

Standard Paper

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

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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 amphila-cinulata* 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 atros-triata* 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

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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. Canéz 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 Mongkolsuk *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:isoamylalcohol (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 ddH₂O. 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

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 (6 α -acetoxyhopane-22-ol, above atranorin), zeorin, T2 (spathulene, 16 β -acetoxyhopane-22-ol, below zeorin), T3 (6 α ,16 β -diacetoxyhopane-22-ol), T4 (16 β -acetoxyhopane-6 α , 22-diol), T5 (6 α -acetoxyhopane-16 β , 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 μ m thick 4. **Heterodermia dactyliza** group
Lobes generally sympodially branched, often confluent, tips not incurved, lower surface without cortex, upper cortex generally under 150 μ m 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 \rightarrow 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 \rightarrow orange-red or red, with depsidones 5
- 5(4) Thallus K+ yellow \rightarrow red, with salazinic acid **H. phyllalbicans** M. F. Souza & Aptroot
Thallus K+ yellow \rightarrow orange-red, with norstictic and dissectic acid **H. dissecta** (Kurok.) D. D. Awasthi
- 6(1) Thallus with soredia 7
Thallus without soredia 10

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 pseudocyphephae	H. diademata (Taylor) D. D. Awasthi
	Thallus without pseudocyphephae	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 <i>et al.</i>
	Lower surface without pigment	H. namaquana Brusse
5(2)	Lower surface with orange pigment	H. neocomosa M. P. Rodríguez <i>et al.</i>
	Lower surface without pigment	6
6(5)	Lower surface veined	H. mobergiana Michlig <i>et al.</i>
	Lower surface not veined	7

- 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

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. spatulifera Moberg	
16(14)	Thallus K+ yellow → red, with salazinic acid	H. hypocaustia (Yasuda ex Räsänen) D. D. Awasthi	
	Thallus K+ yellow → orange-red, with norstictic acid		17
17(16)	Soralia labriiform	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 pseudocypbellae; main lobes over 1 mm wide	H. flabellata (Fée) D. D. Awasthi	
	Secondary lobes with pseudocypbellae; 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.	

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*, *phylloidia* 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 lacinate 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-diacetoxypopane-22-ol (T3), 6α-acetoxypopane-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*, *phylloidia* 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. *Phylloidia* 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-acetoxypopane-22-ol (T1), 6α,16β-diacetoxypopane-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.

