* 0.1–0.4 × 0.1 mm, pale ochraceous to black, mostly simple, rarely sparingly dichotomously branched.

*Apothecia* regularly present, sessile, 0.5–1.0 mm, laminal; margin with soredia; disc concave, epruinose, brown; *ascospores* ellipsoid, 1-septate, thick-walled, 20–24 × 11–13 µm, without sporoblastidia, lumina spade-shaped.

*Chemistry.* Atranorin, salazinic acid, zeorin, often 6α,16β-diacetoxyhopane-22-ol (T3), and sometimes also 16β-acetoxyhopane-6α, 22-diol (T4). Thallus K+ yellow → red.

*Etymology.* The name refers to the species being similar to *H. albicans* but with phyllidia.

*Distribution and ecology.* Known only from Mato Grosso do Sul State, in Cerrado forest.

*Discussion.* This species is most similar to *H. albicans* but it has phyllidia instead of soredia.

*Additional specimens examined.* **Brazil:** *Mato Grosso do Sul*: same locality as the type, 2020, *Aptroot* & *Souza* 80836–80839 & 80864; Terenos, 2010, *Spielmann* 8090 (all CGMS).

### *Heterodermia spielmannii* M. F. Souza & Aptroot sp. nov.

MycoBank No.: MB 839899

Similar to *H. hypoleuca* but with salazinic acid.

Type: Brazil, Rio Grande do Sul, Piratini, corticolous, 21 July 2011, *Spielmann* 9351 (CGMS—holotype).

(Fig. 5B & C)

*Thallus* mineral grey, rather tightly adnate, up to 6.0 cm wide, 101–250 µm thick; upper cortex 30–50 µm thick, lower cortex lacking. *Lobes* with anisotomic ramifications, occasionally leaving large interspaces, mostly laterally overlapping, 1.0–2.0 × 0.7–1.0 mm, convex, lobe tips widening, flabellate. *Soredia*, *phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate without yellow pigment. *Cilia* 1.0–2.5 × 0.1–0.2 mm, black, mostly perpendicularly branched, projecting outwards.

*Apothecia* 1.0–6.0 mm, laminal; margin dentate, often convoluted; disc concave, pruinose, brown; *ascospores* 8 per ascus, ellipsoid, distinctly curved, 1-septate, thick-walled, 30–35 × 13–16 µm,

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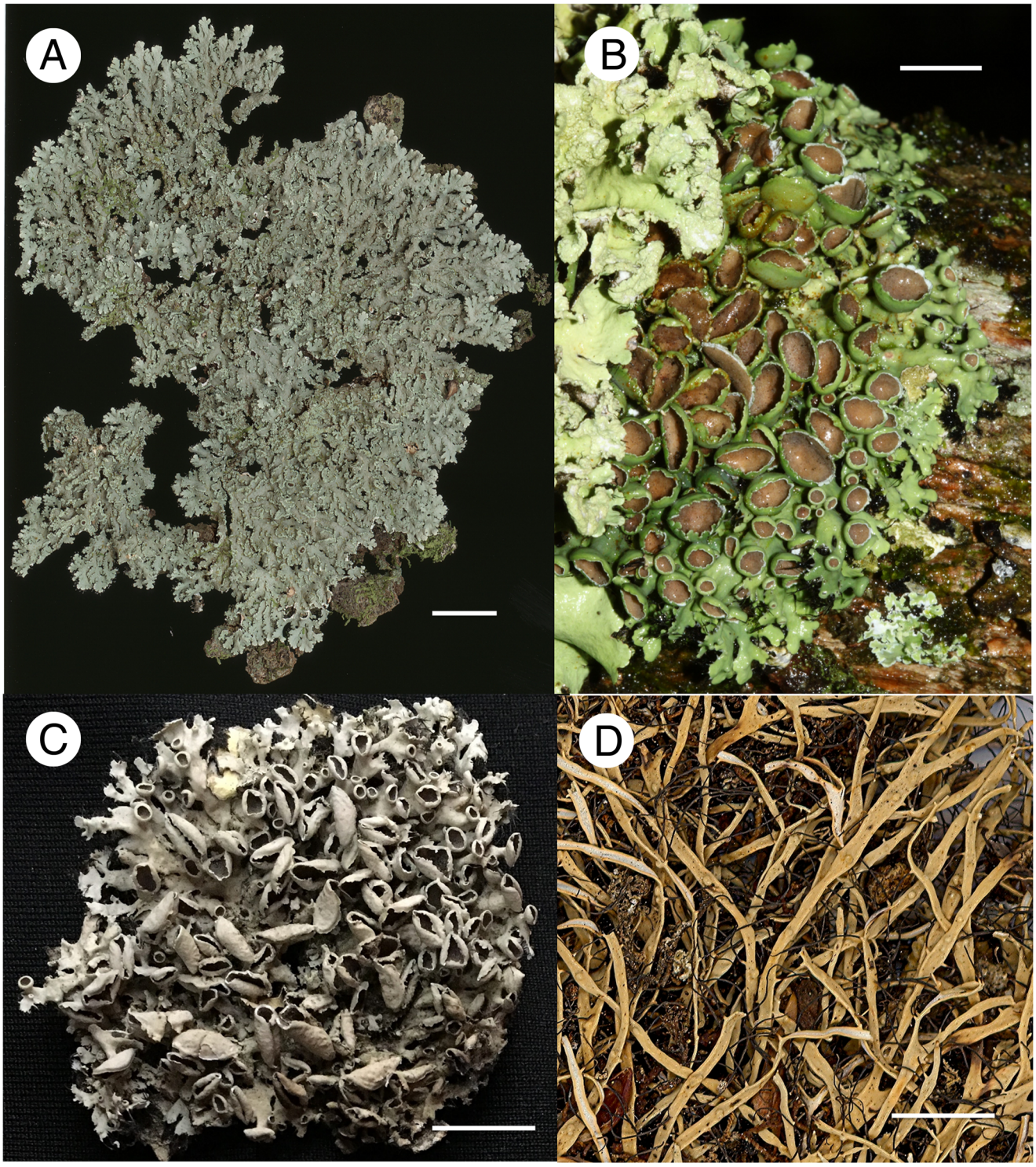


