

New species of the *Heterodermia comosa*-group (Physciaceae, lichenized Ascomycota) from southern South America

Andrea MICHLIG^{a,b*}, María Pía RODRÍGUEZ^{a,c}, André APTROOT^d,
Nicolás NIVEIRO^{a,b,c} & Lidia Itatí FERRARO^{a,b,c}

^a*Instituto de Botánica del Nordeste (IBONE-UNNE-CONICET),
Sargento Cabral 2131, CC 209, CP 3400, Corrientes, Argentina*

^b*Facultad de Ciencias Exactas y Naturales y Agrimensura (FACENA, UNNE),
Av. Libertad 5470, CP 3400, Corrientes, Argentina*

^c*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET),
Argentina*

^d*ABL Herbarium, Gerrit van der Veenstraat 107, NL-3762 XK Soest,
The Netherlands*

Abstract – A revision of the specimens from southern South America deposited at CTES herbarium identified as *Heterodermia comosa* (Eschw.) Follmann & Redón was made. As a result, four new species, viz. *H. mobergiana* Michlig, M.P. Rodríguez & Aptroot, *H. neocomosa* M.P. Rodríguez L.I. Ferraro & Aptroot, *H. ramosociliata* M.P. Rodríguez, Michlig & Aptroot, and *H. solediosa* Michlig, L.I. Ferraro & Aptroot, all closely related to *H. comosa*, are here proposed. Each species is described, illustrated and commented. A distribution map is also presented.

Laminal cilia / norstictic acid / pigments / soredia

INTRODUCTION

The *Heterodermia comosa*-group comprises species with a foliose to subfruticose thallus, with usually ascending, spatulate or paddle-shaped lobes, and white marginal rhizines at least when young, somewhat darkened at tips (Mongkolsuk *et al.*, 2015). This group was previously included in *Anaptychia* sect. *Polyblastidium* ser. *Podocarpae* by having ascospores with sporoblastidia at maturity and ascending lobes (Kurokawa, 1962).

Characters that are used to distinguish species within the *Heterodermia comosa*-group include the presence/absence of cilia on the upper surface and/or amphithecia and, as in other groups within *Heterodermia s. lat.*, the mode of reproduction (soralia versus apothecia), underside pigmentation (type and colour), and medullary chemistry (Lücking *et al.*, 2008).

* Corresponding author: andrea.michlig@yahoo.com

However, for *Heterodermia comosa* (Eschw.) Follmann & Redón, a widely distributed species in tropical and subtropical regions (Moberg, 2011), character statements differ between authors, resulting in confusion around the species delimitation. Thus, *H. comosa* has been treated as non-soresiate (Moberg, 2011; Moberg & Nash, 1999, 2002), or as often soresiate with soredia on the underside of lobe tips when sterile (Kurokawa, 1962; Swinscow & Krog, 1976; Aptroot, 1987; Scutari, 1995; Sipman, 1995; Chen, 2001; Elix, 2011; Michlig & Ferraro, 2012; Rodríguez *et al.*, 2012; Mongkolsuk *et al.*, 2015); and with a white non-pigmented lower surface (Moberg & Nash, 1999, 2002; Martins, 2007) or with a yellow to ochraceous pigmentation in the lower surface, K negative (Swinscow & Krog, 1976; Kashiwadani *et al.*, 1990; Chen, 2001; Moberg, 2011; Rodríguez *et al.*, 2012) or reacting K+ purple (Elix, 2011; Mongkolsuk *et al.*, 2015). Kurokawa (1962) mentioned that specimens from South America contain considerable quantities of an ochraceous pigment on the lower surface, which is unknown in specimens from other regions, while Elix (2011) and Mongkolsuk *et al.* (2015) suggest that the palaeotropical specimens may be different from the neotropical material at species level. In addition, although the type of ascospores was considered as an important character to distinguish series within the genus (Kurokawa, 1962), they have been reported in *H. comosa* as being of *Polyblastidium*-type (Kurokawa, 1962; Swinscow & Krog, 1976; Martins, 2007; Elix, 2011; Mongkolsuk *et al.*, 2015), *Pachysporaria*-type with or without sporoblastidia (Moberg, 2011) or without sporoblastidia (Lyngé, 1924; Moberg & Nash, 1999, 2002).

Recent molecular studies in the *H. obscurata* group support the phylogenetic significance of the mode of reproduction, underside pigmentation, and medullary chemistry in the genus (Lücking *et al.*, 2008). Therefore, we supposed that specimens currently identified as *H. comosa* may well consist of a mixture of several, maybe undescribed taxa. The analysis of a large collection of *H. comosa*-like specimens kept in CTES provided an opportunity to test our hypothesis. While they all keyed out as *H. comosa* with one or the other of the traditional keys, several different taxa were recognizable, four of which we propose here as new species. We could not use other existing names, as we are not aware of heterotypic synonyms of *H. comosa*. The most likely candidate, *H. subcomosa* (Nyl.) Elix, is a very different species with squamules on the apothecium margin, an arachnoid lower cortex and only marginal cilia (Trass, 1992).

MATERIALS AND METHODS

Nearly 100 samples identified as *Heterodermia comosa* from Argentina, Bolivia, Brazil, and Paraguay deposited at CTES herbarium were studied. Morphological analysis was carried out using standard stereoscopic (Leica MZ6) and compound light microscopes (Leica CME). Apothecia and pycnidia were sectioned by hand with a razor blade and then mounted in tap water for examination. A total of 30 mature spores were measured per sample. The identification of lichen substances was made with spot tests with 10% KOH (K), UV fluorescence, and thin layer chromatography (TLC) with solvent A following standard methods (Orange *et al.*, 2010). The terms cilia and marginal rhizines are used following Mongkolsuk *et al.* (2015).

