

## A revisionary synopsis of the *Trypetheliaceae* (Ascomycota: *Trypetheliales*)<sup>‡</sup>

André APTROOT and Robert LÜCKING

**Abstract:** A revisionary synopsis is presented for the family *Trypetheliaceae*, based on a separately published phylogenetic analysis of a large number of species, morpho-anatomical and chemical study of extensive material, and revision of numerous type specimens. A total of 418 species is formally accepted in this synopsis, distributed among 15 genera as follows: *Aptrootia* (3), *Architrypethelium* (7), *Astrothelium* (242), *Bathelium* (16), *Bogoriella* (29), *Constrictolumina* (9), *Dictyomeridium* (7), *Distothelia* (3), *Marcelaria* (3), *Nigrovothelium* (2), *Novomicrothelia* (1), *Polymeridium* (50), *Pseudopyrenula* (20), *Trypethelium* (16), and *Viridothelium* (10). All accepted genera, including new genera described separately in this issue, are keyed out and briefly described and discussed, and keys are provided for all accepted species within each genus. Entries with full synonymy and brief descriptions, and in part also discussions, are provided for all accepted species, except those newly described elsewhere in this issue, which are cross-referenced in the corresponding keys. The description of the newly defined genera takes into account phylogeny in combination with morpho-anatomical features with the result that they are mostly recognizable by a combination of thallus, ascoma and ascospore features. Most species previously assigned to the genera *Astrothelium*, *Campylothelium*, *Cryptothelium*, and *Trypethelium*, based on a schematic concept of ascoma morphology and ascospore septation, are now included in a single genus, *Astrothelium*, with highly variable ascoma morphology and ascospore septation but invariably with astrothelioid ascospores (at least when young), that is diamond-shaped lumina, and a well-developed, corticate, usually olive-green thallus that often covers the ascomata. While the genera *Aptrootia* (large, brown, muriform ascospores), *Architrypethelium* (large, mostly 3-septate ascospores), and *Pseudopyrenula* (ecorticate, white thalli and astrothelioid ascospores) are maintained, *Trypethelium* is redefined to include species with raised, pseudostromatic ascomata and multiseptate ascospores with thin septa. The sister group of *Trypethelium* is the genus *Marcelaria*, with brightly coloured pseudostromata and muriform ascospores. *Bathelium* is now limited to species with strongly raised, fully exposed pseudostromata and septate to muriform ascospores with thin septa. Several genera are recognized for more basal lineages with mostly ecorticate, white thalli and solitary, exposed ascomata previously assigned to *Arthopyrenia*, *Mycocomirothelia* and *Polymeridium*, viz. *Bogoriella*, *Constrictolumina*, *Dictyomeridium*, and *Novomicrothelia*. In addition, separate genera are accepted for the *Trypethelium tropicum* (*Nigrovothelium*) and *T. virens* (*Viridothelium*) groups. In addition, a refined species concept resulting from phylogenetic studies is employed which pays particular attention to morphological features of the thallus and ascomata. Of a total of 526 names checked, 107 remain synonyms of accepted names and a further eight are newly excluded from the family. Based on these repositions, the following 146 new combinations are proposed, including reinstatement of numerous names previously subsumed into synonymy: *Architrypethelium columbianum* (Nyl.) Aptroot & Lücking comb. nov., *A. grande* (Kremp.) Aptroot & Lücking comb. nov., *Astrothelium aeneum* (Eschw.) Aptroot & Lücking comb. nov., *A. alboverrucum* (Makhija & Patw.) Aptroot & Lücking comb. nov., *A. amazonum* (R. C. Harris) Aptroot & Lücking comb. nov., *A. ambiguum* (Malme) Aptroot & Lücking comb. nov., *A. andamanicum* (Makhija & Patw.) Aptroot comb. nov., *A. annulare* (Spreng.) Aptroot & Lücking comb. nov., *A. aurantiacum* (Makhija & Patw.) Aptroot & Lücking comb. nov., *A. auratum* (R. C. Harris) Aptroot & Lücking comb. nov., *A. aureomaculatum* (Vain.) Aptroot & Lücking comb. nov., *A. basilicum* (Kremp.) Aptroot & Lücking comb. nov., *A. bicolor* (Taylor) Aptroot & Lücking comb. nov., *A. buckii* (R. C. Harris) Aptroot & Lücking comb. nov., *A. calosporum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. cartilagineum* (Fée) Aptroot & Lücking comb. nov., *A. cecidiogenum* (Aptroot & Lücking) Aptroot & Lücking comb. nov., *A. ceratinum* (Fée) Aptroot & Lücking comb. nov.,

A. Aptroot (corresponding author): ABL Herbarium, G.v.d.Veenstraat 107, NL-3762 XK Soest, The Netherlands. Email: andreaproot@gmail.com

R. Lücking: Botanischer Garten und Botanisches Museum, Königin-Luise-Strasse 6–8, 14195 Berlin, Germany; Research Associate, Integrative Research

Center, The Field Museum, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA.

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*A. chapadense* (Malme) Aptroot & Lücking comb. nov., *A. chrysoglyphum* (Vain.) Aptroot & Lücking comb. nov., *A. chrysostomum* (Vain.) Aptroot & Lücking comb. nov., *A. cinereosellum* (Kremp.) Aptroot & Lücking comb. nov., *A. cinereum* (Müll. Arg.) Aptroot & Lücking comb. et stat. nov., *A. confluens* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. consimile* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. deforme* (Fée) Aptroot & Lücking comb. nov., *A. defossum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. degenerans* (Vain.) Aptroot & Lücking comb. nov., *A. dissimilum* (Makhija & Patw.) Aptroot & Lücking comb. nov., *A. effusum* (Aptroot & Sipman) Aptroot & Lücking comb. nov., *A. endochryseum* (Vain.) Aptroot & Lücking comb. nov., *A. exostemmatidis* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. fei* (C. F. W. Meissn.) Aptroot & Lücking comb. nov., *A. ferrugineum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. galligenum* (Aptroot) Aptroot & Lücking comb. nov., *A. gigantoporum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. indicum* (Upreti & Ajay Singh) Aptroot & Lücking comb. nov., *A. infossum* (Nyl.) Aptroot & Lücking comb. nov., *A. infuscatulum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. irregulare* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. keralense* (Upreti & Ajay Singh) Aptroot & Lücking comb. nov., *A. kunzei* (Fée) Aptroot & Lücking comb. nov., *A. leioplacum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. lugescens* (Nyl.) Aptroot & Lücking comb. nov., *A. luridum* (Zahlbr.) Aptroot & Lücking comb. nov., *A. macrocarpum* (Fée) Aptroot & Lücking comb. nov., *A. macrosporum* (Makhija & Patw.) Aptroot & Lücking comb. nov., *A. marcidum* (Fée) Aptroot & Lücking comb. nov., *A. megaleium* (Kremp.) Aptroot & Lücking comb. nov., *A. megalophthalmum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. megalostomum* (Vain.) Aptroot & Lücking comb. nov., *A. megaspermum* (Mont.) Aptroot & Lücking comb. nov., *A. meiophorum* (Nyl.) Aptroot & Lücking comb. nov., *A. meristosporoides* (P. M. McCarthy & Vongsheew.) Aptroot & Lücking comb. nov., *A. meristosporum* (Mont. & Bosch) Aptroot & Lücking comb. nov., *A. neogalbineum* (R. C. Harris) Aptroot & Lücking comb. nov., *A. nigratum* (Müll. Arg.) Aptroot & Lücking comb. et stat. nov., *A. nigrorufum* (Makhija & Patw.) Aptroot & Lücking comb. nov., *A. nitidiusculum* (Nyl.) Aptroot & Lücking comb. nov., *A. octosporum* (Vain.) Aptroot & Lücking comb. nov., *A. oligocarpum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. olivaceofuscum* (Zenker) Aptroot & Lücking comb. nov., *A. papillosum* (P. M. McCarthy) Aptroot & Lücking comb. nov., *A. papulosum* (Nyl.) Aptroot & Lücking comb. nov., *A. peranceps* (Kremp.) Aptroot & Lücking comb. nov., *A. phaeoethelium* (Nyl.) Aptroot & Lücking comb. nov., *A. phlyctaena* (Fée) Aptroot & Lücking comb. nov., *A. porosum* (Ach.) Aptroot & Lücking comb. nov., *A. praetervisum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. pseudoplatystomum* (Makhija & Patw.) Aptroot & Lücking comb. nov., *A. pseudovariatum* (Upreti & Ajay Singh) Aptroot & Lücking comb. nov., *A. puiggarii* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. pulcherrimum* (Fée) Aptroot & Lücking comb. nov., *A. pupula* (Ach.) Aptroot & Lücking comb. nov., *A. purpurascens* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. pustulatum* (Vain.) Aptroot & Lücking comb. nov., *A. rufescens* (Müll. Arg.) Aptroot & Lücking comb. et stat. nov., *A. sanguinarium* (Malme) Aptroot & Lücking comb. nov., *A. santessonii* (Letr.-Gal.) Aptroot & Lücking comb. nov., *A. saxicola* (Malme) Aptroot & Lücking comb. nov., *A. scoria* (Fée) Aptroot & Lücking comb. nov., *A. scorizum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. sierraleonense* (C. W. Dodge) Aptroot & Lücking comb. nov., *A. sikkimense* (Makhija & Patw.) Aptroot & Lücking comb. nov., *A. spectabile* (Aptroot & Ferraro) Aptroot & Lücking comb. nov., *A. sphaerioides* (Mont.) Aptroot & Lücking comb. nov., *A. stramineum* (Malme) Aptroot & Lücking comb. nov., *A. straminicolor* (Nyl.) Aptroot & Lücking comb. nov., *A. subcatervarium* (Malme) Aptroot & Lücking comb. nov., *A. subdiscretum* (Nyl.) Aptroot & Lücking comb. nov., *A. subdisjunctum* (Müll. Arg.) Aptroot & Lücking comb. nov., *A. subdissocians* (Nyl. ex Vain.) Aptroot & Lücking comb. et stat. nov., *A. superbium* (Fr.) Aptroot & Lücking comb. nov., *A. tenue* (Aptroot) Aptroot & Lücking comb. nov., *A. thelotremoides* (Nyl.) Aptroot & Lücking comb. nov., *A. tryptelhelizans* (Nyl.) Aptroot & Lücking comb. nov., *A. tuberculosum* (Vain.) Aptroot & Lücking comb. nov., *A. ubianense* (Vain.) Aptroot & Lücking comb. nov., *A. variatum* (Nyl.) Aptroot & Lücking comb. nov., *A. vezdae* (Makhija & Patw.) Aptroot & Lücking comb. nov., *B. bathelium austroafricanum* (Zahlbr.) Aptroot & Lücking comb. nov., *B. nigroporum* (Makhija & Patw.) Aptroot & Lücking comb. nov., *Bogoriella alata* (Groenh. ex Aptroot) Aptroot & Lücking comb. nov., *B. annonacea* (Müll. Arg.) Aptroot & Lücking comb. nov., *B. apposita* (Nyl.) Aptroot & Lücking comb. nov., *B. captiosa* (Kremp.) Aptroot & Lücking comb. nov., *B. collopsora* (Vain.) Aptroot & Lücking comb. nov., *B. confluens* (Müll. Arg.) Aptroot & Lücking comb. nov., *B. conothelena* (Nyl.) Aptroot & Lücking comb. nov., *B. decipiens* (Müll. Arg.) Aptroot & Lücking comb. nov., *B. exigua* (Müll. Arg.) Aptroot & Lücking comb. nov., *B. fumosula* (Zahlbr.) Aptroot & Lücking comb. nov., *B. hemisphaerica* (Müll. Arg.) Aptroot & Lücking comb. nov., *B. lateralis* (Sipman) Aptroot & Lücking comb. nov., *B. leuckertii* (D. Hawksw. & J. C. David) Aptroot & Lücking comb. nov., *B. macrocarpa* (Komposch, Aptroot & Hafellner) Aptroot & Lücking comb. nov., *B. megaspora* (Aptroot & M. Cáceres) Aptroot & Lücking comb. nov., *B. miculiformis* (Nyl. ex Müll. Arg.) Aptroot & Lücking comb. nov., *B. minutula* (Zahlbr.) Aptroot & Lücking comb. nov., *B. modesta* (Müll. Arg.) Aptroot & Lücking comb. nov., *B. nonensis* (Stirt.) Aptroot & Lücking comb. nov., *B. obovata* (Stirt.) Aptroot & Lücking comb. nov., *B. pachytheca* (Sacc. & Syd.) Aptroot & Lücking comb. nov., *B. punctata* (Aptroot) Aptroot & Lücking comb. nov.,