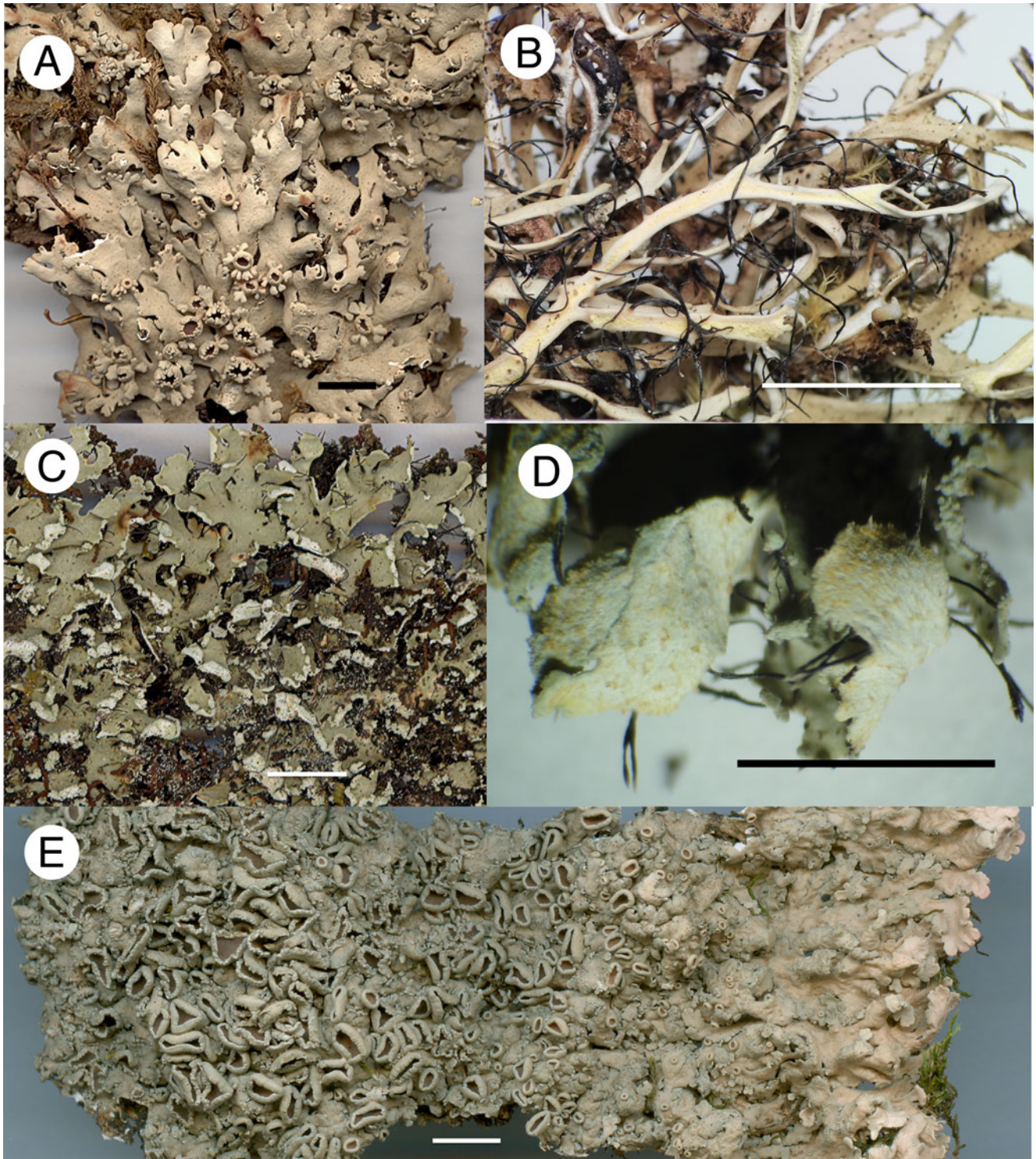


Fig. 1. Holotypes of new species of *Heterodermia*. A, *H. amphilacinulata*. B, *H. caneziae*. C & D, *H. delicatula* (D, lower surface showing the pigment in spots). E, *H. dissecticodiademata*. Scales = 5 mm. In colour online.

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).