**Fig. 5.** Holotypes of new species of *Heterodermia*. A, *H. phyllalbicans*. B & C, *H. spielmannii* (B, field picture when wet). D, *H. sublinearis*. Scales = 5 mm. In colour online.

without sporoblastidia or rarely with one sporoblastidium, lumina angular.

*Chemistry.* Atranorin, zeorin and salazinic acid. Thallus K+ yellow → red.

*Etymology.* Named after our colleague and esteemed teacher, Adriano Afonso Spielmann.

*Distribution and ecology.* Known only from Rio Grande do Sul, in the Pampa biome.

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*Discussion.* This species is similar to *H. hypoleuca* but with salazinic acid.

### *Heterodermia sublinearis* M. P. Marcelli & M. F.N. Martins sp. nov.

MycoBank No.: MB 839900

Similar to *H. boryi* but with tubercles on the upper surface.

Type: Brazil, São Paulo, Campos do Jordão, terricolous, 24 November 1994, *Marcelli* 27567 & *Luchi* (SP—holotype).

(Fig. 5D)

*Thallus* pale ochraceous grey, rather loosely hanging to subfruticose, up to 18 cm wide, 115–130 µm thick; upper cortex 40–80 µm thick, lower cortex lacking. *Lobes* with dichotomous ramifications, leaving large interspaces, not laterally overlapping, 4.0–7.0 × 0.5–1.0 mm, flat to slightly concave, with occasional tubercles of 0.2–0.6 mm diam. *Soredia*, *phyllidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate, but with a broad corticate margin, without pigment. *Cilia* rather copious, black, 0.2 × 2–4 mm, mostly simple, some sparingly dichotomously branched.

*Apothecia* rare, sessile to stalked, 0.7–2.2 mm, subterminal; margin lacinulate; disc concave, pruinose, brown; *ascospores* 8 per ascus, ellipsoid, 1-septate, thick-walled, 35–45 × 15–19 µm, with 2–7 sporoblastidia.

*Chemistry.* Atranorin and zeorin. Thallus K+ yellow.

*Distribution and ecology.* Known only from the states of São Paulo and Minas Gerais, in Atlantic rainforest.

*Discussion.* This species is similar to *H. boryi* but with tubercles on the upper surface.

*Additional specimens examined.* **Brazil:** *São Paulo State*: same locality as the type, 1991, *Marcelli* 12313. *Minas Gerais*: Parque Estadual do Ibitipoca, corticolous, 1993, *Marcelli* et al. 24384 (all SP).

## *Species newly reported from Brazil*

In this and the following section, 'Species already reported from Brazil', and in Supplementary Material Table S1 (available online), abbreviations of two capital letters outside brackets refer to federal states in Brazil, and are as follows: AL = Alagoas; AP = Amapá; BA = Bahia; CE = Ceará; DF = Distrito Federal; GO = Goiás; MG = Minas Gerais; MS = Mato Grosso do Sul; MT = Mato Grosso; PA = Pará; PE = Pernambuco; PR = Paraná; RJ = Rio de Janeiro; RO = Rondônia; RS = Rio Grande do Sul; SC = Santa Catarina; SE = Sergipe; SP = São Paulo. In the text, states are listed from northwest to southeast, in the order usually followed in floristic literature in Brazil.

*Heterodermia barbifera* (Nyl.) Kr. P. Singh — Database records: SP, *Sipman* 41068, 41120 (B).

*Heterodermia crocea* R. C. Harris — Specimen examined: PE, *Cáceres* & *Aptroot* 21958 (ISE). Database record: SC (B).

*Heterodermia cubensis* (Kurok.) Trass — Database record: MG, *Henschen* (UPS).

*Heterodermia hypocaesia* (Yasuda ex Räsänen) D. D. Awasthi — Specimen examined: MS, *Aptroot* & *Souza* 80792 (CGMS).

*Heterodermia lamelligera* (Taylor) Trass — Specimen examined: MS, *Aptroot* 82645 (CGMS).

*Heterodermia major* (Nyl.) Trevis. — Specimens examined: MG, *Canêz* 12; RS, 11 specimens examined including *Aptroot* 79646, *Canêz* 4467 and *Spielmann* 15 (all CGMS). This species differs from *H. diademata*, with which it has often been confused and synonymized, mostly by the absence of pseudocyphellae.

*Heterodermia mobergiana* Michlig *et al.* — Specimens examined: MT, *Souza* & *Aptroot* 101; MG, *Spielmann* 7655; PR, *Aptroot* & *Souza* 82018; SC, *Aptroot* 79697; RS, 13 specimens examined including *Aptroot* 79321, *Canêz* 266 and *Spielmann* 681 (all CGMS). This species has been only recently described and differentiated from *H. comosa*. Many old reports of *H. comosa* may refer to *H. mobergiana*, which is the most common species of the *H. comosa* group in Brazil.