*B. queenslandica* (Müll. Arg.) Aptroot & Lücking comb. nov., *B. socialis* (Zahlbr.) Aptroot & Lücking comb. nov., *B. striguloides* (Sérus. & Aptroot) Aptroot & Lücking comb. nov., *B. subfallens* (Müll. Arg.) Aptroot & Lücking comb. nov., *B. thelena* (Ach.) Aptroot & Lücking comb. nov., *B. triangularis* (Aptroot) Aptroot & Lücking comb. nov., *B. xanthonica* (Komposch, Aptroot & Hafellner) Aptroot & Lücking comb. nov., *Constrictolumina esenbeckiana* (Fée) Lücking, M. P. Nelsen & Aptroot comb. nov., *C. leucostoma* (Müll. Arg.) Lücking, M. P. Nelsen & Aptroot comb. nov., *C. lyrata* (R. C. Harris) Lücking, M. P. Nelsen & Aptroot comb. nov., *C. majuscula* (Nyl.) Lücking, M. P. Nelsen & Aptroot comb. nov., *C. malacciuula* (Nyl.) Lücking, M. P. Nelsen & Aptroot comb. nov., *C. porospora* (Vain.) Lücking, M. P. Nelsen & Aptroot comb. nov., *Dictyomeridium amylosporium* (Vain.) Aptroot, M. P. Nelsen & Lücking comb. nov., *D. campylothelioides* (Aptroot & Sipman) Aptroot, M. P. Nelsen & Lücking comb. nov., *D. immersum* (Aptroot, A. A. Menezes & M. Cáceres) Aptroot, M. P. Nelsen & Lücking comb. nov., *D. isohypocrellinum* (Xavier-Leite, M. Cáceres & Aptroot) Aptroot, M. P. Nelsen & Lücking comb. nov., *D. parapropionens* (Aptroot, M. Cáceres & E. L. Lima) Aptroot, M. P. Nelsen & Lücking comb. nov., *Distothelia rubrostoma* (Aptroot) Aptroot & Lücking comb. nov., *Phyllobatheium chlorogastricum* (Müll. Arg.) Aptroot & Lücking comb. nov., *Pseudopyrenula cubana* (Müll. Arg.) Aptroot & Lücking comb. nov., *Viridothelium cinereoglaucescens* (Vain.) Lücking, M. P. Nelsen & Aptroot comb. nov., *V. indutum* (Stirt.) Aptroot & Lücking comb. nov., and *V. megaspermum* (Makhija & Patw.) Aptroot & Lücking comb. nov. In addition, six replacement names are proposed: *Astrothelium campylocartilagineum* Aptroot & Lücking nom. nov., *A. grossoides* Aptroot & Lücking nom. nov., *A. octosporoides* Aptroot & Lücking nom. nov., *A. scoriiothelium* Aptroot & Lücking nom. nov., *A. pyrenastrosulphureum* Aptroot & Lücking nom. nov., and *Batheium prinolucens* Aptroot & Lücking nom. et stat. nov. Along with this, 57 lectotypes are newly designated. Most species (392 out of 418) are illustrated, with a total of 697 images in 59 plates, including 406 type specimens. Where appropriate, taxa are briefly discussed. New country or continental records are listed for many species in their revised circumscription. A checklist of taxa described or placed in genera belonging in *Trypetheliaceae* but previously excluded from the family, and their current names, is also provided.

**Key words:** Brazil, Colombia, Ecuador, French Guiana, Guyana, Indonesia, lichen, Papua New Guinea, Puerto Rico, Solomon Islands, taxonomy, Venezuela

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## Introduction

The family *Trypetheliaceae* is an almost strictly tropical lineage of nearly exclusively corticolous (very rarely saxicolous), lichenized fungi (Fig. 1). The first members of this family were encountered towards the end of the 18th century on pieces of medicinal bark (mainly *Cinchona* for quinine) that had been collected in South American forests (Zenker 1827). The conspicuous, often brightly coloured ascomata with complex structures intrigued lichenologists of the time and both Acharius (1817*a, b*) and Fée (1831) wrote monographs of what was then known as the genus *Trypethelium*, treating 10 and 19 species, respectively. More species became known especially from Australia, Brazil and Borneo, which were described in separate papers, mostly by Eschweiler (1824, 1833), Krempelhuber (1875), Montagne (1851, 1856) and Müller (1884, 1885). During this time, a further synopsis of the family was made by Trevisan (1861).

After this initial burst of activity, which concluded with Malme's treatment of species gathered during the first Regnellian Expedition in Brazil (Malme 1924), relatively few species were added for a long time, and for many species only the type was known. In the meantime, the genus *Trypethelium* had been split into smaller entities and various classification systems had been proposed and applied, particularly by Müller (1884, 1885), Nylander (1863), Vainio (1890) and Zahlbruckner (1922, 1924, 1928). These studies doubled the number of names accepted in the *Trypetheliaceae* solely through reclassifications. Halfway through the 20th century, this led to the situation where almost as many names existed in the family as there had been specimens collected and illustrated by the only monograph published around that time, by Letrouit-Galinou (1957, 1958), on the genus *Laurera*. In part, the genera of *Trypetheliaceae* were also mixed with those of *Pyrenulaceae* since the overall ascoma morphology was considered more important than anatomical





FIG. 1. Mosaic of six *Astrothelium* species (and one *Phaeographis*) on a tropical rainforest tree at Los Amigos Biological Station in Amazonian Peru. Left, with orange pseudostromata, *A. kunzei*; centre, with white pseudostromata, *A. rufescens*; upper right, with green thallus, *A. cf. cecidiogenum*; right, mottled-green-yellow thallus, *A. subscoria*; lower right, small thallus, *A. nitidiusculum*; lower middle and left, *A. aeneum*.

features such as hamathecium structure and ascospore type (e.g. Dodge 1953). Both these character complexes clearly separate the two families, which are not even closely related; molecular phylogenetic studies placed *Pyrenulaceae* in Eurotiomycetes and *Trypetheliaceae* in Dothideomycetes (Del Prado *et al.* 2006; Nelsen *et al.* 2009; Schoch *et al.* 2009a, b).