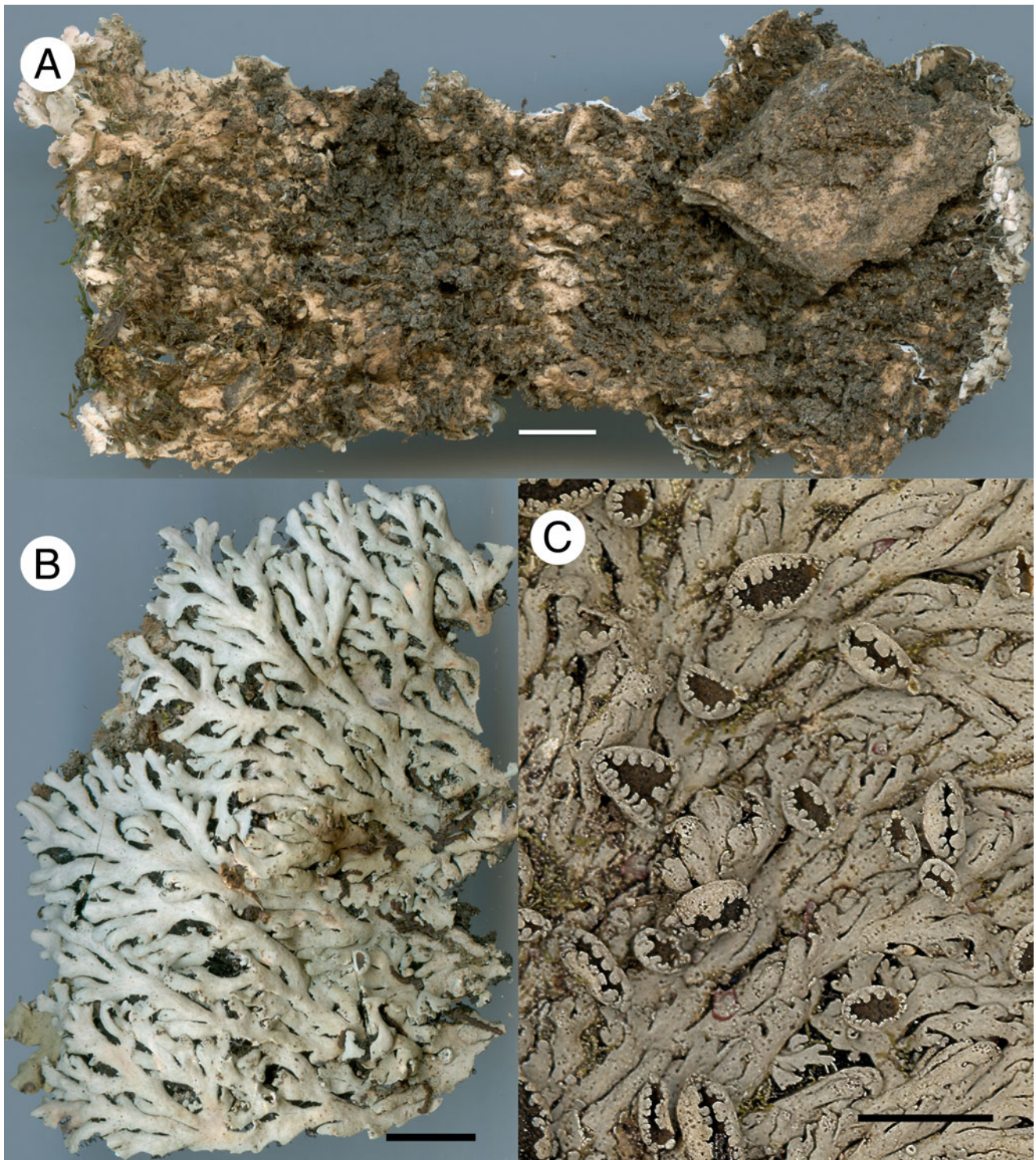


Fig. 2. Holotypes of new species of *Heterodermia*. A, *H. dissectocodiademata* (lower surface). B, *H. dissecticoflabellata*. C, *H. flavodactyliza*. Scales = 5 mm. In colour online.

(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*, *phylloidia* 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 \times 0.05 mm, on

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, 6 α ,16 β -diacetoxyhopane-22-ol (T3), 6 α -acetoxyhopane-16 β , 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*, *phylidia* 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, 6 α ,16 β -diacetoxyhopane-22-ol (T3), 16 β -acetoxyhopane-6 α , 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*, *phylidia* 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