*Heterodermia pseudospeciosa* (Kurok.) W. L. Culb. — Specimens examined: MT, *Souza* & *Aptroot* 36 (CGMS); MS, *Aptroot* & *Souza* 80803 (CGMS); SP, *Cáceres* & *Aptroot* 13690 (ISE); RS, *Cáceres* & *Aptroot* 22200 (ISE). Database records: MG (UPS), RJ (NY). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia rugulosa* (Kurok.) Wetmore — Specimen examined: SP, *Canêz* 2452 (CGMS).

*Heterodermia spinigera* (Kurok.) Trass — Specimen examined: RS, *Canêz* 4459 (CGMS).

## *Species already reported from Brazil*

One reference per state per species is given.

*Heterodermia africana* (Kurok.) M. F. Souza & Aptroot comb. et stat. nov. MycoBank No.: MB 839901. Basionym: *Anaptychia magellanica* var. *africana* Kurok., *Journal of the Hattori Botanical Laboratory* **37**, 604 (1973). — Reported from SP (Martins 2007).

*Heterodermia albicans* (Pers.) Swinscow & Krog — Reported from AP (Cáceres & Aptroot (2016), specimen is *H. tremulans*); PE (Moreira de Barros & Xavier Filho 1972); AL (Menezes *et al.* 2013); MS (Osorio 1992); SP (Kalb 1982*c*); PR (Osorio 1977*b*); RS (Spielmann 2006). Database record: RJ (LSU). Additional state records: MT, *Aptroot* & *Souza* 81542 & 81965 (CGMS); SC, *Canêz* 1413 (CGMS).

*Heterodermia allardii* (Kurok.) Trass — Reported from MG and SP (Moberg 2011).

*Heterodermia appendiculata* (Kurok.) Swinscow & Krog — Reported from MG (Aptroot 2002).

*Heterodermia borphyllidiata* (Kalb & Meesim) M. F. Souza & Aptroot comb. nov. MycoBank No.: MB 839902. Basionym: *Leucodermia borphyllidiata* Kalb & Meesim, *Phytotaxa* **235**, 33 (2015). — Reported from MG (Mongkolsuk *et al.* (2015), as *Leucodermia borphyllidiata*).

*Heterodermia boryi* (Fée) Kr. P. Singh & S. R. Singh — Reported from AL (Oliveira Júnior *et al.* 2020); BA (Kalb 1982*b*); PR (Osorio 1977*a*); RS (Spielmann 2006). Additional state records: MT, *Souza* & *Aptroot* 4 (CGMS); MG, *Canêz* 1869 (CGMS).

*Heterodermia casarettiana* (A. Massal.) Trevis. — Reported from PA (Brako *et al.* 1985); PE (Moreira de Barros & Xavier Filho 1972); MG (Aptroot 2002); SP (Martins 2007), PR (Osorio

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1977*b*); RS (Spielmann 2006). Database records: RJ (B), MT (UPS). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia circinalis* (Zahlbr.) W. A. Weber — Reported from SP (Martins 2007).

*Heterodermia comosa* (Eschw.) Follmann & Redon — Reported from PA (Mongkolsuk *et al.* 2015). Also reported from SC by Reginaldo & Gumboski (2019); BA (Moreira Barros & Xavier Filho 1972); MT (Kurokawa 1962); MG (Aptroot 2002); RJ (Cengia Sambo 1940); SP (Marcelli 1991); SC (Marcelli 1992); RS (Spielmann 2006). Database record: DF (LSU). This species was until recently taken in a wide sense (Michlig *et al.* 2017), and most of the records above may refer to *Heterodermia mobergiana*.

*Heterodermia corallophora* (Tayl.) Skorepa — Reported from MG (Kurokawa 1962); RJ (Zahlbruckner 1902); SP (Marcelli 1991); PR (Osorio 1977*b*); RS (Spielmann 2006). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia corcovadensis* (Kurok.) Elix — Reported from RJ (Kurokawa 1962). Additional state records: MG, *Canêz* 1816, 1818 (CGMS); RS, *Canêz* 3768 (CGMS).

*Heterodermia dactyliza* (Nyl.) Swinscow & Krog — Reported from BA (Aptroot & Cáceres 2018); MG (Aptroot 2002). Database records: PA (UPS), RJ (UPS).

*Heterodermia dendritica* (Pers.) Poelt — Reported from MG (Aptroot 2002). Database records: GO (ASU), RJ (B), SP (B). Additional state record: RS, *Canêz* 4464 (CGMS).

*Heterodermia diademata* (Taylor) D. D. Awasthi — Reported from PA (Brako *et al.* 1985); MT (Lynge 1924); MS (Aptroot & Spielmann 2020); RJ (Cengia Sambo 1940); SP (Martins 2007); RS (Spielmann 2006). Since the species was often confused with *Heterodermia major*, some of the records above may refer to this species.

*Heterodermia dissecta* (Kurok.) D. D. Awasthi — Reported from PE (Cáceres 2007); AL (Menezes *et al.* 2013).

*Heterodermia fertilis* Moberg — Reported from MG (Moberg 2011).