Aside from two papers published by Johnson (1940, 1959) on North American *Trypetheliaceae* and an anatomical study of the endoperidermal thallus of *Trypethelium eluteriae* (Lambright & Tucker 1980), serious taxonomic and systematic treatments of the *Trypetheliaceae* were only taken up again by Harris with his studies on Amazonian species (Harris 1986) and a revision of *Polymeridium*

(Harris 1993). Previously, Eriksson (1981) had briefly treated the family in his conspectus of bitunicate Ascomycetes and elaborated a detailed evolutionary scheme for the supposedly closely related *Trypetheliaceae* and *Pyrenulaceae*. The work by Harris (1986, 1993) redefined the family in a restricted sense and adopted a generic division based on thallus type, ascoma disposition, and ascospore type that has been in use since then. However, Harris (1995) and other workers (Aptroot *et al.* 2008) also recognized that this system was at least in part artificial, resulting in cases such as in the *Astrothelium variolosum*-*Trypethelium nitidiusculum* complex where a single specimen could be partly assigned to one genus and partly to another (Harris 1995). Further systematic treatments



were provided by Aptroot (1991), introducing the new genus *Architrypethelium*, and Harris (1998), with a revision of the genus *Pseudopyrenula*. Harris's work in particular triggered further inventories and taxonomic studies of the family, particularly in India but also in the Neotropics and Australia, describing many new taxa (Upreti & Singh 1987; Makhija & Patwardhan 1988, 1992, 1993; McCarthy & Kantvilas 1993; McCarthy 1995; Aptroot & Ferraro 2000; Aptroot *et al.* 2008; Aptroot 2009*a, b*). At the time when Harris (1986) published his Amazonian studies, Hawksworth (1986) provided a revision of the genus *Mycromicrothelia*, a genus at the time not thought to be related to *Trypetheliaceae* but recently found to include many species falling in lineages at the base of the family (Nelsen *et al.* 2009, 2011, 2014; Lücking *et al.* 2016*a*) and now redispositioned in the genera *Bogoriella* and *Novomicrothelia* (Lücking *et al.* 2016*a*).

Notably, the *Trypetheliaceae* were the subject of several detailed studies about ascospore anatomy and ontogeny (Sweetwood *et al.* 2012) and pigment chemistry (Mathey & Hoder 1978; Mathey 1979; Mathey *et al.* 1980), as well as potential pharmaceutical properties of their chemical compounds (Manojlovic *et al.* 2010). Ecological and ecogeographical papers with details on *Trypetheliaceae* were published by Komposch & Hafellner (2000) on canopy and savanna species in Venezuela, Aptroot *et al.* (2008) on pyrenocarpous lichens in Costa Rica, Rivas Plata *et al.* (2008) on the correlation between family-level diversity and environmental parameters related to the conservation status of tropical forest ecosystems, and Aptroot (2009*b*) on diversity and endemism of *Trypetheliaceae* and *Pyrenulaceae* in Malaysia.

The systematics of the family regained interest with the advent of molecular phylogenetic methods. An initial study by Del Prado *et al.* (2006) demonstrated the placement of *Trypetheliaceae* within Dothideomycetes, and phylogeny of the family was refined through subsequent work by Nelsen *et al.* (2009, 2011, 2014) and Lücking *et al.* (2016*a*), showing that lichenized species of *Arthopyrenia* and *Mycromicrothelia* also belong

here, and laying the groundwork for a much revised genus and species concept (Aptroot *et al.* 2013*a*; Hyde *et al.* 2013; Aptroot & Cáceres 2014; Nelsen *et al.* 2014; Luangsuphabool *et al.* 2016; Lücking *et al.* 2016*a*). This also stimulated further inventory work in several parts of the tropics, with the discovery of many new taxa (Aptroot & Cáceres 2013, 2016; Aptroot *et al.* 2013*b*, 2016*a, b*; Lima *et al.* 2013; Córdova-Chávez *et al.* 2014; Weerakoon & Aptroot 2014; Flakus *et al.* 2016; Luangsuphabool *et al.* 2016; Lücking *et al.* 2016*b*). The order *Trypetheliales* was eventually established for the family (Aptroot *et al.* 2008; Hyde *et al.* 2013), and recently a second family, *Polycoccaceae*, including lichenicolous fungi, was included in this order (Ertz *et al.* 2015).

In the present work, we provide a concise synopsis of the family *Trypetheliaceae* to account for the numerous changes that have taken place based on recent phylogenetic studies and a new assessment of the delineation of genera and species within the family. Together with the other papers included within this special issue, this should give a complete overview of the current knowledge of the family. We realize that this synopsis cannot be a definitive monographic treatment; the gaps in knowledge about this megadiverse group of tropical lichens are too large and still many taxa are known only from few or single collections. While available sequence data and revision of phenotypic characters suggest that the concept presented here reflects genus and species boundaries more accurately than previous treatments, we expect that this synopsis will also trigger many further studies. These, we anticipate, would be based on a much more thorough sampling of individual geographical regions, which will unearth novel taxa and also require further revision of *Trypetheliaceae* species. Furthermore, additional types of old names to be assigned to this family will undoubtedly surface.

## Material and Methods

Identification and descriptive work was carried out in Soest, using an OLYMPUS SZX7 stereomicroscope and

an OLYMPUS BX50 compound microscope with interference contrast, connected to a NIKON Coolpix digital camera, as well as at the Field Museum in Chicago, using a LEICA MS5 dissecting microscope and a ZEISS Axioskop 2 compound microscope, in part connected to JENOPTIK ProgRes C3 and C5 digital microscope cameras. Further digital images were taken with CANON Powershot SX20IS, NIKON F301 and Sony Alpha 33 DSLR digital cameras.

Sections of thalli and ascomata were cut by hand with a razor blade and examined with squash preparations on material mounted in water, KOH and Lugol's solution. All measurements are given for water mounts. Illustrated thin sections were made by Dr Felix Schumm using a Wild M3 stereomicroscope, an Olympus BX51 compound microscope with interference contrast, a Canon EOS 40D camera with MP-E 65 mm and a Mic HM 560 cryotome. Specimens were measured and illustrated in tap water, unless marked with IKI (mounted in iodine) or LCB (mounted in lactophenol cotton blue).

Chemistry was analyzed by means of a UV lamp and K-tests using 10% KOH solution, both on thallus and ascoma portions including medulla and on sections. Many specimens, including most types (where not previously analyzed), were also investigated using thin-layer chromatography (TLC) in solvents A and/or C (Orange *et al.* 2010).

Well over 2000 specimens were examined for this study, including most types. Where possible, types were studied through loans or visits to the corresponding major herbaria; in some cases we relied on digitized type specimens available through the Global Plants Initiative (GPI) at JSTOR (<https://plants.jstor.org>). To complete our own 352 images of type specimens accumulated through studies over the past decades, we added 54 partial images of selected type specimens posted on JSTOR to the plates published here to highlight specific morphological features required for taxon identification, reproduced with permission from the curators at BM (Figs 31E, 34H, 41L, 44F, 49F, 51I, 52K), G (Figs 13F, 15B, 16J & K, 18C & K, 19G, 23C & E, 26G, 28J, 29B & F, 32H, 33B, 35B & I, 37A, G & H, 39G, 44K & L, 52F, 53I, 54F & G, 57G), H (Figs 13D & I, 15H, 18G, 20E, 21A, 27F, 35H, 38I, 43A, B & J, 44B, 48A, 49G), and S (Figs 31D, 39I, 42H, 54A). Quite a number of additional type species not shown here are available through GPI at JSTOR and can be consulted there in case of doubts. Except for types, specimens studied are not cited in full; instead, we summarize the known distribution and give selected new country records. Distributions are given in geographical order following the *Flora Neotropica* style, from NW to SE, starting with North America and ending with Australia and Oceania.

The numerous collections made by Charles Wright in the 19th century in Cuba, which have been studied (and distributed in exsiccatae) by Tuckerman (1864), Nylander (1876), and Müller (1885, 1894) was an important reference. The citation of these exsiccatae or the corresponding collections has been somewhat ambiguous in the literature, usually giving Wright as editor or with the exsiccate number as his collection number. However, Wright did not perform identification work on his lichen

collections; instead they were organized and edited by Tuckerman (as *Caroli Wright Lichenes Insulae Cubae* or *Lich. Ins. Cub.*) and Müller (as *Graphideae Cubenses* (a cl. *C. Wright lectae et a cl. W. Nylander determinatae*) or *Graph. Cub.*, as *Lichenes Cubenses* (a cl. *Wright lecti et a cl. W. Nylander pr. p. determinati*) or *Lich. Cub.*, and as *Verrucariae Cubenses* or *Verr. Cub.*) (<http://indexs.botanischestaatssammlung.de>) using a numbering system separate from Wright's collection numbers. Wright's original collection numbers are usually not available for his Cuban lichen collections (if he numbered them at all) and they will be cited as *Wright s. n.*

For the general section, a selection of morphological and anatomical images was provided by Felix Schumm and for the taxonomic section we also included images of five new species of *Astrothelium* described elsewhere in this issue (Luangsuphabool *et al.* 2016), provided by Ek Sangvichien.

### Morphology, Anatomy and Chemistry

Morphological, anatomical and chemical characters in *Trypetheliaceae* are variable and, as in other species-rich families of tropical lichens such as *Graphidaceae* and *Pyrenulaceae*, provide a broad array of features for taxonomic and systematic purposes, which in the past have not been fully explored due to the lack of a phylogenetic framework to assess the validity of individual characters, in particular the external morphology of thallus and ascomata. This framework is now available (Nelsen *et al.* 2014; Lücking *et al.* 2016a); it shows that morphological variation changes with evolutionary history within the family. The typical and often unique characters of *Trypetheliaceae*, particularly the astrothelioid ascospores and the thin, net-like hamathecium, often with coarse inspersion, are mostly developed in derived lineages, whereas the more basal lineages are not particularly different from similar, lichenized forms in other, often unrelated orders, such as *Monoblastiales*, *Strigulales* and even certain *Pyrenulales*.