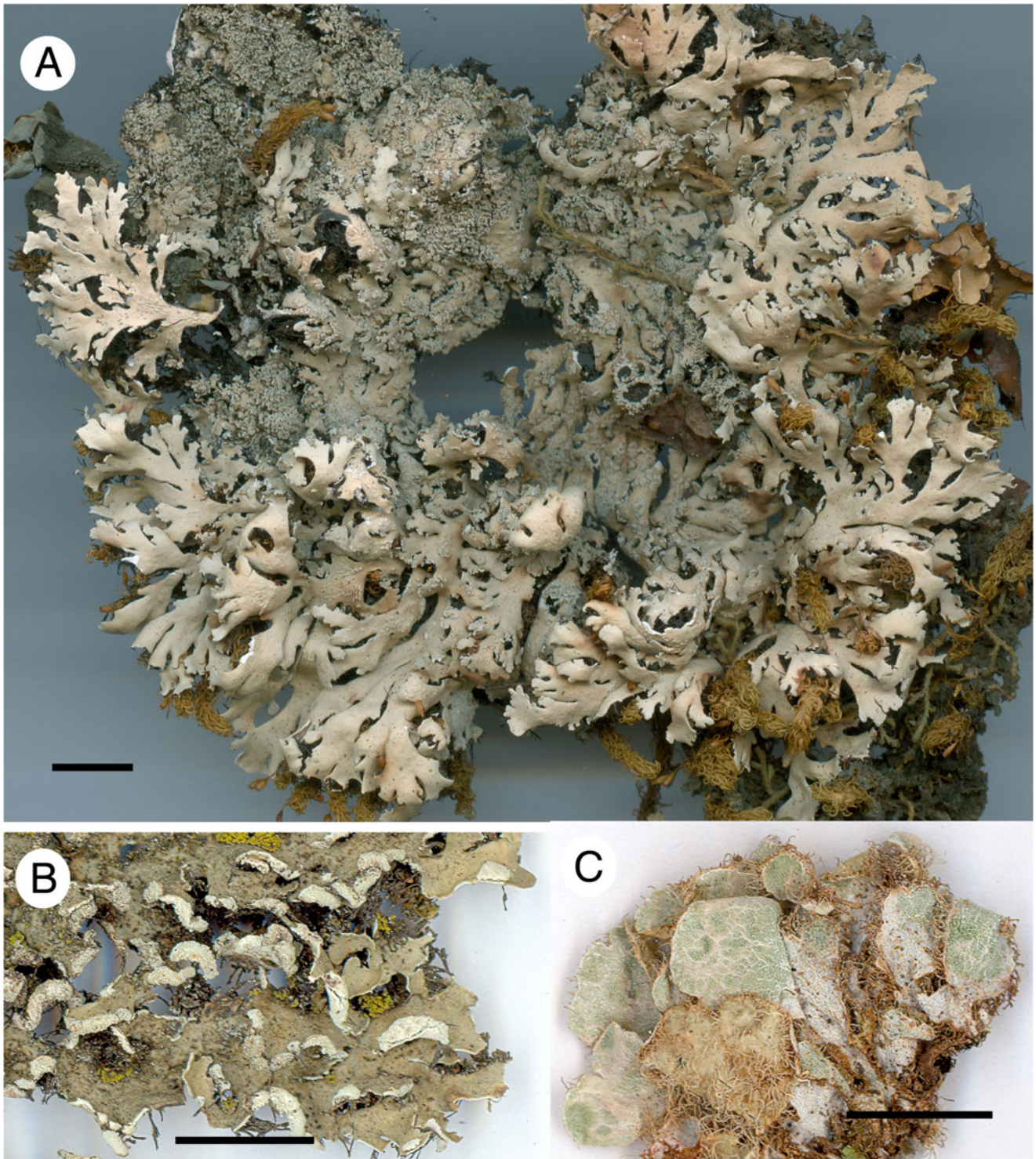


Fig. 3. Holotypes of new species of *Heterodermia*. A, *H. flavulifera*. B, *H. labiata*. C, *H. macrosoriata*. Scales = 5 mm. In colour online.

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 × 0.1–0.2 mm, 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-acetoxypopane-6α, 22-diol (T4), emodin and 5,7-dichloroemodin. Thallus K+ yellow; pigment K+ purple.

Etymology. Bearing yellow spots.

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 \times 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 \times 0.1–0.2 mm, mostly black, simple when young, soon becoming squarrosely branched, projecting outwards.

Apothecia unknown.

Chemistry. Atranorin, norstictic acid, zeorin and 6 α ,16 β -diacetoxyhopane-22-ol (T3). Thallus K⁺ yellow \rightarrow 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 \times 0.1 mm, mostly whitish, simple.

Apothecia unknown.

Chemistry. Atranorin, norstictic acid and zeorin. Thallus K⁺ yellow \rightarrow 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 \times 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 \times 0.1 mm, mostly black, simple, projecting outwards.

Apothecia unknown.

Chemistry. Atranorin, zeorin, 6 α ,16 β -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.