RESULTS

We can distinguish four different morphological species in the investigated material from Argentina. They are described and illustrated below, and compared to *H. comosa*. A concise overview of the characters is given in Table 1.

***Heterodermia mobergiana* Michlig, M.P. Rodríguez & Aptroot, *sp. nov.* Figs 1-8**

Mycobank: MB 819856

Holotype: ARGENTINA, Corrientes, Santo Tomé, 35 km SW of Santo Tomé, in marginal forest of Cuay Chico, 4 February 1979, L. Ferraro *et al.* 1485 (CTES).

Diagnosis: This species of the *Heterodermia comosa*-aggregate can be recognized by the following combination of features: ciliate thallus, cilia concolorous with the thallus, *Polyblastidium*-type ascospores, 30-35(-36) × 16-20 µm in size, and an ecorticate, arachnoid, lower surface, without soredia, granules or pigments.

Thallus subfruticose, whitish grey, corticolous, 3 to 4.5 cm in diameter; lobes sublinear, ascending, 2.5-3.5 mm wide, contiguous to partially overlapped, usually convex when fertile, with rounded apices when sterile; margin entire to irregularly incised, with marginal rhizines; marginal rhizines concolorous with the thallus, distributed along the margin, initially simple (Fig. 3) but becoming irregularly branched, commonly anastomosing, 0.2-1 mm long when simple. *Upper surface* continuous, smooth to slightly rugose, emaculate, epruinose, moderately ciliate; cilia concolorous with the thallus, simple to irregularly branched, commonly anastomosing (Fig. 4) or fixed to the upper cortex or rarely to the lower surface. *Medulla* white, lax. *Lower surface* without cortex, arachnoid, without granules or soredia, predominantly veined (Fig. 5), uniformly white, without pigment; rhizines absent, sometimes with cilia arising from veins (Fig. 6). *Apothecia* abundant, slightly convex to plane, usually large, 2.5-7 mm in diameter, commonly stipitate, terminal to subterminal; amphithecium smooth to slightly rugose, sparsely to moderately ciliate (Fig. 8), with simple cilia, 0.1-0.6 mm long, emaculate, usually breaking away from the apothecial wall and forming lobules (Fig. 7); amphithecial lobules irregular, ciliate at the margin, ecorticate on the upper surface; disc brown, pruinose, not covered by a pigment; asci clavate, eight-spored; ascospores brown, subglobose to ellipsoid with a median constriction, *Polyblastidium*-type (with 1-3 sporoblastidia), 30-35(-36) × 16-20 µm. *Pycnidia* submarginal, emergent, conspicuous, ostiole black to whitish; conidia bacilliform, 3-5 µm long.

Chemistry: cortex K+ yellow, UV-; medulla K+ yellow, UV-; lower surface UV-; containing atranorin (major), zeorin (major), 6α-acetoxypopane-16β, 22-diol (minor).

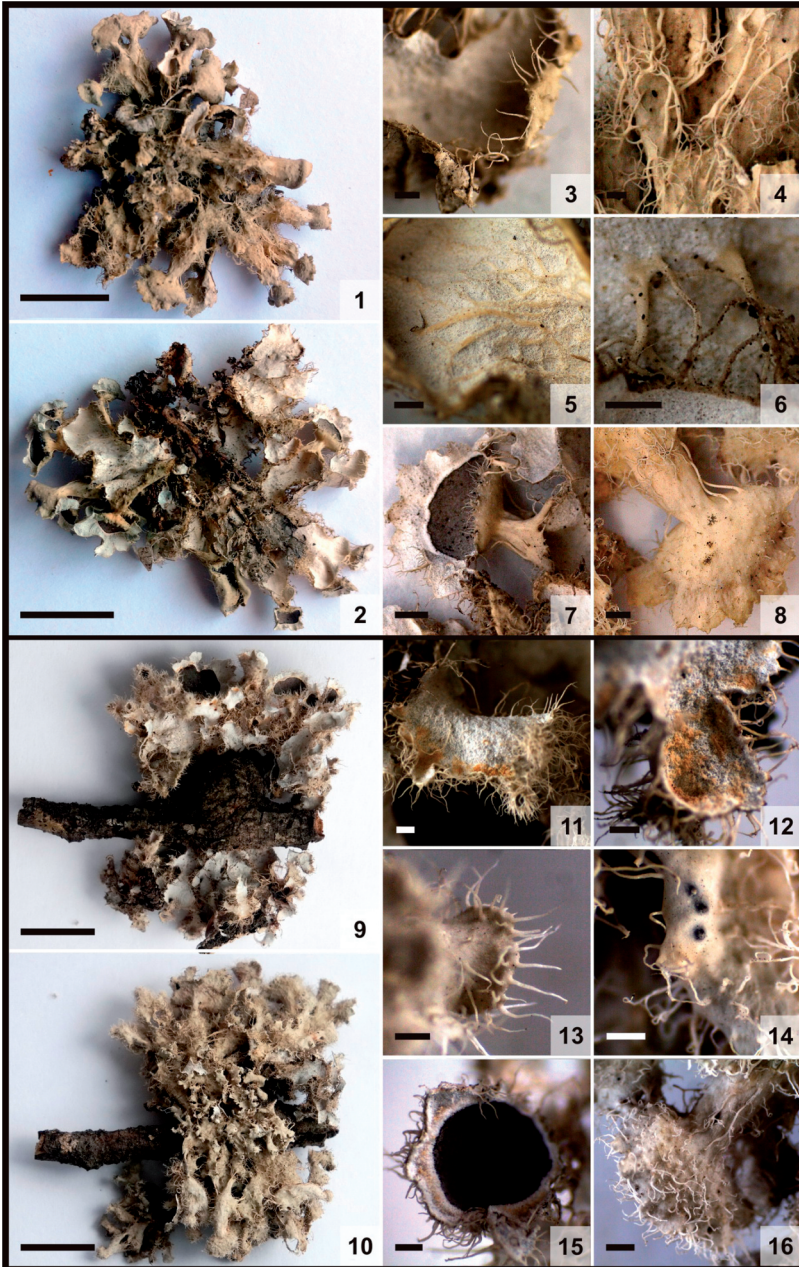
Distribution: Only known from its type locality (Fig. 27).