*Heterodermia flabellata* (Fée) Awasthi — Reported from PA (Brako *et al.* 1985); PE (Moreira de Barros & Xavier Filho 1972); MS (Aptroot & Spielmann 2020); MG (Aptroot 2002); SP (Martins 2007); SC (Kurokawa 1962); RS (Spielmann 2006). Additional state record: PR, *Aptroot* & *Souza* 82268 (CGMS). Database records: MT (UPS), RJ (UPS).

*Heterodermia flavosquamosa* Aptroot & Sipman — Reported from SP (Martins 2007); RS (Spielmann 2006). Additional state record: MS, *Aptroot* 80517 (CGMS). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia galactophylla* (Tuck.) W. Culb. — Reported from PA (Brako *et al.* 1985); AL (Oliveira Júnior *et al.* 2020); SE (Cáceres *et al.* 2014); MT (Mongkolsuk *et al.* 2015); MG (Kalb 1984); RJ (Cengia Sambo 1940); SP (Marcelli 1992); SC (Marcelli 1992); RS (Spielmann 2006). Additional state record: PR, *Aptroot* & *Souza* 82170 (CGMS).

*Heterodermia hypochracea* (Vain.) Swinscow & Krog — Reported from SP (Martins 2007); PR (Eliasaro *et al.* 2012); RS (Spielmann 2006).

*Heterodermia hypoleuca* (Ach.) Trevis. — Reported from MT (Lynge 1924); MG (Vainio 1890); RJ (Cengia Sambo 1940); SC (Müller 1891*a*); RS (Spielmann 2006).

*Heterodermia isidiophora* (Vain.) D. D. Awasthi — Reported from RS (Benatti & Marcelli 2017). Database record: MG (UPS). Additional state record: RJ, *Spielmann* 10084 (CGMS). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia japonica* (M. Sâto) Swinscow & Krog — Reported from RO (Aptroot & Cáceres (2014), specimen is *H. obscurata*); AL (Oliveira Júnior *et al.* 2020); SE (Cáceres *et al.* 2014); BA (Marcelli 1992); MT (Lynge 1924); MS (Lynge 1924); RJ (Mongkolsuk *et al.* 2015); SP (Marcelli 1992); SC (Marcelli 1992); RS (Spielmann 2006). Database record: GO (UPS). Additional state records: PE, *Cáceres* & *Aptroot* 22023 (ISE); MG, *Canêz* 1821, 1824 (CGMS); PR, *Aptroot* & *Souza*, 6 specimens including 82005 (all CGMS).

*Heterodermia lepidota* Swinscow & Krog — Reported from SP (Martins 2007).

*Heterodermia leucomelos* (L.) Poelt — Reported from PA (Müller 1891*b*); PE (Moreira de Barros & Xavier Filho 1972); AL (Nusbaumer *et al.* 2015); MG (Vainio 1890); RJ (Cengia Sambo 1940); SP (Nagaoka & Marcelli 1989); SC (Müller 1891*a*); RS (Spielmann 2006).

*Heterodermia lutescens* (Kurok.) Follm. — Reported from AL (Oliveira Júnior *et al.* 2020); MG (Aptroot 2002); RJ (Mongkolsuk *et al.* 2015); SP (Martins 2007); RS (Spielmann 2006). Database records: GO (UPS), PR (UPS). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia magellanica* (Zahlbr.) Swinscow & Krog — Reported from MG (Aptroot 2002); SP (Martins 2007); PR (Eliasaro *et al.* 2012); RS (Spielmann 2006). Database record: RJ (B). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia microphylla* (Kurok.) Skorepa — Reported from BA (Aptroot & Cáceres 2018); MS (Fleig & Riquelme 1991); RJ (Mongkolsuk *et al.* 2015); SP (Mongkolsuk *et al.* 2015); RS (Spielmann 2006). Additional state records: MG, *Canêz* 1864 (CGMS); PR, *Aptroot* & *Souza* 82151; SC, *Aptroot* 78408 (all CGMS).

*Heterodermia namaquana* Brusse — Reported from SP (Martins 2007). Additional state record: MG, *Canêz* 1867 (CGMS). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia neocomosa* M. P. Rodríguez *et al.* — Reported from MS (Michlig *et al.* 2017).

*Heterodermia obscurata* (Nyl.) Trevis. — Reported from PA (Brako *et al.* 1985); CE (Alves 2014); AL (Oliveira Júnior *et al.* 2020); PE (Moreira de Barros & Xavier Filho 1972); SE (Cáceres *et al.* 2014); BA (Aptroot & Cáceres 2018); MG (Aptroot 2002); RJ (Zahlbruckner 1902); SP (Marcelli 1992); PR (Osorio 1977*b*); SC (Marcelli 1992); RS (Spielmann 2006). Additional state records: RO, *Cáceres* & *Aptroot* 11009 (ISE); MT, *Souza* & *Aptroot* 5, 43 and *Aptroot* & *Souza* 81963 (CGMS); MS, *Aptroot* & *Souza* 80471, 80823, 80965 (CGMS).

*Heterodermia palpebrata* (Tayl.) Trass — Reported from Brazil but state not indicated (Meyen & Flotow 1843).

*Heterodermia podocarpa* (Bél.) D. D. Awasthi — Reported from PA (Brako *et al.* 1985); PE (Moreira de Barros & Xavier Filho 1972); MT (Lynge 1924); MG (Kalb 1982*a*); RJ (Müller 1891*b*); SP (Martins 2007); SC (Müller 1891*a*); RS (Spielmann 2006).