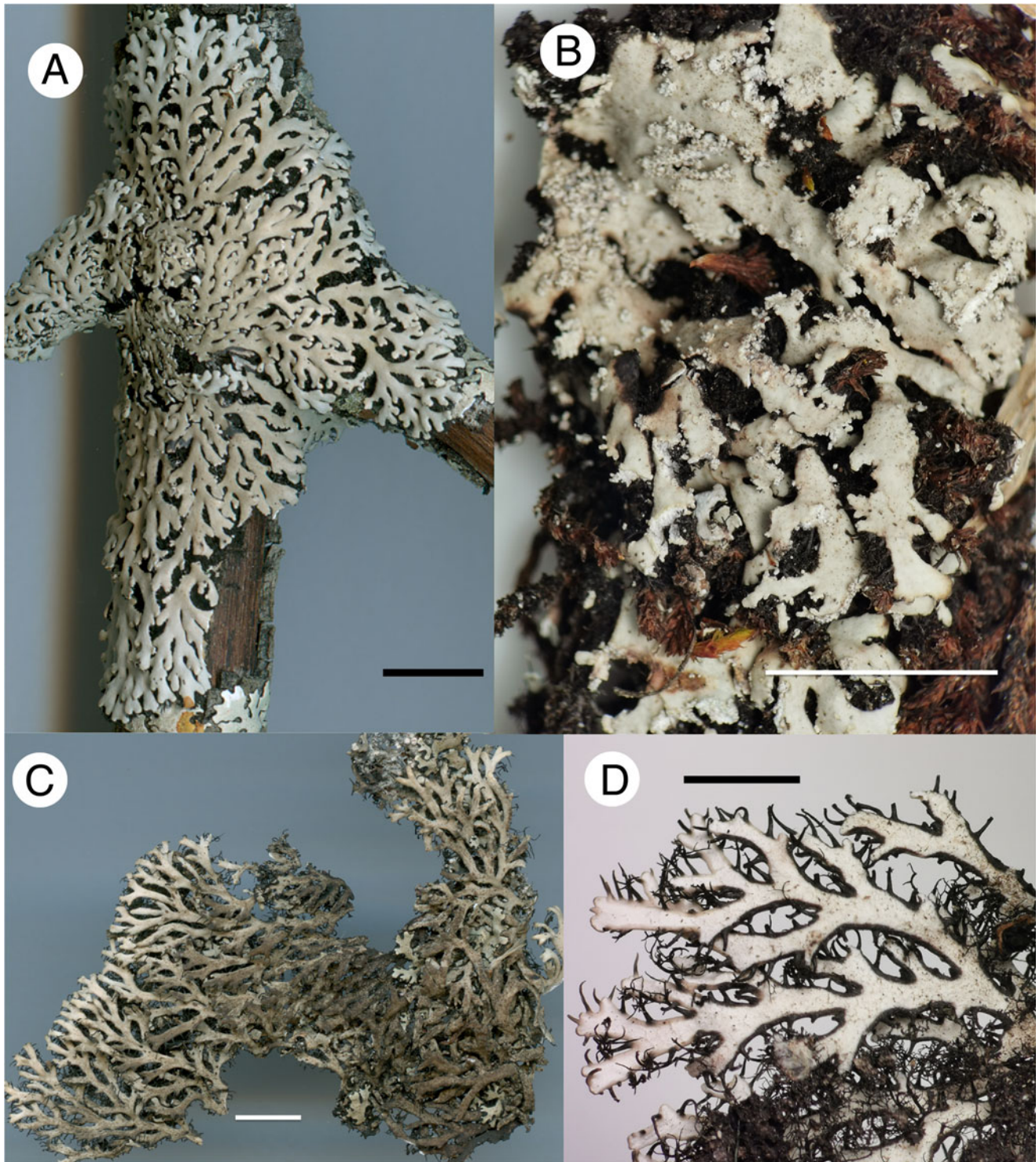


Fig. 4. Holotypes of new species of *Heterodermia*. A, *H. minor*. B, *H. necrocea*. C & D, *H. nigromarginata* (D, lower surface showing the black margins). Scales = 5 mm. In colour online.

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 necrocea* 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).

(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-acetoxypopane-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-acetoxypopane-22-ol (T1), zeorin, 6α,16β-diacetoxypopane-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-diacetoxypopane-22-ol (T3), and sometimes also 16β-acetoxypopane-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,