Comments: *Heterodermia mobergiana* is characterized by its ciliate thallus, with cilia concolorous with the thallus, the *Polyblastidium*-type ascospores [30-35 (-36) × 16-20 µm in size], and the ecorticate arachnoid lower surface, without soredia, granules or pigments. The invalid name *Heterodermia breviciliata* ined. (Martins, 2007) may well refer to the same species.

Given all the differences between descriptions in the literature, the current circumscription of *Heterodermia comosa* is broader than originally defined by Eschweiler (in Martius, 1828) based on material from Brazil. As none of this material is left, Moberg & Nash (1999) designed an epitype from Minas Gerais (Brazil-UPS), which they consider the most similar to the figures and description of Martius

Table 1. Comparison of the new species of the *Heterodermia comosa*-group with *H. comosa* [based on Moberg & Nash (1999)]

	<i>H. mobergiana</i>	<i>H. neocomosa</i>	<i>H. ramosociliata</i>	<i>H. sorediosa</i>	<i>H. comosa</i>
lobes	convex when fertile 2.5-3.5 mm wide	convex when fertile 1.3-3.1 mm wide	convex and reflexed, markedly widened at tips 0.5-1.5 mm wide (-3.5 mm at tips)	convex and reflexed, slightly widened at tips 1.5-3 mm wide	convex up to 5 mm wide
marginal rhizines	concolorous with thallus simple to irregular along the margin	concolorous with thallus simple to irregular along the margin	initially concolorous, turning brownish to grayish to completely black richly irregularly branched dense at lobe sides and axils, scarce at tips	concolorous with thallus simple to irregular or dichotomous along the margin	whitish simple to irregular along the margin
cilia	moderate concolorous with thallus	abundant to moderate concolorous with thallus	absent -	abundant concolorous with somewhat darkened tips	abundant to moderate whitish
lower surface pigment	predominantly veined absent	sometimes slightly veined abundant, orange, K+	not veined scarce, orange, K+	rarely slightly veined moderate to scarce, orange, K+	not veined yellow-brown, K+ (Mongkolsuk <i>et al.</i> , 2015)
rhizines	sometimes with cilia arising from veins	with cilia arising from veins	absent	occasionally sparsely ciliate on veins	absent
soredia	absent	absent	sorediate at tips	sorediate at tips	absent
apothecia	abundant	abundant	rare	absent	common
amphithecium	sparsely to moderately ciliate, lobulate	abundantly to moderately ciliate, lobulate	eciliate, elobulate	-	ciliate, lobulate
pigment	without pigment	orange, K+	not seen (immature)	-	without pigment
ascospores	<i>Polyblastidium</i> -type 30-35 (-36) × 16-20 µm	<i>Pachysporaria</i> -type (18-) 20-31 (-33) × (8-) 10-15 (-16) µm	not seen (immature apothecia) -	-	<i>Pachysporaria</i> -type 31-34 × 13.0-15.5 µm
depsidone	absent	absent	norstictic acid	absent	absent
terpene	6α-acetoxypopane-16β, 22-diol	16β-acetoxypopane-6α, 22-diol	16β-acetoxypopane-6α, 22-diol	16β-acetoxypopane-6α, 22-diol	6α-acetoxypopane-16β, 22-diol (Mongkolsuk <i>et al.</i> , 2015)



Figs 1-16. **1-8.** *Heterodermia mobergiana* (holotype): **1-2.** Complete thallus. **3.** Lobe tips with marginal rhizines. **4.** Laminal cilia. **5.** Arachnoid lower surface with veins. **6.** Cilia arising from the lower side of the upper cortex. **7.** Apothecia with lobules ciliate at margins and no pigment rounding the disc. **8.** Amphithecia with scarce cilia. **9-16.** *Heterodermia neocomosa* (holotype): **9-10.** Complete thallus. **11.** Lower surface with pigment near lobe margins. **12.** Pigment below apothecia. **13.** Marginal rhizinate. **14.** Laminal cilia and pycnidia. **15.** Apothecia with pigment rounding the disc. **16.** Cilia on the amphithecia. Scale bar: 1-2, 9-10 = 1 cm; 3-7, 11-15 = 0.5 mm; 8, 16 = 1 mm.

(1828). The overall appearance of the epitype is in accordance with *H. mobergiana*, including the absence of soralia (Moberg & Nash, 1999). However, it has *Pachysporaria*-type ascospores, without sporoblastidia, differing thus from *H. mobergiana*.

The new species is distinguished from *Heterodermia neocomosa* by its *Polyblastidium*-type ascospores, larger in size [30-35(-36) × 16-20 µm versus (18-) 20-31(-33) × (8-)10-15(-16) µm], the absence of pigments on the lower surface and around the disc, and the medullary 6α-acetoxypentane-16β, 22-diol.

Among the non-sorediate species of the *Heterodermia comosa* group, *Polyblastidium*-type ascospores are also present in *H. cubensis* (Kurok.) Trass and *H. peruviana* (Kashiw. & Kurok.) Kurok., but both differ in having medullary norstictic acid, with additional salazinic acid in the former (Kashiwadani *et al.*, 1990). *Heterodermia peruviana* also differs in having a yellow, K negative pigment.