*Heterodermia propagulifera* (Vain.) Dey — Reported from SP (Marcelli 1991); RS (Spielmann 2006). Additional state records: MT, 5 specimens including *Souza* & *Aptroot* 21, 143; MG, *Canêz* 1805, 1817, 1865, *Spielmann* 7632, 7675; PR, *Aptroot* & *Souza* 82075; SC, *Canêz* 2901 (all CGMS).

*Heterodermia sorediosa* Michlig *et al.* — Reported from AL (Oliveira Júnior *et al.* 2020). Additional state record: MS, *Aptroot* 79049 (CGMS).

*Heterodermia spathulifera* Moberg & Purvis — Reported from Brazil but state not indicated (Moberg 2011); according to the database in UPS the specimens are from MG and SP.

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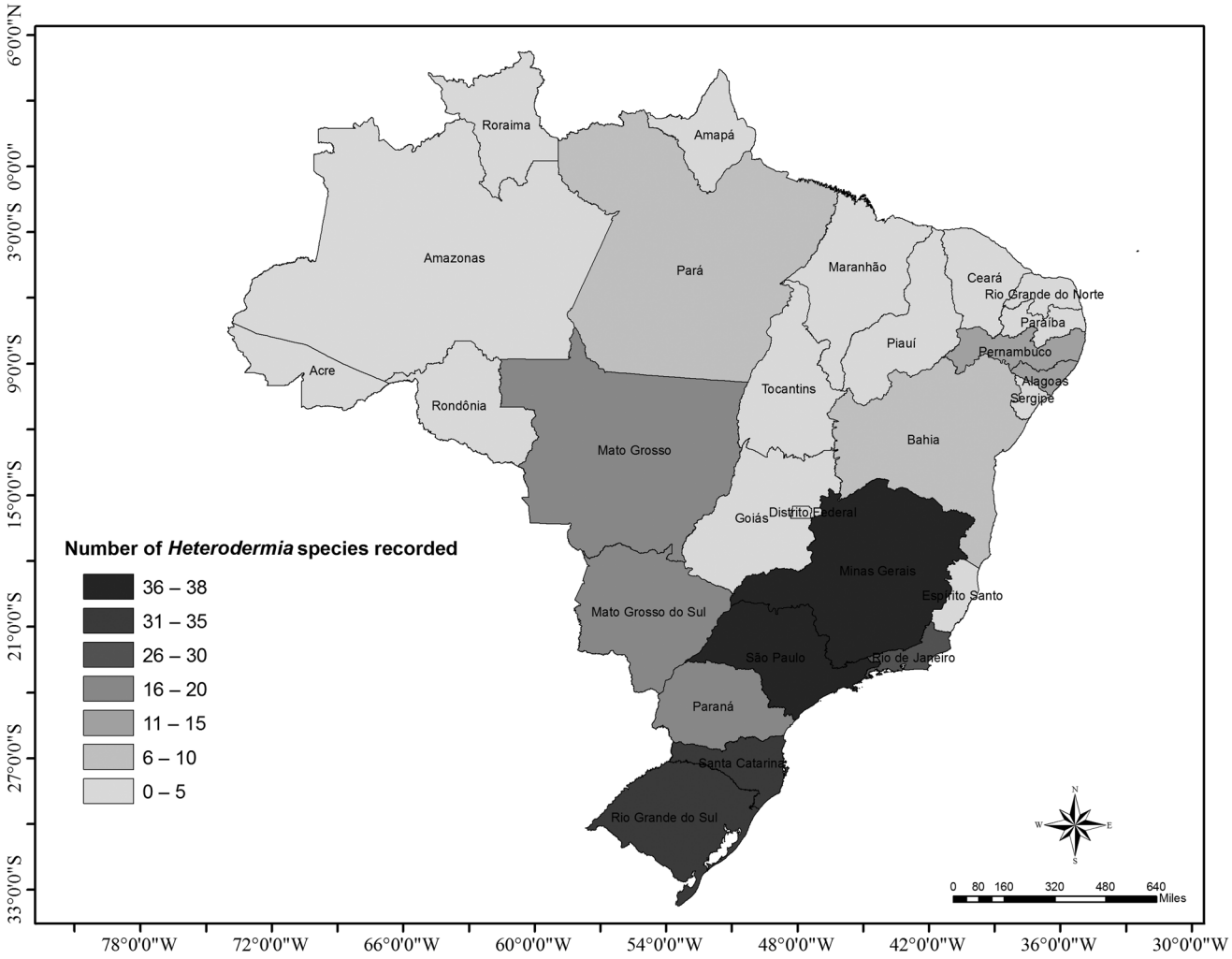


**Fig. 6.** Map of Brazil with an indication of the number of recorded *Heterodermia* species per state. Geographic coordinate system: SIRGAS 2000.

*Heterodermia speciosa* (Wulf.) Trevis. — Reported from PA (Brako *et al.* 1985); CE (Alves 2014); AL (Oliveira Júnior *et al.* 2020); BA (Marcelli 1992); MS (Fleig & Riquelme 1991); MG (Aptroot 2002); RJ (Vainio 1890); SP (Marcelli 1992); SC (Marcelli 1992); RS (Spielmann 2006). Additional state records: MT, *Souza* & *Aptroot* 36 and *Aptroot* & *Souza* 81544 (CGMS).