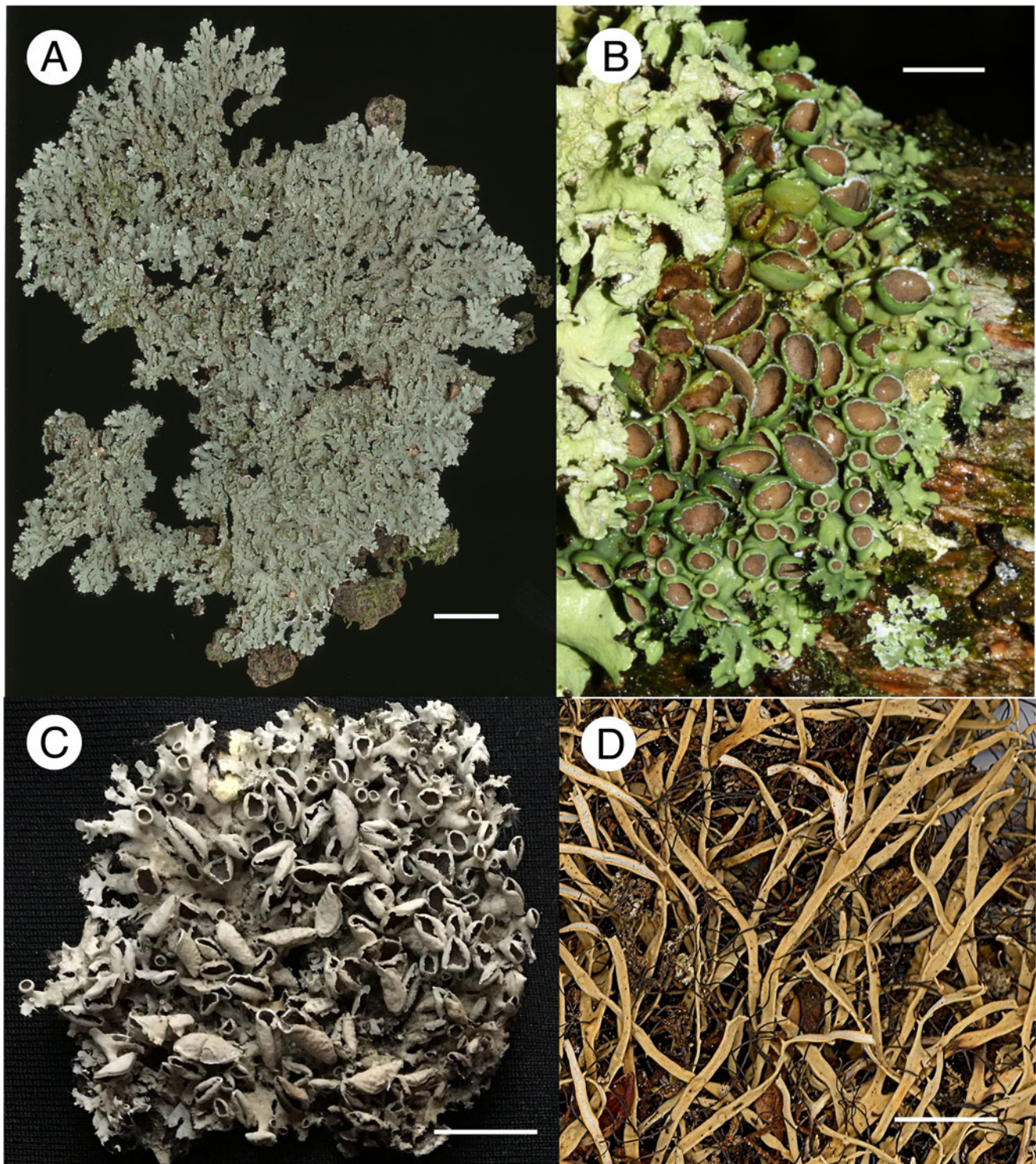


Fig. 5. Holotypes of new species of *Heterodermia*. A, *H. phyllalbicans*. B & C, *H. spielmannii* (B, field picture when wet). D, *H. sublinearis*. Scales = 5 mm. In colour online.

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.

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*, *phylidia* and *isidia* absent. *Medulla* white. *Lower surface* ecorticate, but with a broad corticate margin, without pigment. *Cilia* rather copious, black, 0.2 × 2–4 µm, 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 1982c); PR (Osorio 1977b); 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 1982b); PR (Osorio 1977a); 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


- 1977b); 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 1977b); 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 (Lyngé 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 (Lyngé 1924); MG (Vainio 1890); RJ (Cengia Sambo 1940); SC (Müller 1891a); 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. Sato) 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 (Lyngé 1924); MS (Lyngé 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 1891b); 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 1891a); 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 1977b); 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 (Lyngé 1924); MG (Kalb 1982a); RJ (Müller 1891b); SP (Martins 2007); SC (Müller 1891a); 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.

- 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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