### Thallus morphology

Various characters can be assessed with regard to thallus morphology, including whether the thallus is (partially) endoperidermal, the presence of a cortex, the development of surface structures, colour and the associated pigment chemistry (see also below).



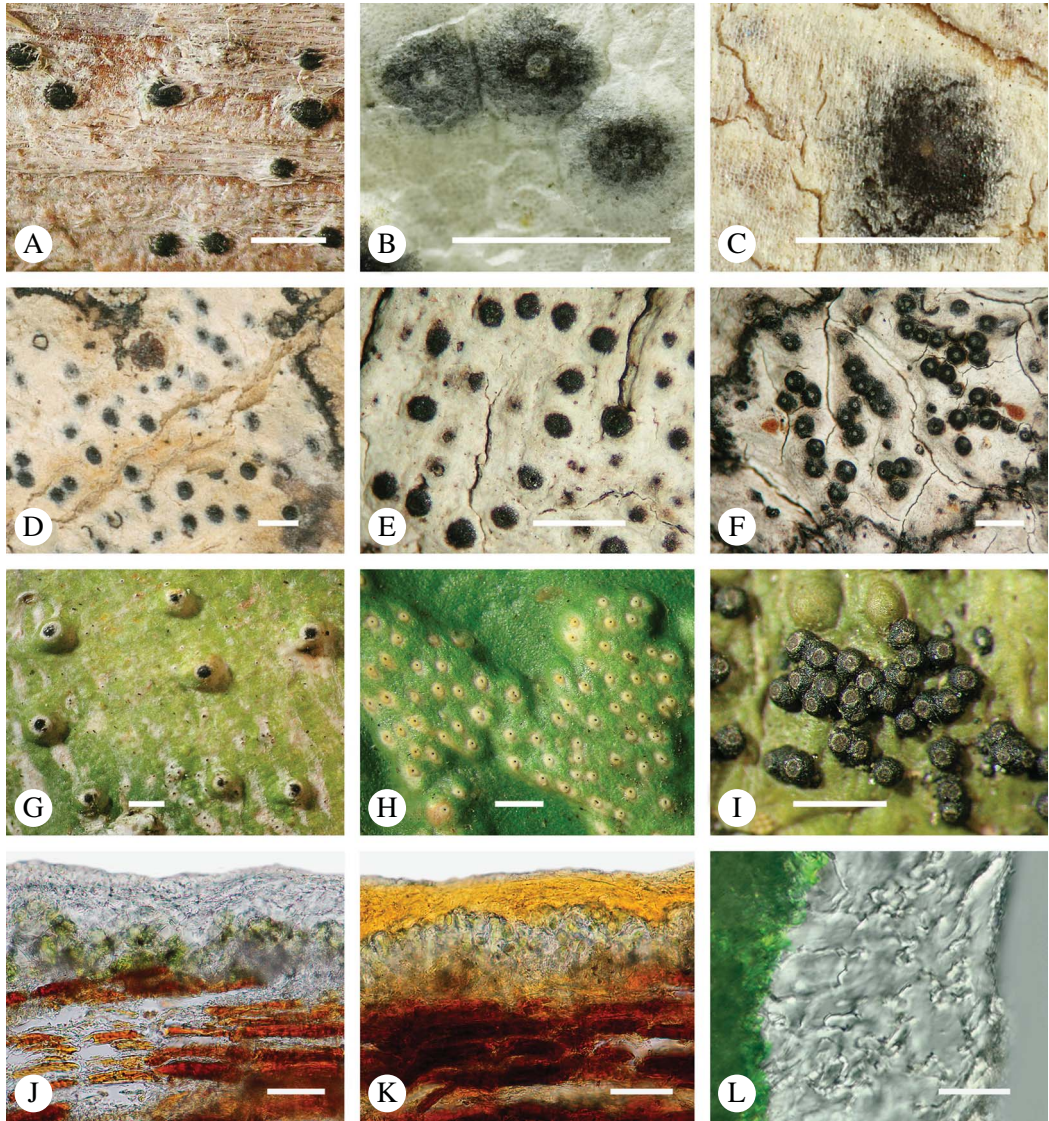


FIG. 2. Thallus morphology and anatomy in *Trypetheliaceae*. A–C, endoperidermal thallus with outline of periderm cells visible; A, *Bogoriella modesta*; B, *Constrictolumina majuscula*; C, *Bogoriella megaspora*. D–F, ecorticate, whitish thallus with black prothallus line; D, *B. miculiformis*; E, *Polymeridium catapastum*; F, *P. subcinereum*. G–I, corticate, (olive-)green thallus; G, *Astrothelium megaspermum*; H, *A. intermedium*; I, *Nigrovothelium tropicum*. J–L, anatomy of epiperidermal thallus showing gelatinized cortex, photobiont layer, and periderm; J & K, *Astrothelium tuberculosum*; L, *Architrypethelium grande*. Scales: A–I = 1 mm; J–L = 20  $\mu$ m. (Images B, C, J & K by F. Schumm).

Basal lineages in the family, such as former species of *Arthopyrenia* and *Mycomicrothelia* now dispositioned in the genera *Bogoriella*, *Constrictolumina*, and *Novomicrothelia*, as well as the genera *Dictyomeridium*, *Distothelia*,

*Polymeridium*, and *Pseudopyrenula*, almost invariably have an ecorticate, whitish thallus that is often endoperidermal (Fig. 2A–F), with scattered photobiont cells; further structures except for a black prothallus line (Fig. 2F) are



usually absent and the ascomata are usually exposed and black (Fig. 2A–F). Except for *Pseudopyremula*, this correlates with the presence of non-astrothelioid ascospores with thin or uniformly thickened septa and rectangular to rounded, but not diamond-shaped, lumina (see below).

In more derived lineages, the thallus is almost invariably corticate and mostly has an olive-green colour when fresh (Fig. 2G–I). The cortex is epiperidermal and often massive, consisting of a loose network of anastomosing hyphae (similar to the hamathecium, but more irregular; see below) embedded in a gelatinous matrix and becoming more dense and orange-yellow in K; the photobiont layer and medulla (if developed) are either epiperidermal or partly endoperidermal (Fig. 2J–L).

While most species have a smooth to uneven thallus (Fig. 3A–C), a particular feature in *Trypetheliaceae* rarely found in other families such as *Graphidaceae*, is the formation of a verrucose-papillose to bullate or folded thallus surface (Fig. 3D–I). In section, these structures either include amorphous white crystal masses or mainly consist of a strongly thickened cortex, with anastomosing hyphae embedded in a gelatinous matrix (Fig. 3J & K). In these cases, in which the thallus might even appear squamulose (Fig. 3I), the photobiont layer is often vertically arranged (Fig. 3J & K), suggesting adaptation to high light intensities, for example in the rainforest canopy where such *Trypetheliaceae* primarily occur. The available phylogenetic data suggest that such thallus structures are species-specific, although habitat-induced variation has been shown in other groups, such as *Graphis pseudocinerea* in *Graphidaceae* (Lücking *et al.* 2011).

Independent of the surface structure, many *Trypetheliaceae* seem to produce thickened bark, which suggests gall formation. This is particularly seen in relation to the ascomata, which often emerge from beneath the upper periderm layers of the bark (see below). However, galls in the strict sense should produce abnormal growth of the periderm, in particular the inner, living layers, viz. the cork cambium (phellogen),

which due to its meristematic nature is predestined to produce abnormal growth reactions. In most *Trypetheliaceae*, the endoperidermal thallus portion is developed only in the upper, dead layers of the periderm (Fig. 3J & K), the cork (phellem), and rather than causing growth of the periderm, the thickening appears to be caused by uplifting of the upper layers, particularly above the ascomata (see below). However, some cases have been observed with true gall formation due to growth of the cork (Fig. 3L). Further studies, particularly on the ontogeny of the thallus and ascomata, are needed to properly understand this phenomenon and its biological implications.

### Ascoma morphology

The ascomata in *Trypetheliaceae* provide some of the richest character sets for taxonomic purposes but at the same time have provided stumbling blocks to properly recognizing and classifying the variation encountered in this family. Several characters can be assessed when analyzing ascoma morphology: 1) arrangement of the ascomata relative to the thallus, 2) orientation of the ostioles, 3) ascoma emergence, 4) degree of thallus cover, 5) configuration of the ostiolar area, and 6) pigmentation (see also below).