*Heterodermia squamulosa* (Degel.) W. L. Culb. — Reported from SP (Marcelli 1992); PR (Eliasaro *et al.* 2012); RS (Spielmann 2006). Database record: RJ (LSU), MS (UPS). Additional state records: MT, 5 specimens including *Souza* & *Aptroot* 105 and *Aptroot* & *Souza* 81582 (CGMS). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia stellata* (Vain.) W. A. Weber — Reported from MG (Mongkolsuk *et al.* 2015); SP (Martins 2007). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia subcitrina* Moberg — Reported from Brazil but state not indicated (Moberg 2011); according to the database in UPS the specimen is from RS.

*Heterodermia tremulans* (Müll. Arg.) Culb. — Reported from CE (Aptroot & Cáceres 2016); PE (Moreira de Barros & Xavier Filho 1972); AL (Oliveira Júnior *et al.* 2020); BA (Aptroot & Cáceres 2018); MS (Aptroot & Spielmann 2020); MG (Kurokawa 1962); RJ (Mongkolsuk *et al.* 2015); SP (Mongkolsuk *et al.* 2015); PR (Eliasaro *et al.* 2012); RS (Spielmann 2006). Additional state records: AP, *Cáceres* & *Aptroot* 27215 (ISE); MT, *Aptroot* & *Souza* 81660 (CGMS). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia trichophora* (Kurok.) Trass — Reported from RJ (Moberg 2011); SP (Moberg 2011); PR (Eliasaro *et al.* 2012); RS (Spielmann 2006).

*Heterodermia vulgaris* (Vain.) Follm. & Redón — Reported from AL (Oliveira Júnior *et al.* 2020); MS (Osorio 1992); MG (Moberg 2011); RJ (Mongkolsuk *et al.* 2015); SP (Marcelli 1991); PR (Osorio 1977*a*); RS (Spielmann 2006). Database record: DF (LSU). Also reported from SC by Reginaldo & Gumboski (2019).

*Heterodermia* sp. 1. — About to be described from SC (Reginaldo & Gumboski 2019).

*Heterodermia* sp. 2. — About to be described from SC (Reginaldo & Gumboski 2019).

## *Further species described from Brazil*

The species mentioned below have been described from Brazil but are still not validly published. Their tentative identity is given below.

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*H. kalbii* M. F. N. Martins & M. P. Marcelli, *ined.*: probably = *H. magellanica*.
*H. velata* M. P. Marcelli & M. N. Benatti, *ined.*: probably = *H. obscurata*.

## Discussion

*Heterodermia* species are very unevenly dispersed over Brazil (Fig. 6). Not a single species is known from most of the Amazonian states, and from two states just one species is recorded. In the Northeast Region, more species occur but mostly in the Atlantic rainforest. Most species occur in the Southeast and South Regions of the country, including Mato Grosso and Mato Grosso do Sul. Based on our data, the states of Minas Gerais, São Paulo and Rio Grande do Sul are richest in species, each state containing (with a large overlap of species) more than half of the total *Heterodermia* mycota of the country.

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**Author ORCIDs.** André Aptroot, 0000-0001-7949-2594; Adriano Spielmann, 0000-0003-0137-0807.

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## References

**Alves MME** (2014) *Levantamento das espécies de liquens em áreas de cerrado na Chapada do Araripe – CE*. Master's thesis, Universidade Regional de Cariri.

**Aptroot A** (1988) *Pyxinaceae* (Lichens). *Flora of the Guianas Series E* **1**, 1–59.

**Aptroot A** (2002) New and interesting lichens and lichenicolous fungi in Brazil. *Fungal Diversity* **9**, 15–45.

**Aptroot A and Cáceres MES** (2014) A key to the microfoliose, foliose and related crustose lichens from Rondônia, Brazil, with the description of four new species. *Lichenologist* **46**, 783–799.

**Aptroot A and Cáceres MES** (2016) Two new lecanoroid *Caloplaca* (*Teloschistaceae*) species from gneiss inselbergs in equatorial Brazil, with a key to tropical lecanoroid species of *Caloplaca* s. lat. *Lichenologist* **48**, 201–207.

**Aptroot A and Cáceres MES** (2018) New species and records of lichens from inselbergs and surrounding Atlantic rain forest in the Chapada Diamantina (Bahia, Brazil). *Herzogia* **31**, 359–373.

**Aptroot A and Spielmann AA** (2020) New lichen species and records from the Serra da Bodoquena, Mato Grosso do Sul, Brazil, the westernmost Atlantic rain forest. *Archive for Lichenology* **17**, 1–25.

**Benatti MN and Marcelli MP** (2017) Foliose *Physciaceae* from the State Park of Cantareira, São Paulo State, Brazil. *Iheringia* **27**, 255–266.

**Brako L, Dibben MJ and Amaral I** (1985) Preliminary notes on the macrolichens of Serra do Cachimbo, northcentral Brazil. *Acta Amazonica* **15**, 123–135.

**Cáceres MES** (2007) Corticolous crustose and microfoliose lichens of northeastern Brazil. *Libri Botanici* **22**, 1–168.

**Cáceres MES and Aptroot A** (2016) First inventory of lichens from the Brazilian Amazon in Amapá State. *Bryologist* **119**, 250–265.

**Cáceres MES, Nascimento EL, Aptroot A and Lücking R** (2014) Liquens brasileiros: novas descobertas evidenciam a riqueza no Norte e Nordeste do país. *Boletim do Museu de Biologia Mello Leitão* **35**, 101–119.