Heterodermia neocomosa M.P. Rodríguez, L.I. Ferraro & Aptroot, *sp. nov.*

Figs 9-16

Mycobank: MB 819857

Holotype: ARGENTINA, Formosa, Bermejo, Formosa Natural Reserve, surroundings of the eastern access of the Reserve, 24°17'51" S, 61°47'38" W, 170 m, 7 May 2012, A. Michlig *et al.* 2867 (CTES).

Diagnosis: Differing from *Heterodermia comosa* in the smaller, *Pachysporaria*-type ascospores.

Thallus subfruticose, whitish grey, corticolous, 1.5 to 5 cm in diameter; lobes sublinear, ascending, 1.3-3.1 mm wide, crowded, usually convex when fertile; margin crenate to irregularly incised, with marginal rhizines; marginal rhizines concolorous with the thallus, distributed along the margin, simple to irregularly branched (Figs 13 & 14), sometimes anastomosing, 0.3-1.3(-2.2) mm long. *Upper surface* continuous, smooth to slightly rugose, emaculate, epruinose, abundantly to moderately ciliate; cilia concolorous with the thallus, simple to irregularly branched, less commonly dichotomous, sometimes anastomosing or fixed to the upper cortex or rarely to the lower surface, 0.4-3.5 mm long. *Medulla* white, lax. *Lower surface* without cortex, arachnoid, without granules or soredia, sometimes slightly venose, white, with an orange pigment K+ dark red to brownish, usually abundant, distributed in patches or often irregularly, usually more concentrated near the thallus margin (Fig. 11) and at the base of the stipe (Fig. 12); rhizines absent but occasionally sparsely ciliate (with cilia arising from veins). *Apothecia* abundant, initially slightly convex to cupuliform with entire margin, but usually becoming plane, usually large, 0.6-10 mm in diameter, stipitate, terminal to subterminal; amphithecium smooth to slightly rugose, ciliate with simple cilia (Fig. 16), 0.4-1(-1.5) mm long, emaculate, usually breaking away from the apothecial wall and forming lobules (Fig. 15); amphithecial lobules irregular, occasionally branched, ciliate at the margin, ecorticate on the upper surface; disc brown to dark gray, rarely pinkish, pruinose, rounded by an orange pigment, K+ dark red (Fig. 15); asci clavate, eight spored; ascospores brown, subglobose to ellipsoid with a median constriction, *Pachysporaria*-type (without sporoblastidia), (18-)20-31(-33) × (8-)10-15(-16) µm. *Pycnidia* mostly submarginal, sometimes marginal, emergent, conspicuous, usually abundant, ostiole black to whitish; conidia bacilliform, 3-5 µm long.

Chemistry: cortex K+ yellow, UV-; medulla K+ yellow, UV-; lower surface UV-; containing atranorin (major), zeorin (major to minor), 16β-acetoxypentane-6α, 22 diol (major to minor), and 7-chloroemodin (minor to trace).

Additional specimens examined: ARGENTINA, Chaco, Comandante Fernández, Nat. Route N° 95, between Presidencia Roque Sáenz Peña and Tres Isletas, kilometers before the junction with Prov. Route N° 44, 26°33'44.4" S, 60°18'26.6" W, 108 msm, in a *Schinopsis balansae* forest, on *Schinopsis balansae*, 11 February 2010, A. Michlig & N. Niveiro 2161 (CTES); Donovan, 13 km from La Verde, Estancia 2 Tranqueras, on *Prosopis*, 21 September 1982, A. Schinini 22798 (CTES); La Leonesa, near the stream Canguí Grande, in edge of road, 16 November 1995, L. Ferraro *et al.* 5254 (CTES); Primero de Mayo, Colonia Benítez, 15 July 1978, A. Schinini 15319 (CTES); Quitilipi, Colonia La Tambora, 31 September 1977, L. Ferraro 1193 (CTES); Corrientes, Saladas, San Lorenzo, San Lorenzo river, 20 April 1973, A. Schinini & C. Quarín 6450 (CTES); San Cosme, Paso de la Patria, San Juan stream, 9 September 1985, L. Ferraro & T. Nash 3216 (CTES); Formosa, Bermejo, Laguna Yema, in Chaco forest, edge of road, 25 April 2009, L. Ferraro 9153 (CTES); Salta, Rivadavia, Route 81, 18 Km W of Cap. Page, 25 November 1994, A. Krapovickas 46474 (CTES); San Martín, 15 km W of Hickman-Pozo del Milagro, epiphyte on sparse trees, sandy soil, 9 December 1972, A. Schinini *et al.* 17597 (CTES). BOLIVIA, Chuquisaca, Luis Calvo, El Salvador, 670 m, epiphyte of forage value, 4 June 1991, C. Toledo 2994c (CTES); Santa Cruz, Cordillera, Isla Verde Farm, on the shore of Izozog "bañados", Parapeti river, poorly drained Chaco forest with *Aspidosperma triternatum* and *Trithrinax campestris*, 20 straight NE of the farm, 300 m, 17 August 1997, A. Fuentes & G. Navarro 2000 (CTES); Tarija, Caingua, 15 km N de Villa Montés, n/d, A. Krapovickas *et al.* 6462 (CTES). BRASIL: Mato Grosso do Sul, Corumbá, 19°49' S-57°49' W, 23 October 1988, V. Pott & A. Pott 699 (CTES). PARAGUAY, Chaco, Mayor Pedro Lagerenza, 20° S, 60°45' W, 15 April 1978, A. Schinini & E. Bordas 15258 (CTES); Nueva Asunción, Trans Chaco route, 21°26' S, 61°25' W, on dry fallen branches in open xerophytic forest, March 1979, A. Schinini 16617 (CTES).

Distribution: This is a relatively common species, distributed over northern Argentina, Brazil, Bolivia and Paraguay (Fig. 27). It grows over shrub branches, in relatively open situations.