Ascomata arrangement can vary from regularly dispersed over the thallus (solitary), to confluent, aggregate, and pseudostromatic (Fig. 4A–L), with the ostioles apical, eccentric (lateral) or fused, in which case the shared portion of the ostiole might be apical or lateral (Fig. 5A–L). Ascoma arrangement can best be assessed when comparing distances between individual ascomata. In dispersed ascomata (Fig. 4A–C), random measurement of paired distances will result in a broad, continuous distribution of distance measures. In contrast, aggregate or pseudostromatic ascomata (Fig. 4E–L) will give a bimodal distribution of randomly measured distances, reflecting small distances between ascomata belonging to the same cluster versus large distances between ascomata belonging to different clusters. In specimens with partially confluent ascomata (Fig. 4D), the distribution

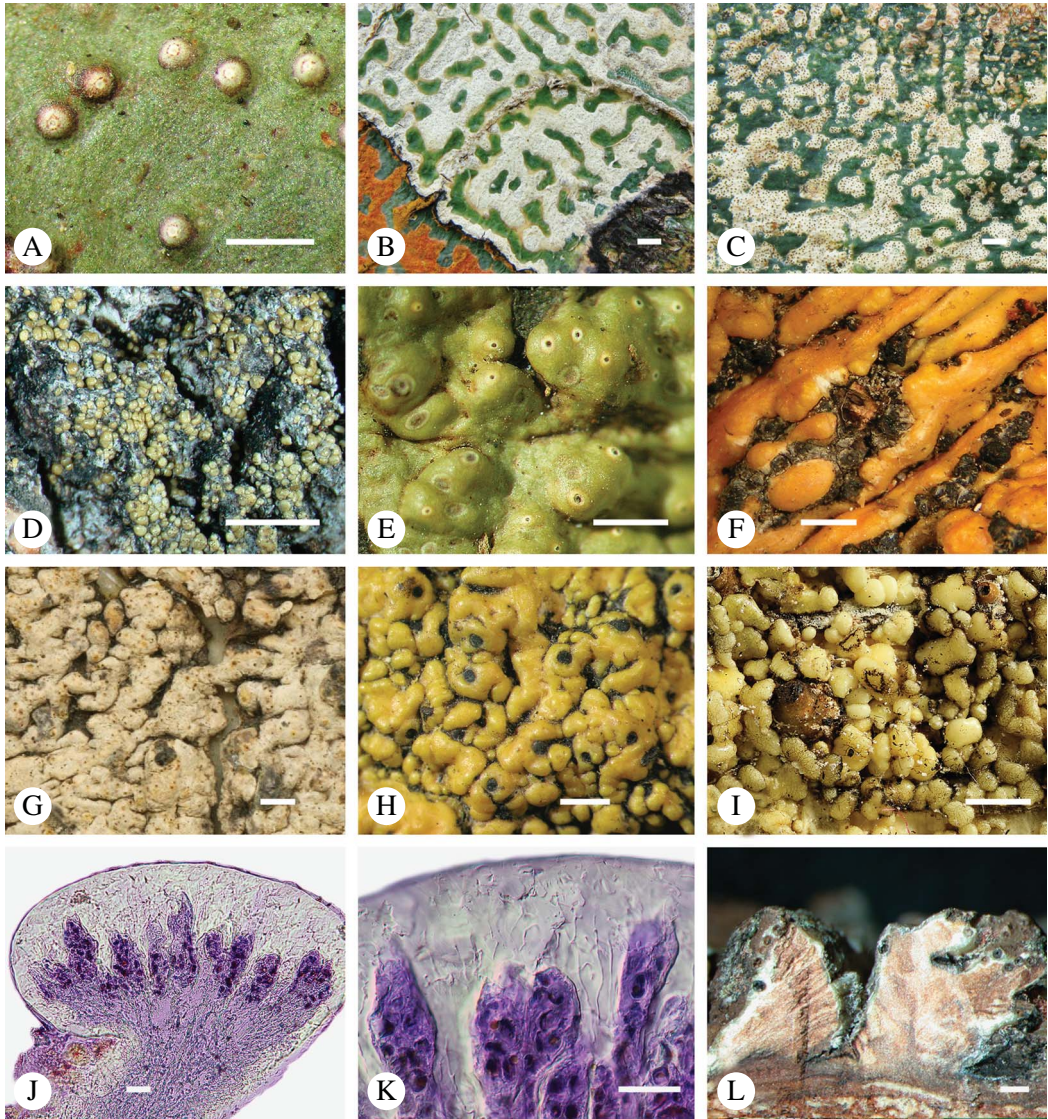


FIG. 3. Thallus surface morphology in *Trypetheliaceae*. A–C, surface smooth to uneven, following the contours of the bark; A, *Astrothelium nitidiusculum*; B & C, *A. rufescens*. D, surface papillose-verrucose, *A. papillosum*. E, surface bullate, *A. tuberculosum*. F & G, surface bullate-folded; F, *A. megalophthalmum*; G, *A. versicolor*. H & I, surface verrucose-bullate-squamulose; H, *Aptrootia elatior*; I, *Astrothelium puiggarii*. J & K, section through bullate 'squamules' showing gelatinized cortex and vertically arranged photobiont layer, *A. puiggarii*. L, true gall formation, *A. ceratinum*. Scales: A–I & L = 1 mm; J & K = 20  $\mu$ m. (Images J & K by F. Schumm).

will be intermediate between the two extremes. To distinguish between aggregate and pseudostromatic clusters, pseudostromata are defined here as areas that differ from the surrounding thallus in either structure (e.g.

being strongly emergent; Fig. 4E), colour (often whitish or dominated by black excipular tissue; Fig. 4F–K), or chemistry (e.g. pigment or lichexanthone limited to the pseudostromata; Fig. 4L), or a combination of these.



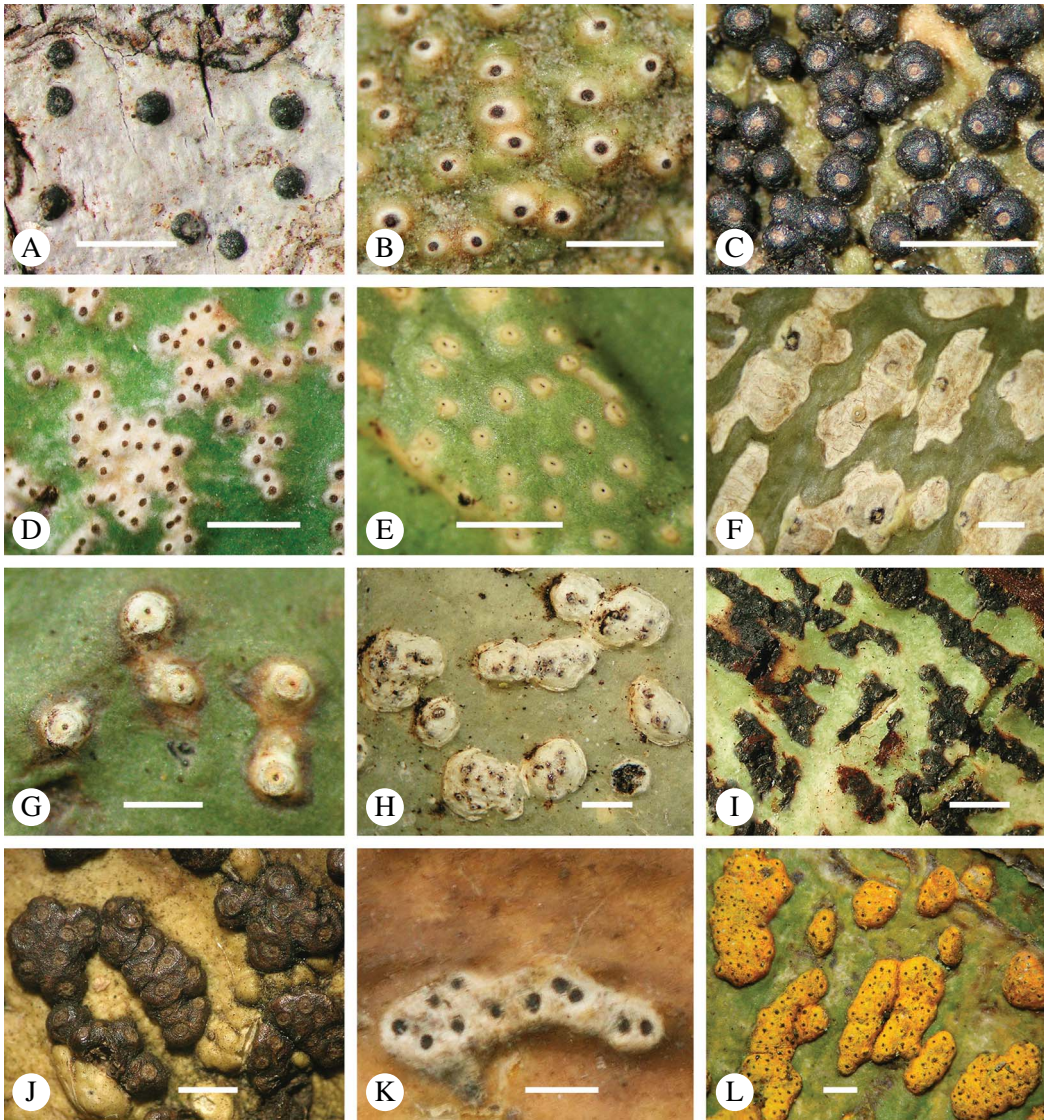


FIG. 4. Ascoma arrangement in *Trypetheliaceae*. A, solitary, dispersed, *Pseudopyrenula subnudata*; B, solitary, dense, *Astrothelium floridanum*; C, solitary, crowded, *Nigrovothelium tropicum*; D, solitary to confluent, *Astrothelium nitidiusculum*; E, pseudostromatic by emergence, *A. intermedium*; F, pseudostromatic by colour contrast, *A. norisianum*; G, with fused ostioles, fused ascomata dispersed, *A. eustomum*; H, with fused ostioles, fused ascomata pseudostromatic, *A. interjectum*; I, pseudostromatic with exposed ascomata and linear-reticulate pseudostromata, *A. neogalbineum*; J, pseudostromatic with exposed, prominent sessile ascomata, *Bathelium mastoideum*; K, pseudostromatic with erumpent to prominent pseudostromata with white cover, *Astrothelium sphaerioides*; L, pseudostromatic with prominent to sessile pseudostromata covered by pigment, *Trypethelium eluteriae*. Scales = 1 mm.