**Cengia Sambo M** (1940) Licheni del Brasile. *Annali di Botanica* **22**, 19–41.

**Chen J-B and Wang D-P** (2001) The lichen family *Physciaceae* (*Ascomycota*) in China III. Ten species of *Heterodermia* containing depsidones. *Mycotaxon* **77**, 101–105.

**Eliasaro S** (1992) *Liquens do gênero* Heterodermia (Pyxinaceae - Ascomycotina) *no Rio Grande do Sul, Brasil*. Master's thesis, Universidade Federal do Rio Grande do Sul.

**Eliasaro S and Fleig M** (1994) Novas ocorrências de *Heterodermia* (Líquens - *Pyxinaceae*) no Rio Grande do Sul, Brasil. *Acta Botanica Brasilica* **8**, 59–64.

**Eliasaro S, Gerlach ACL and Gumboski EL** (2012) Novos registross de fungos liquenisados para o estado do Paraná, Brasil. *Revista Brasileira de Biociências* **10**, 507–512.

**Fleig M and Riquelme I** (1991) Liquens de Piraputanga, Mato Grosso do Sul, Brasil. *Acta Botanica Brasilica* **5**, 3–12.

**Gardes M and Bruns T D** (1993) ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**, 113–118.

**Jungbluth P and Marcelli MP** (2012) Identificação de *Physciaceae* s.l. foliosas brasileiras. *Glalia* **4**, 65–101.

**Kalb K** (1982*a*) *Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel II (No. 41–80)*. Neumarkt/Opf.

**Kalb K** (1982*b*) *Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel III (No. 81–120)*. Neumarkt/Opf.

**Kalb K** (1982*c*) *Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel V (No. 161–200)*. Neumarkt/Opf.

**Kalb K** (1984) *Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel VIII (No. 301–350)*. Neumarkt/Opf.

**Kurokawa S** (1962) A monograph of the genus *Anaptychia*. *Beihefte zur Nova Hedwigia* **6**, 1–115.

**Kurokawa S** (1998) A catalogue of *Heterodermia* (*Physciaceae*) [*Heterodermia* (*Physciaceae*) kataloog]. *Folia Cryptogamica Estonica* **32**, 21–25.

**Lendemer JC** (2009) A synopsis of the lichen genus *Heterodermia* (*Physciaceae*, lichenized *Ascomycota*) in eastern North America. *Opuscula Philolichenum* **6**, 1–36.

**Lücking R, del Prado R, Lumbsch HT, Will-Wolf S, Aptroot A, Sipman HJM, Umaña L and Chaves LJ** (2008) Phylogenetic patterns of morphological and chemical characters and reproductive mode in the *Heterodermia obscurata* group in Costa Rica (*Ascomycota*, *Physciaceae*). *Systematics and Biodiversity* **6**, 31–41.

**Lücking R, Hodkinson BP and Leavitt SD** (2017) The 2016 classification of lichenized fungi in the *Ascomycota* and *Basidiomycota* – approaching one thousand genera. *Bryologist* **119**, 361–416.

**Lynge B** (1924) On South American *Anaptychiae* and *Physciae*. *Videnskapsselska Skrifter, Matematik-Naturvissenschaftlike Klasse* **2**, 1–47, 5.

**Marcelli MP** (1991) Aspects of the foliose lichen flora of the southern-central coast of Sao Paulo State, Brazil. In Galloway DJ (ed.), *Tropical Lichens: Their Systematics, Conservation, and Ecology*. Oxford: Clarendon Press, pp. 150–170.

**Marcelli MP** (1992) Ecologia Liquênica nos Manguezais do Sul-Sudeste Brasileiro. *Bibliotheca Lichenologica* **47**, 1–288.

**Marcelli MP** (2013) Identificação de espécies em *Heterodermia* (*Ascomycetes: Physciaceae*). In *Livro de Resumos do Sexto Encontro do Grupo Brasileiro de Liquenólogos*, pp. 19–22.

**Marcelli MP and Martins MFN** (2007) Variabilidade subgenérica e específica em *Heterodermia* (*Ascomycetes: Physciaceae*). In *Anais da Segunda Reunião Brasileira de Estudos Liquenológicos, Porto Alegre*, pp. 35–41.

**Marcelli MP, Jungbluth J, Benatti MN, Spielmann AA, Canêz LS, Cunha IPR and Martins MFN** (2007) Some new species and combinations of Brazilian lichenized fungi. *Bibliotheca Lichenologica* **96**, 209–227.

**Martins MFN** (2007) *O gênero* Heterodermia (Physciaceae, Ascomycota *liquenizados) no Estado de São Paulo, Brasil*. Master's thesis, São Paulo State University.

**Menezes AA, Xavier-Leite AB, Aptroot A and Cáceres MES** (2013) New lichen species from the Caatinga in Chapada do Araripe, northeastern Brazil. *Bryologist* **116**, 302–305.

**Meyen J and Flotow J** (1843) Lichenes Exotici (Observationes in itinere circum terram institutae (1830–1832)): Lichenes. *Nova Acta Academiae Caesareae Leopoldino-Carolinae* **19**(Suppl.), 209–232.

**Michlig A, Rodríguez MP, Aptroot A, Niveiro N and Ferraro LI** (2017) New species of the *Heterodermia comosa*-group (*Physciaceae*, lichenized *Ascomycetes*) from southern South America. *Cryptogamie, Mycologie* **38**, 155–167.

**Moberg R** (1990) The lichen genus *Physcia* in Central and South America. *Nordic Journal of Botany* **10**, 319–342.

**Moberg R** (2011) The lichen genus *Heterodermia* (*Physciaceae*) in South America – a contribution including five new species. *Nordic Journal of Botany* **29**, 129–147.