Comments: *Heterodermia neocomosa* is characterized by its upper surface and amphithecia with cilia which are completely concolorous with the thallus, the white ecorticate arachnoid lower surface with an orange pigment K+ dark red distributed in irregular patches and also rounding the apothecial disc, the *Pachysporaria*-type ascospores, (18-)20-31(-33) × (8-)10-15(-16) µm in size, and the absence of soralia or granules on the underside.

The overall appearance of the epitype of *H. comosa* is in accordance with *H. neocomosa*, including the absence of soralia, even though Moberg & Nash (1999) did not mention any pigment on the lower surface or apothecia and reported larger ascospores, as commonly found in literature for the species (31-34 × 13-15.5 µm), which is clearly differing from *H. neocomosa*.

There are a few additional species within the genus with laminal cilia, which are closely related with this species: *Heterodermia ciliatomarginata* (Linder) Essl., *H. cubensis*, *H. erinacea* (Ach.) W. A. Weber, *H. namaquana* Brusse, *H. peruviana*, and *H. sinocomosa* J. B. Chen. Among these, *H. cubensis* and *H. peruviana* are the taxa most similar to *H. neocomosa*, as both have ascendant lobes, marginal rhizines and laminal cilia, an ecorticate and esorediate lower surface, and subapical to apical apothecia with crenate to lobulate margin and ciliate receptacle. However, both species differ from *H. neocomosa* in the type and size of the ascospores, the pigment in the lower surface, and in their medullary chemistry (Kurokawa, 1962; Kashiwadani *et al.*, 1990). In *H. cubensis* and *H. peruviana*, the

ascospores are of *Polyblastidium*-type and usually large ($33-42 \times 16-20 \mu\text{m}$ and $28-38 \times 13-18 \mu\text{m}$ respectively), while in *H. neocomosa* they lack sporoblastidia and are smaller ($18-28 \times 10-16 \mu\text{m}$). In *H. cubensis* the pigment is absent, while in *H. peruviana* it is yellow and K negative (Kashiwadani *et al.*, 1990) differing from the material studied where the pigment is orange and K⁺ dark red to brownish. *Heterodermia peruviana* and *H. cubensis* have norstictic acid, associated with salazinic acid in the latter, which is absent in *H. neocomosa* (Kashiwadani *et al.*, 1990).

Heterodermia erinacea and *H. namaquana* are rather similar species with lobes somewhat narrower and elongate, smaller, *Physcia*-type ascospores [$16-24 \times 7.5-10 \mu\text{m}$ and $(14-17)-17-22.5 \times 6-8 \mu\text{m}$ respectively], cilia mostly marginal or submarginal, not frequently laminal, commonly simple, and white but also darkening towards the tips (Brusse, 1992; Esslinger & Bratt, 1998). The latter also differs from *H. neocomosa* in having a lower surface sorediate at lobes tips, with some cilia originating from the upper surface (Brusse, 1992; Esslinger & Bratt, 1998). *Heterodermia ciliatomarginata* is a saxicolous species, also with small, *Physcia*-type ascospores [$12-17(-20) \times 6-7.5 \mu\text{m}$] and cilia white or darkening in upper parts, but clearly differs in its lower surface which is composed of agglutinated medullary hyphae forming a more or less smooth, but dull, lower cortex, and the absence of zeorine (Esslinger & Bratt, 1998).

Heterodermia sinocomosa is similar to *H. neocomosa* in having a K⁺ pigment and abundant laminal and marginal cilia, but they are shorter (0.7-2 mm long), and white or pellucid at the base, turning dark brown or blackish towards the apices (Chen, 2001). It also differs in having much narrower lobes (0.7-1.5 mm wide), with pruina near the apices.

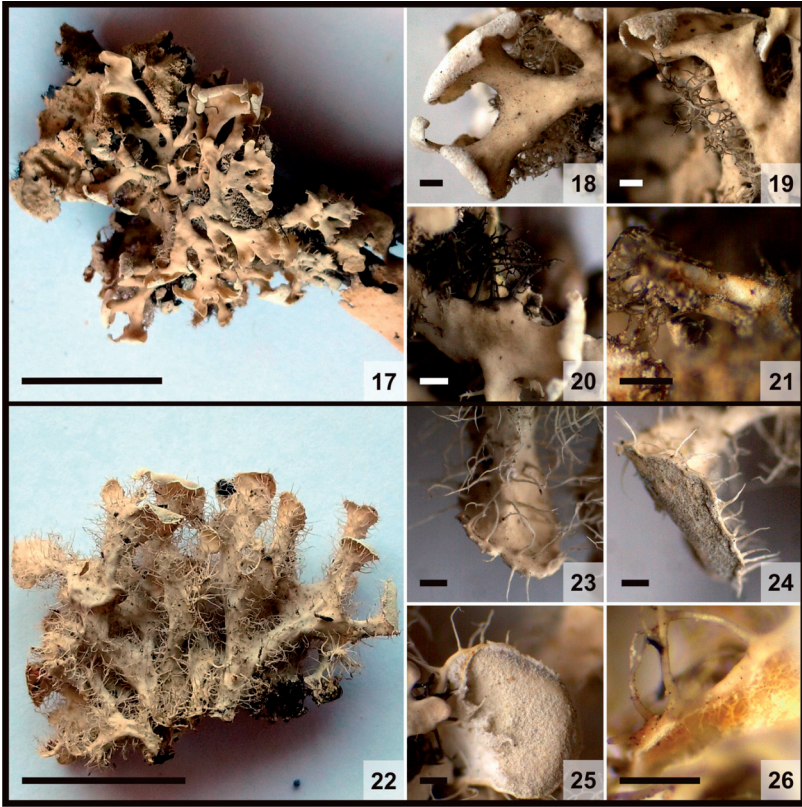
***Heterodermia ramosociliata* M.P. Rodríguez, Michlig & Aptroot, *sp. nov.* Figs 17-21**

Mycobank: MB 819858

Holotype: ARGENTINA, Misiones, Guaraní, Predio Guaraní, near the guests housing, on *Sebastiania commensoniana*, 18 September 1998, S. Tressens 5984 (CTES).