Thus, aggregate ascomata in which the associated thallus is similar to the surrounding thallus and which lack specific features are not

considered pseudostromatic. This applies in particular to fused ascomata with a shared ostiole in many species of *Astrothelium*, in



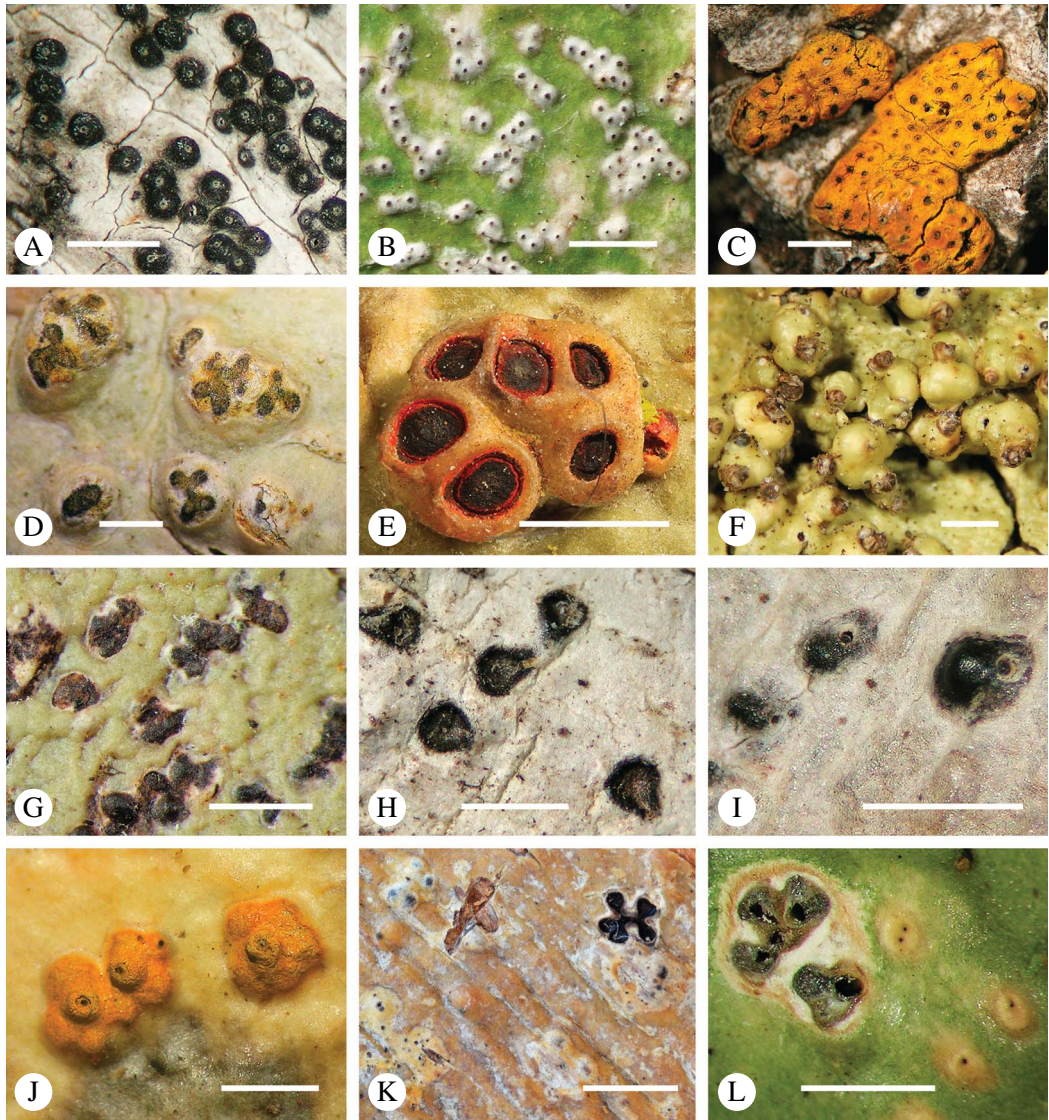


FIG. 5. Ascoma disposition and orientation of ostioles in *Trypetheliaceae*. A–C, ostioles apical, separate, A, *Polymeridium subcinereum*; B, *Astrothelium nitidiusculum*; C, *Trypethelium subeluteriae*. D, ostioles apical, with ostiolar areas forming lobate pattern, *T. astroideum*. E, ostioles apical, ostiolar area separated from covering thallus by a split, *Marcelaria purpurina*. F–I, ostioles lateral, eccentric, separate, pointing in various directions, F, *Astrothelium gigasporum*; G, *A. scorizum*; H, *Polymeridium simulans*; I, *Dictyomeridium proponens*. J–L, ostioles lateral, eccentric, centrally fused to form a shared channel leading to various chambers, J, *Astrothelium macrocarpum*; K, *A. marcidum*; L, *A. intermedium*. Scales = 1 mm.

which the thallus associated with the ascomata is not particularly differentiated.

For ascoma emergence, we apply here the same criteria and terminology as used in *Graphidaceae* and the genus *Graphis*

(Lücking 2009), since this feature has often been imprecisely treated in the literature and the term emergent has been used for morphologies ranging from slightly emergent to sessile. Here we define four states: 1) immersed,



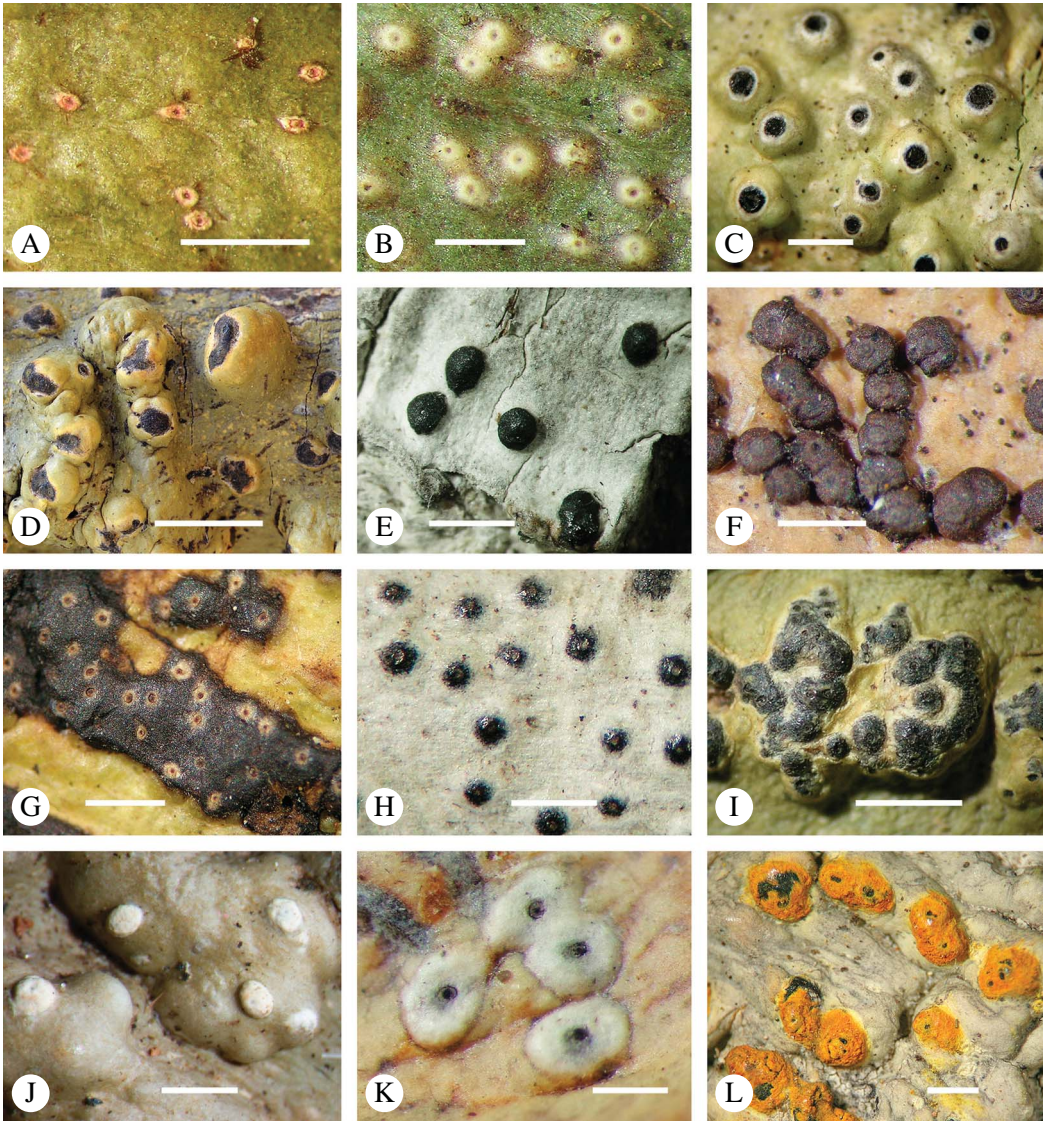


FIG. 6. Ascoma emergence and thallus cover in *Trypetheliaceae*. A, immersed, *Astrothelium calosporum*. B, erumpent, *A. nitidiusculum*. C, prominent, *A. megaspermum*. D, sessile, *A. fallax*. E–G, fully exposed, without thallus cover; E, *Pseudopyrenula dubia*; F, *Bathelium porinosporum*; G, *Astrothelium infuscatulum*. H, with basal thalline cover, *Polymeridium amyloideum*. I, with lateral thalline cover, *Astrothelium straminicolor*. J, with complete thalline cover, *A. megeustumum*. K, whitish and exposed ostiolar area, *A. fijiense*. L, with pigment cover, *A. macrocarpum*. Scales = 1 mm.

if more than 3/4 of the ascoma is beneath the thallus level (Fig. 6A); 2) erumpent, if more than 1/4 to 1/2 of the ascoma is above thallus level (Fig. 6B); 3) prominent, if more than 1/2 of the ascoma is above thallus

level and the base is expanded outwards to vertical (Fig. 6C); 4) sessile, if more than 3/4 of the ascoma is above thallus level and the base is constricted (Fig. 6D). This terminology also applies to pseudostromata

as a whole. A special feature of some *Trypetheliaceae* is that the ascomata can be deeply immersed, well below the thallus and often deep into the periderm, up to 2 mm and occasionally up to 5 mm below the thallus surface. This is not restricted to a certain taxonomic group but occurs, for example, in *Astrothelium* (Fig. 6A), *Polymeridium*, and *Pseudopyrenula*. Ascomata that are deeply immersed in the periderm are rare in lichens, otherwise mostly known from *Pyrenulaceae*.