**Moberg R and Nash TH, III** (1999) The genus *Heterodermia* in the Sonoran Desert area. *Bryologist* **102**, 1–14.

**Mongkolsuk P, Meesim S, Poengsungnoen V, Buaruang K, Schumm F and Kalb K** (2015) The lichen family *Physciaceae* in Thailand – II. Contributions to the genus *Heterodermia* sensu lato. *Phytotaxa* **235**, 1–66.

**Moreira de Barros Barros L and Xavier Filho L** (1972) Catalogo dos liquens do herbario do Departamento de Botanica da Universidade Federal de Pernambuco. In *XXIII Congresso Nacional Botanica, 16–23-Janeiro 1972*, Garanhuns, Brazil, pp. 45–55.

**Müller J** (1891*a*) Lichenes Catharinenses a cl. E. Ule in Brasilia prov. Santa Catharina lecti. *Hedwigia* **5**, 235–243.

**Müller J** (1891*b*) Lichenes Schenckiane a cl. Dr. H. Schenck, Bonnensi, in Brasiliae orientalis prov. Santa Catharina, Parana, Rio de Janeiro, Minas Geraes et Pernambuco lecti. *Hedwigia* **5**, 219–234.

**Murray MG and Thompson WF** (1980) Rapid isolation of high molecular weight plant DNA. *Nucleic Acids Research* **8**, 4321–4325.

**Nagaoka LY and Marcelli MP** (1989) Líquens da área de reserva do Parque Estadual das Fontes do Ipiranga. *Acta Botanica Brasilica* **3**(2, Suppl. 1), 95–98.

**Nusbaumer L, Cáceres MES, Aptroot A, Gibertoni TB and Horak E** (2015) Fungos e liquens. In Studer A, Nusbaumer L and Spichiger R (eds), *Biodiversidade da Reserva Biológica de Pedra Talhada (Alagoas, Pernambuco - Brasil). Boissiera*, *Volume 68*. Geneva: Conservatoire et Jardin Botaniques, pp. 563–580.

**Oliveira Junior I de, Aptroot A, Cavalcante JG, Košuthová A and Cáceres MES** (2020) Two further new lichen species from the Atlantic Forest remnant Pedra Talhada (Alagoas, Brazil), with a list of species. *Bryologist* **123**, 617–632.

**Orange A, James PW and White FJ** (2001) *Microchemical Methods for the Identification of Lichens*. London: British Lichen Society.

**Osorio HS** (1977*a*) Contribution to the lichen flora of Brazil II. Lichens from Guarapuava, Paraná State. *Dusenia* **10**, 101–102.

**Osorio HS** (1977*b*) Contribution to the lichen flora of Brazil III. Lichens from western Paraná. *Acta Biologica Paranaense* **6**, 3–7.

**Osorio HS** (1992) Contribution to the lichen flora of Brazil. XXIX. *Comunicaciones Botánicas del Museo de Historia Natural de Montevideo* **5** (98), 1–6.

**Reginaldo JDG and Gumboski EL** (2019) *Estudos taxonômicos em* Heterodermia *s. lat* (Ascomycota *liquenizados,* Physciaceae*) no Estado de Santa Catarina*. Graduation Report, Universidade da Região de Joinville.

**Rodriguez JM, Estrabou C and Quiroga G** (2012) The genus *Heterodermia* (*Lecanorales - Physciaceae*) in Central North of Argentina. *Acta Botanica Brasilica* **26**, 1000–1005.

**Schumm F and Elix JA** (2015) *Atlas of Images of Thin Layer Chromatograms of Lichen Substances*. Norderstedt: Books on Demand GmbH.

**Scutari NS** (1995) Los macrolíquenes de Buenos Aires, I: *Dirinaria*, *Heterodermia* e *Hyperphyscia* (*Physciaceae*, *Ascomycotina*). *Darwiniana* **33**, 149–176.

**Spielmann AA** (2006) Checklist of lichens and lichenicolous fungi of Rio Grande do Sul (Brazil). *Caderno de Pesquisa, Série Biologia* **18**(2), 7–125.

**Stamatakis A** (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**, 2688–2690.

**Swinscow TDV and Krog H** (1976) The genera *Anaptychia* and *Heterodermia* in East Africa. *Lichenologist* **8**, 103–138.

**Taylor T** (1847) New lichens, principally from the herbarium of Sir William J. Hooker. *Journal of Botany* **6**, 148–197.

**Trass H** (1992) Synopsis of the lichen genus *Heterodermia* (*Ascomycotina*, *Physciaceae* sive *Pyxinaceae*). *Folia Cryptogamica Estonica* **29**, 1–24.

**Vainio EA** (1890) Étude sur la classification et la morphologie des lichens du Brésil, I. *Acta Societatis pro Fauna et Flora Fennica* **7**, 1–247.

**White TJ, Bruns T, Lee S and Taylor JW** (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In Innis MA, Gelfand DH, Sninsky JJ and White TJ (eds), *PCR Protocols: A Guide to Methods and Applications*. New York: Academic Press, pp. 315–322.

**Zahlbruckner A** (1902) Studien über brasilianische Flechten. *Sitzungsberichte der kaiserlichen Akademie für Wissenschaften Wien, Mathematisch.-Naturwisschenschaflichen Classe* **3**(Avt. 1), 357–432.

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