Diagnosis: This species of the *Heterodermia comosa*-aggregate is characterized by convex, reflexed lobes, markedly widened at tips, and richly branched marginal rhizines which are white turning brownish to completely black, and medullary norstictic acid. The lower surface is mostly white, with small quantities of pigment at convex areas of lobes where no soredia or granules are developed, which reacts K⁺ dark red to brownish and easily becomes hidden by marginal rhizines.

Thallus foliose, whitish grey, corticolous, 1 to 2.5 cm in diameter; lobes sublinear, 0.5-1.5 mm wide, partially overlapped to crowded, usually convex and then reflexed with widened tips (1.8-3.5 mm wide) (Fig. 18); margin entire to irregularly incised, with marginal rhizines; marginal rhizines initially concolorous with the thallus, but turning brownish to grayish and finally completely black, dense at lobe sides and axils but scarce at lobe apices, richly irregularly branched (Figs 18-20). *Upper surface* continuous, smooth to slightly rugose, emaculate, epruinose, eciliate. *Medulla* white. *Lower surface* without cortex, arachnoid at center, becoming sorediate at tips turning the lobes reflexed, not veined, white, with an orange to ochraceous pigment K⁺ dark red to brownish (Fig. 21), scarce, mostly restricted to small patches of non-granulate surface; rhizines absent. *Apothecia* rare, only immature ones seen, slightly convex, 0.4-0.6 cm in diameter, adnate to substipitate, laminal; amphithecium smooth, eciliate, emaculate, elobulate; ascospores not seen. *Pycnidia* not seen.



Figs 17-26. **17-21.** *Heterodermia ramosociliata* (holotype): **17.** Complete thallus. **18.** Convex lobes widened and sorediate at tips. **19.** Branched marginal rhizines with darkened tips. **20.** Completely black marginal rhizines. **21.** Pigment on the lower surface. **22-26.** *Heterodermia sorediosa* (holotype): **22.** Complete thallus. **23.** Convex lobe with laminal cilia and marginal rhizines. **24.** Reflexed lobe tips with marginal rhizines. **25.** Soralia at lobe tips with farinose soredia. **26.** Pigment on the lower surface. Scale bar: 17, 22 = 1 cm; 18-21, 23-25 = 0.5 mm.

Chemistry: cortex K+ yellow, UV-; medulla K+ yellow, UV-; lower surface UV-; containing atranorin (major), zeorin (major), norstictic acid (major), 6 α -acetoxyhopane-16 β , 22-diol (major), and 7-chloroemodin (trace).

Additional specimen examined: ARGENTINA, Salta, Santa Victoria, Baritú National Park, shortly after the entry to the rustic camping area “El Ukumar”, in an open environment, 22°25'39.2''S, 64°44'20.6''W, 1118 m, on fallen branches, 21 April 2009, A. Michlig *et al.* 1219b (CTES).

Distribution: Known only from Argentina (Fig. 27).

Comments: *Heterodermia ramosociliata* is characterized by its convex, reflexed lobes markedly widened at tips and the richly branched marginal rhizines which are white turning brownish to completely black, and the medullary norstictic acid. The lower surface is mostly white, with only small quantities of pigment at convex areas of lobes where no soredia or granules are developed, which reacts K+ dark red to brownish and easily becomes hidden by marginal rhizines. While there are no apothecia in the holotype, the paratype has two eciliate, immature apothecia.

This new species clearly differs from *H. comosa* by its eciliate thallus with richly branched marginal rhizines, and the medullary norstictic acid.

The most closely related species are *Heterodermia galactophylla* (Tuck.) W. L. Culb. and *H. allardii* (Kurok.) Trass, both with soralia beneath lobes apices and branched marginal rhizines, but both differ in the colour of the marginal rhizines and the medullary chemistry. Although *H. allardii* has medullary norstictic acid, the marginal rhizines are uniformly white (Kurokawa, 1962; Moberg, 2011), while *H. galactophylla* has white to somewhat darkened marginal rhizines (Kurokawa, 1962; Moberg, 2011) but lacks norstictic acid and is reported to contain japonene (Mongkolsuk *et al.*, 2015), which is absent in *H. ramosociliata*. Kurokawa (1962) also reported salazinic acid for *H. allardii*, which was not detected in our species. Incidentally, the identification of salazinic acid has been questioned; it is connorstictic acid according to Elix (2011).

Other related species without laminal cilia are *Heterodermia echinata* (Taylor) W. L. Culb., *H. barbifera* (Nyl.) Kr. P. Singh, *H. podocarpa* (Bél.) D. D. Awasthi, and *H. stellata* (Vain.) W. A. Weber, but they are clearly different as they lack soralia (Kurokawa, 1962). Among these, *H. barbifera* and *H. podocarpa* share with *H. ramosociliata* the medullary norstictic acid, but the former also differs in having sublinear-elongate lobes, and cilia forming mats along the margins (Kurokawa, 1962), while the later has simple to irregularly branched marginal rhizines but not mat-forming (Mongkolsuk *et al.*, 2015).

***Heterodermia solediosa* Michlig, L.I. Ferraro & Aptroot, *sp. nov.* Figs 22-26**

Mycobank: MB 819859

Holotype: ARGENTINA, Misiones, Guaraní, Predio Guaraní, near the guests housing, on *Sebastiania commensoniana*, 18 September 1998, S. Tressens 5990 (CTES).

Diagnosis: This species of the *Heterodermia comosa*-aggregate is characterized by its laminal cilia, concolorous with the thallus or occasionally with darkened tips, the paddle-shaped lobes reflexed at tips, and the arachnoid to finely granulate lower surface with farinose soredia towards lobe apices, and an orange to ochraceous pigment, which is K+ dark red to brownish.