With regard to the degree of thallus cover, the following states are distinguished, also based on classifications developed for *Graphidaceae* and *Graphis* (Lücking 2009): 1) absent, ascomata are fully exposed from the base (Fig. 6E–G); 2) basal, only the base up to *c.* 1/4 of the ascoma is covered (Fig. 6H); 3) partial, the ascomata are covered with thallus up to about 3/4 except the area surrounding the ostiole (Fig. 6I); 4) complete, only the ostiole or ostiolar spot remains visible (Fig. 6J). This scheme also applies to pseudostromata or thallus warts with aggregated ascomata (Fig. 6K & L). The configuration of the ostiolar area is also an important taxonomic character, including its visibility as a narrow dot (Fig. 6B) or broad spot (Fig. 6C & D), its colour (mostly black, sometimes white; Fig. 6J), and the presence of a differently coloured, ring-shaped band around the ostiole (usually whitish), which can be sharp and regular (Fig. 6C) or diffuse and often irregular (Fig. 6B & G). In some cases, the entire ascoma is covered with a layer different from the thallus, which is often the case in pseudostromata but can also be found in species with solitary ascomata (Fig. 6K).

### Ascoma anatomy

The internal anatomy of the ascomata including the pseudostromata has not been well studied, even though it has the potential to provide useful taxonomic and systematic characters. For instance, Makhija & Patwardhan (1993) made a typology of pseudostroma configurations found in *Trypethelium*, but more data are needed to fully assess the importance of their categories. Letrouit-Galinou (1957, 1958) also classified the ascomata of the artificial

genus *Laurera* according to wall structures which have subsequently been used, in part, to disperse the species studied over various lineages, including *Marcelaria*, *Bathelium*, and *Astrothelium*. Notably, the species belonging to *Marcelaria* were placed in different categories by Letrouit-Galinou (1957, 1958), although the main difference is the nature of the pigments present on and in the pseudostromata (Schumm & Aptroot 2012; Aptroot *et al.* 2013a).

The ascomata in *Trypetheliaceae* develop either superficially above the periderm or emerge from beneath the periderm and while this appears to be species-specific, both epiperidermal and endoperidermal ascomata can be found in different species of the same genus. For example, *Architrypethelium grande*, *Astrothelium megaspermum*, *A. porosum*, *A. puiggarii*, *Marcelaria purpurina*, *Nigrovothelium tropicum* and *Trypethelium eluteriae* all produce epiperidermal ascomata or pseudostromata, with the periderm remaining below the ascomata and not included in the covering layers (Fig. 7A–F, J–L). In contrast, in *Astrothelium tuberculosum*, *Constrictolumina majuscula* and *Pseudopyrenula diluta* the ascomata are endoperidermal (Fig. 7G–I). The ascoma wall is (1–)2–3-layered with a brown to carbonized excipulum (Fig. 7B–K), often with a cortical layer similar to the thallus cortex, which might be thin (Fig. 7B) to thick (Fig. 7E & F, K & L) and in the case of pseudostromata with an amorphous medullary layer (Fig. 7C); in species such as *Astrothelium megaspermum*, the upper wall also contains a brownish ‘medullary’ layer which might be homologous to the involucrellum in other pyrenocarpous taxa.

Ascoma anatomy provides a very rich set of characters but we have not yet fully explored these features here as we await more detailed studies. We expect that ascoma and pseudostroma wall anatomy, explored within a phylogenetic framework, will help to further refine genus and species concepts in *Trypetheliaceae*.

### Hamathecium, asci and ascospores

Most *Trypetheliaceae* have a rather uniform hamathecium, consisting of thin, straight,



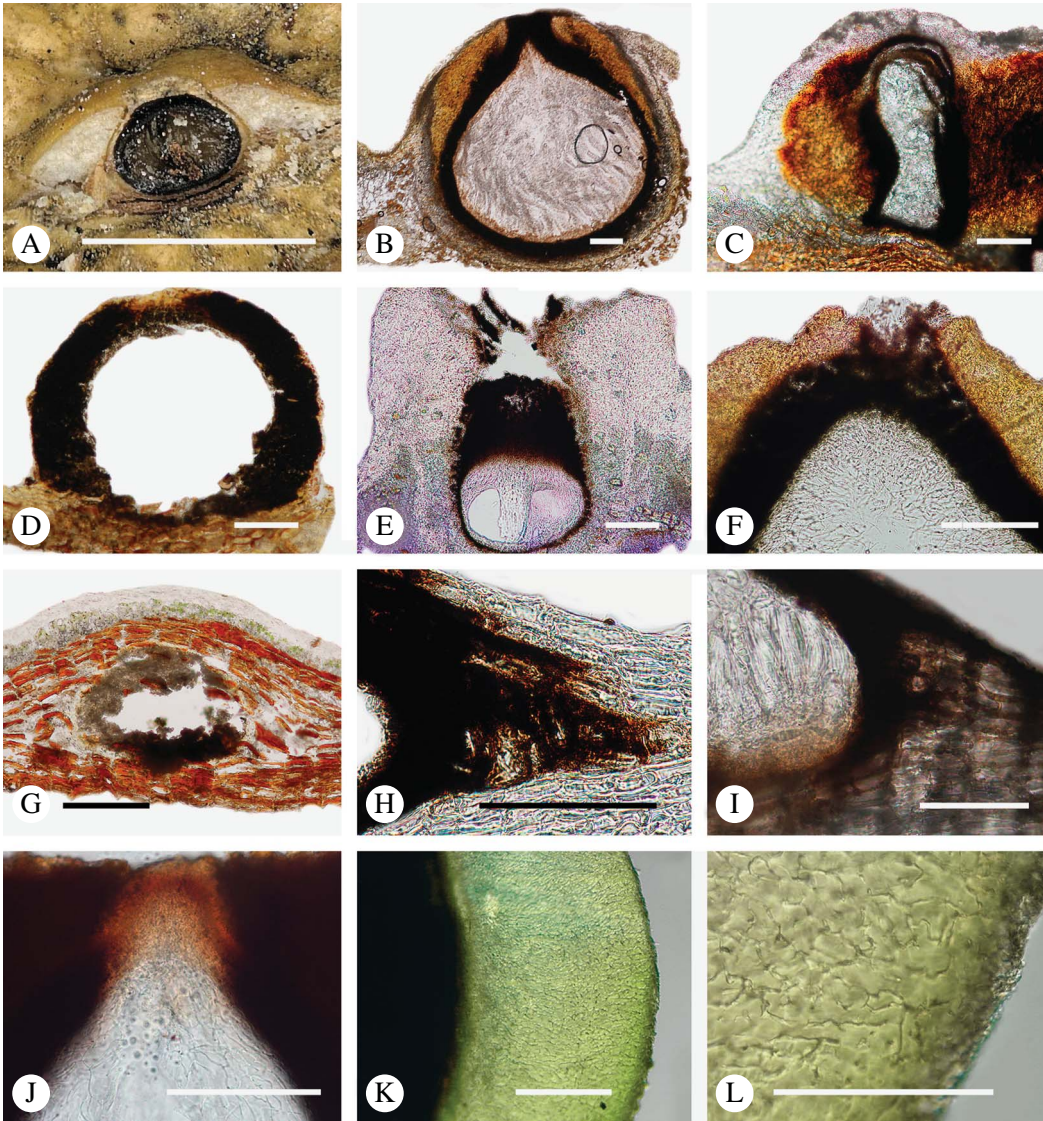


FIG. 7. Ascoma anatomy in *Trypetheliaceae*. A–C, epidermal ascomata with thallus cover; A & B, *Astrothelium megaspermum*; C, *A. porosum*. D, epidermal ascoma with simple wall, *Nigrovothelium tropicum*. E–F, epidermal ascoma with thick cortical layer, E, *Marcelaria purpurina*; F, *Astrothelium puiggarii*. G–I, endoperidermal ascomata, G, *A. tuberosum*; H, *Pseudopyrenula diluta*; I, *Constrictolumina majuscula*. J, ostiolar area, *Trypethelium eluteriae*. K–L, gelatinized cortical layer on ascoma, *Architypethelium grande*. Scales: A = 1 mm; B–K = 100  $\mu$ m; L = 50  $\mu$ m. (Images A–I by F. Schumm).