Thallus subfruticose, whitish, corticolous, 1.5 to 2.5 cm in diameter; lobes paddle-shaped, ascending, 1.5-3 mm wide, crowded, usually convex and reflexed at the tips (Figs 23 & 24); margin entire to irregularly incised, with marginal rhizines; marginal rhizines concolorous with the thallus, distributed along the margin, commonly simple to sometimes irregularly branched or dichotomous, sometimes anastomosing and attached to each other or to the upper surface, 1-2.3 mm long (Figs 23 & 24). *Upper surface* continuous, smooth to slightly rugose, emaculate, epruinose, abundantly ciliate; cilia concolorous with the thallus to occasionally with somewhat darkened tips, simple to irregularly branched, sometimes anastomosing or rarely fixed to the upper cortex, 0.3-1.75 mm long. *Medulla* white, lax. *Lower surface* without cortex, rarely slightly veined, arachnoid to finely granulate, with soralia with farinose soredia towards lobe apices (Fig. 25), white, with an orange to ochraceous pigment K+ dark red to brownish, moderate to scarce, located where soredia or granules are not developed (Fig. 26); rhizines absent but occasionally sparsely ciliate on veins. *Apothecia* absent. *Pycnidia* not seen.

Chemistry: cortex K+ yellow, UV-; medulla K+ yellow, UV-; lower surface UV-; containing atranorin (major), zeorin (major), 16 β -acetoxypopane-6 α , 22-diol (major to minor), and 7-chloroemodin (minor to trace).

Additional specimens examined: ARGENTINA, Corrientes, San Cosme, 3 km from junction with Paso de la Patria, on the way to Puerto González, 21 May 1979, L. Ferraro *et al.* 1933 (CTES); Salta, Anta, El Rey National Park, in “tusca” and “piquillín” forest (on the way to Pozo Verde), on “tusca” branches, *Acacia aroma*, 7 May 1983, S. Chalukián 1970 (CTES); Santa Victoria, Baritú National Park, shortly after the entry to the rustic camping area “El Ukumar”, in an open environment, 22°25′39.2″S, 64°44′20.6″W, 1118 m, on fallen branches, 21 April 2009, A. Michlig *et al.* 1219a (CTES). PARAGUAY, Boquerón, Col. Fernheim, Filadelfia, recreation park for mental health, xerophytic forest, 11 September 1990, R. Vanni *et al.* 2649 (CTES).

Distribution: Known so far only from Argentina and Paraguay (Fig. 27).

Comments: *Heterodermia solediosa* is characterized by its laminal cilia, concolorous with the thallus to occasionally with darkened tips, the paddle-shaped lobes reflexed at tips, and the arachnoid to finely granulate lower surface with farinose soredia towards lobe apices, and an orange to ochraceous pigment, which is K+ dark red to brownish.

Moberg & Nash (1999), when designing the epitype of *H. comosa*, described it as a non-sorediate species, with convex lobes up to 5 mm wide, and whitish cilia, differing thus from *H. solediosa*, which has reflexed and narrower lobes (up to 3 mm), sorediate at tips, and cilia with darkened tips.

Heterodermia follmannii Sipman, *H. namaquana*, *H. archeri* Elix, *H. allardii* and *H. galactophylla* are similar, sorediate species of the *H. comosa*-group. Among them, only *H. follmannii* and *H. namaquana* have a ciliate thallus. The former differs in having linear lobes with black, mostly simple, cilia which arise

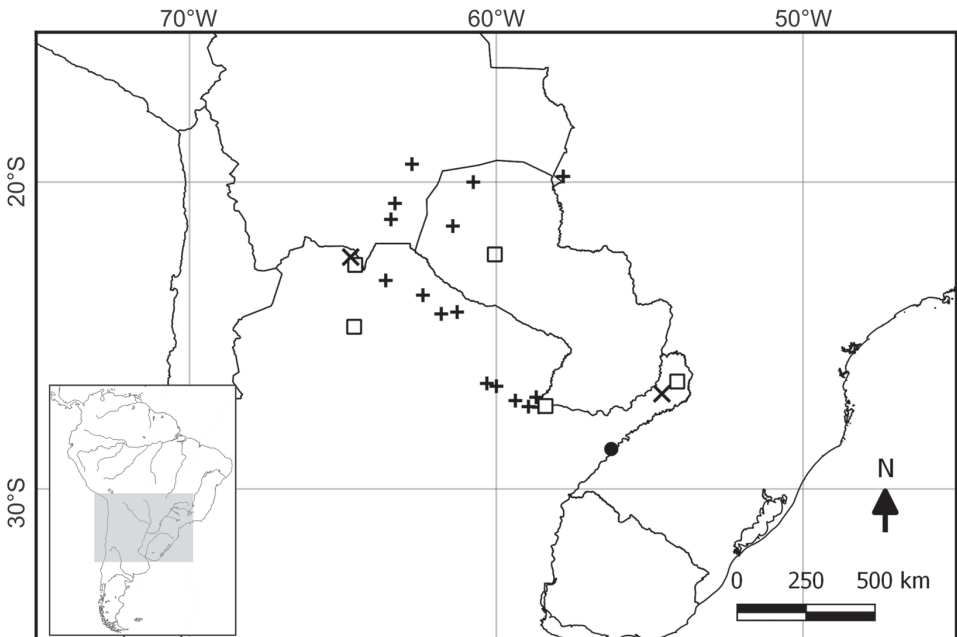


Fig. 27. Map showing the geographic distribution of *H. mobergiana* (●), *H. neocomosa* (+), *H. ramosociliata* (x), *H. solediosa* (□).

from a short pale base (Sipman, 1995), while *H. namaquana* differs in having sublinear lobes, not markedly widened and reflexed at the tips (Brusse, 1992). *Heterodermia archeri*, *H. allardii* and *H. galactophylla* have cilia which become richly branched. The former also differs in lacking pigment, its spathulate soralia and testacein (Mongkolsuk *et al.*, 2015), while *H. allardii* contains norstictic acid (Kurokawa, 1962) and in *H. galactophylla* the marginal rhizines which may turn darkened, the lower surface is uniformly white, and produces japonene (Mongkolsuk *et al.*, 2015).

Acknowledgments. We are grateful to the authorities of the Administración de Parques Nacionales (APN) of Argentina for providing collection permits. This work was funded by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the Secretaría General de Ciencia y Técnica (SGCyT-UNNE).

REFERENCES

- APTROOT A., 1987 — Pyxinaceae (Lichens). In: Görts-van Rijn ARA. (ed.), *Flora of the Guianas, Series E: Fungi and Lichens*. Koeltz Scientific Books, Germany, pp. 1-53.
- BRUSSE F., 1992 — A new species in the lichen genus *Heterodermia*, from coastal Namaqualand. *Bothalia* 22: 183-185.
- CHEN J.B., 2001 — The lichen family Physciaceae (Ascomycota) in China II. Two new species of *Heterodermia*. *Mycotaxon* 77: 101-105.
- ELIX J.A., 2011 — *Heterodermia*, Australian Physciaceae (Lichenised Ascomycota). In: <http://www.anbg.gov.au/abrs/lichenlist/HETERODERMIA.pdf>.
- ESSLINGER T.L. & BRATT C., 1998 — The *Heterodermia erinacea* group in North America, and a remarkable new disjunct distribution. In: Glein MG., Harris RC., Dirig R. & Cole MS. (eds.), *Lichenographia Thomsoniana: North American Lichenology in Honor of John W. Thomson*. Mycotaxon Ltd., Ithaca, NY, pp. 25-36.
- KASHIWADANI H., KUROKAWA S. & MURAKAMI S., 1990 — Enumeration and chemical variations of the lichen genus *Anaptychia* (s. lat.) in Peru. *Bulletin of the National Science Museum, Tokyo*, Ser. B, 16: 174-156.
- KUROKAWA S., 1962 — A monograph of the genus *Anaptychia*. *Beihefte zur Nova Hedwigia* 6: 1-115, 9 plates.
- LÜCKING R., DEL PRADO R., LUMBSCH H.T., WILL-WOLFF S., APTROOT A., SIPMAN H.J.M., UMAÑA L. & CHAVES J.L., 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.
- LYNGE B., 1924 — On South American *Anaptychia*e and *Physcia*e. *Skr. Vid. Math-Naturvidensk. Kl.* 2: 1-49.
- MARTINS M.F.N., 2007 — O gênero *Heterodermia* (Physciaceae, Ascomycota liquenizados) no Estado de São Paulo. Dissertação (mestrado). Universidad Estadual Paulista, Instituto de Biociências de Botucatu, 218 p.
- MARTIUS C.F.P. VON, 1828 — *Icones plantarum cryptogamicarum quas in itinere annis MDCCCXVII-MDCCCXX per Brasiliam jussu et aspiciis Maximiliani Josephi I. Bavariae regis augustissimi instituto/collecit et descripsit*. Monachii, 138 p.
- MICHLIG A. & FERRARO L., 2012 — Diversidad de macrolíquenes del Parque Nacional Mburucuyá (Corrientes, Argentina). *Boletín de la Sociedad Argentina de Botánica* 47: 287-302.
- 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. & NASH T.H., 1999 — The genus *Heterodermia* in the Sonoran desert area. *The Bryologist* 102: 1-14.
- MOBERG R. & NASH T.H., 2002 — *Heterodermia*. In: Nash TH., Ryan BD., Gries C. & Bungartz F. (eds.), *Lichen Flora of the Greater Sonoran Desert Region, Vol. 1*. Lichens Unlimited, Arizona State University, USA, pp. 207-219.

- MONGKOLSUK P., MEESIM S., POENGSUNGNON V., BUARUANG K., SCHUMM F. & KALB K., 2015 — The lichen family Physciaceae in Thailand-II. Contributions to the genus *Heterodermia sensu lato*. *Phytotaxa* 235: 1-66.
- ORANGE A., JAMES P.W. & WHITE F.J., 2010 — *Microchemical methods for the identification of lichens*. 2nd Edition. The British Lichen Society, London, 101 p.
- RODRÍGUEZ J.M., ESTRABOU C. & QUIROGA G., 2012 — El género *Heterodermia* (Lecanorales-Physciaceae) en el centro norte de Argentina. *Acta Botánica Brasilica* 26: 1000-1005.
- SCUTARI N.C., 1995 — Los macrolíquenes de Buenos Aires, I: *Dirinaria*, *Heterodermia* e *Hyperphyscia* (Physciaceae, Ascomycotina). *Darwiniana* 33: 149-176.
- SIPMAN H.J.M., 1995 — *Heterodermia pinnata* sp. nov. and *Heterodermia follmannii* sp. nov. (Physciaceae, Lecanorales), two new lichen species from North Chile, South America. In: Daniels F.J.A., Schulz M. & Peine J. (eds.), *Contributions to Lichenology in honour of Gerhard Follmann*. Cologne, Germany, pp: 329-336.
- SWINSCOW T.D.V. & KROG H., 1976 — The genera *Anaptychia* and *Heterodermia* in East Africa. *Lichenologist* 8: 103-138.
- TRASS H., 1992 — Synopsis of the lichen genus *Heterodermia* (Ascomycotina, Physciaceae sive Pyxinaceae). *Folia Cryptogamica Estonica* 29: 1-24.