much branched and anastomosing paraphyses forming a network embedded in a gelatinous matrix (Fig. 8A). In basal lineages, the paraphyses are usually thicker and less anastomosing and the gelatinous matrix is

less obvious. Hymenial inspersion is common throughout the family and usually occurs as large, irregular, colourless oil droplets lining the paraphyses (Fig. 8B) but it can also form a more amorphous,

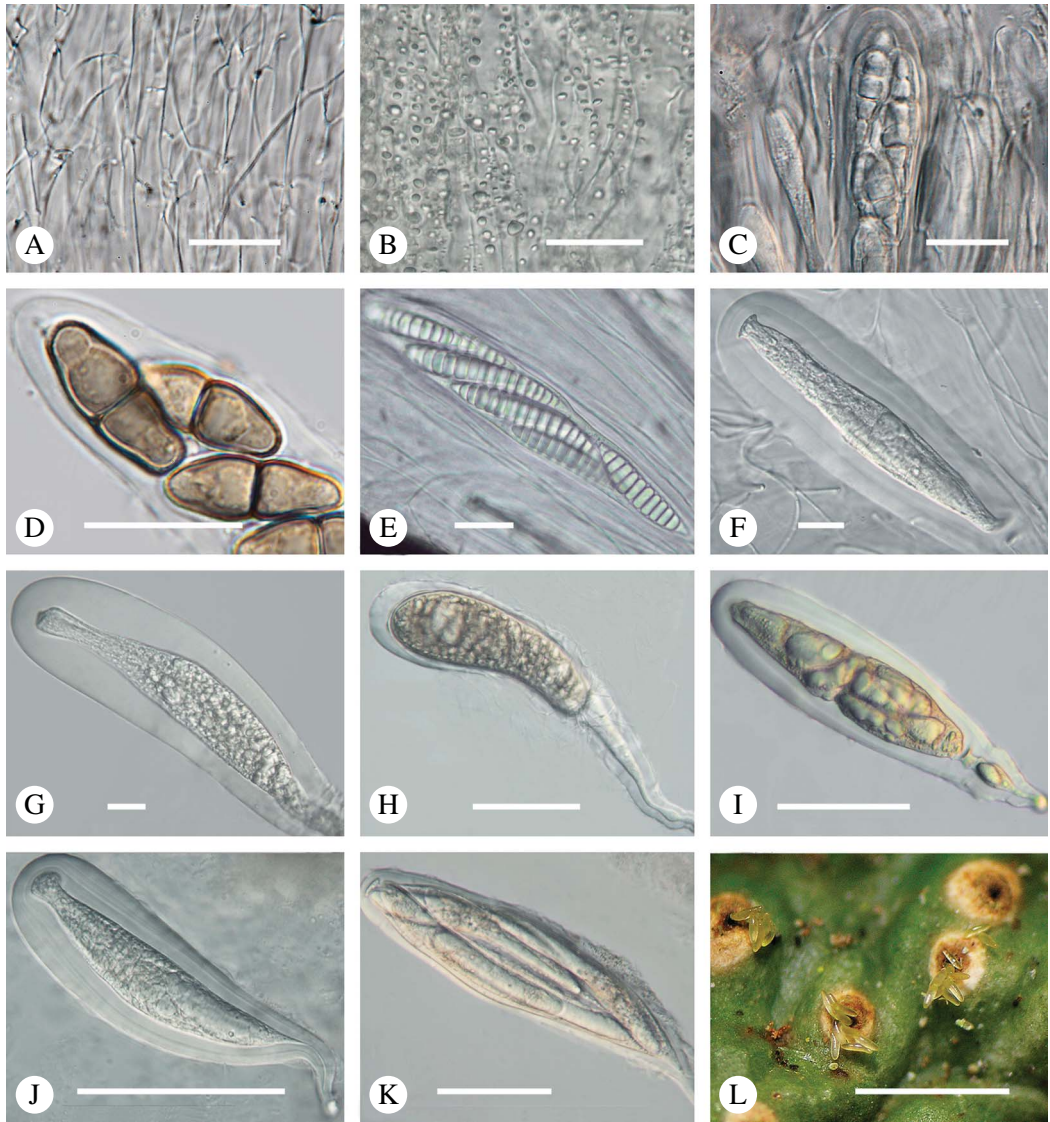


FIG. 8. Hamathecium and asci in *Trypetheliaceae*. A, anatomosing, net-like filaments, *Architrypethelium nitens*. B, inspersion with oil droplets lining the filaments, *Astrothelium megaspermum*. C–E, mature ascus with ascospores; C, *Constrictolumina majuscula*; D, *Novomicrothelia oleosa*; E, *Trypethelium eluteriae*. F–K, young and immature asci showing wall layers and apical apparatus; F, *Aptrootia terricola*; G & H, *A. robusta*; I, *Architrypethelium nitens*; J & K, *Astrothelium megaspermum*. L, ejection of ascospores through ostiole, *A. megaspermum*. Scales: A–G = 20  $\mu$ m; H–K = 100  $\mu$ m; L = 1 mm. (Images C & D by F. Schumm).

sometimes dirty yellow infusion in basal lineages such as *Pseudopyrenula*; in some species, the droplets contain anthraquinones and react with K. In most species, inspersion is found along the ostiolar area while the

hamathecium is clear. For instance, Harris (1995) suggests muriform-spored species of *Bathelium* have an inspersion hamathecium, whereas the inspersion in most of these species is developed only around the ostiole.



The taxonomic importance of hamathecium inspersion (i.e. of the entire hamathecium) has been neglected, except in a few cases, but phylogenetic studies suggest that it is species-specific (Nelsen *et al.* 2014; Lücking *et al.* 2016a). Unfortunately most descriptions, especially of historical names, do not mention this character and hence the status of names for which types have not been available is difficult to resolve. On the other hand, inspersion is usually preserved even in old collections as long as hymenium material is present.

Asci in *Trypetheliaceae* are typically fissitunicate (Eriksson 1981; Aptroot 1991); their internal structure is best observed in species with larger ascospores, as long as the ascospores are young or immature (Fig. 8C–K). Typically the asci have a distinct foot (Fig. 8H & J). The elastic inner wall (endotunica) appears multilayered (Fig. 8J) and the tholus contains a non-staining ring structure. Like ascoma anatomy, ascus structure has not yet been fully studied and explored for taxonomic purposes in this family, but may be helpful to delimit especially the basal lineages.

Besides ascoma morphology, ascospore type is the second most important character complex in *Trypetheliaceae* (Figs 8L, 9A–L). While in the past ascospore septation was mostly used to separate lineages at the genus level, it is now obvious that the nature of the septa and walls provide the most critical characters at a higher taxonomic level (Fig. 9A–L) whereas septation *per se* might separate species but varies considerably at genus level. Astrothelioid ascospores are typical of this family, forming secondary wall thickenings that make the lumina diamond-shaped (Fig. 9G). Very similar ascospores occur in some non-lichenized families such as *Massariaceae*, which Eriksson (1981) used to suggest that they should form part of *Trypetheliaceae*. In fact these families are not closely related to *Trypetheliaceae* (Schoch *et al.* 2009b; Hyde *et al.* 2013). In species of *Trypetheliaceae* with muriform ascospores, in which the lumina are small and their morphology is difficult to assess, the young ascospores in lineages with an astrothelioid

ascospore type undergo a distinctly astrothelioid stage (Fig. 9J & K) (Sweetwood *et al.* 2012). Almost without exception, a given genus has either astrothelioid or non-astrothelioid ascospores. The latter can be assigned to various types, including the multi-septate ascospores with slightly thickened but not astrothelioid septa in *Trypethelium* (Fig. 9E) and *Viridothelium*, or the septate to muriform ascospores in *Bathelium* (Fig. 9F), *Polymeridium* (Fig. 9D) and *Dictyomeridium*. In *Architrypethelium* the ascospores are principally astrothelioid when immature with a reduced endospore when mature, becoming very large with few septa and often including characteristic, needle-shaped crystals (Fig. 9H). Basal lineages formerly placed in *Arthopyrenia* and *Mycomicrothelia* now positioned in the genera *Bogoriella*, *Constrictolumina*, and *Novomicrothelia* have almost invariably 1-septate ascospores with thin or thickened walls and septa but are never astrothelioid (Fig. 9A–D); in *Constrictolumina* these may form secondary invaginations (partial septa), whereas in *Bogoriella* and *Novomicrothelia*, ornamented walls may occur. *Distothelia* has particular ascospores with strong distal thickenings and the lumina near the central septum (Fig. 9C).

Most species in *Trypetheliaceae* have colourless ascospores, but brown ascospores are found in the basal genera *Bogoriella* (Fig. 9B) and *Novomicrothelia*, in most species of *Architrypethelium*, and in *Aptrootia* (Fig. 9K & L), in which the large, muriform ascospores also form a peculiar, easily breakable outer shell (Fig. 9L) (Sweetwood *et al.* 2012).

## Chemistry

The chemistry of the *Trypetheliaceae* is rather simple compared to other tropical, crustose families, such as *Graphidaceae* (Rivas Plata *et al.* 2012; Lumbsch *et al.* 2014), and secondary substances are restricted to two main groups: xanthenes and pigments, mostly anthraquinones.

Lichexanthone is the most commonly found xanthone in the family. It reacts UV+ yellow and can be present on the ascomata, pseudostromata and/or the ostioles, and/or

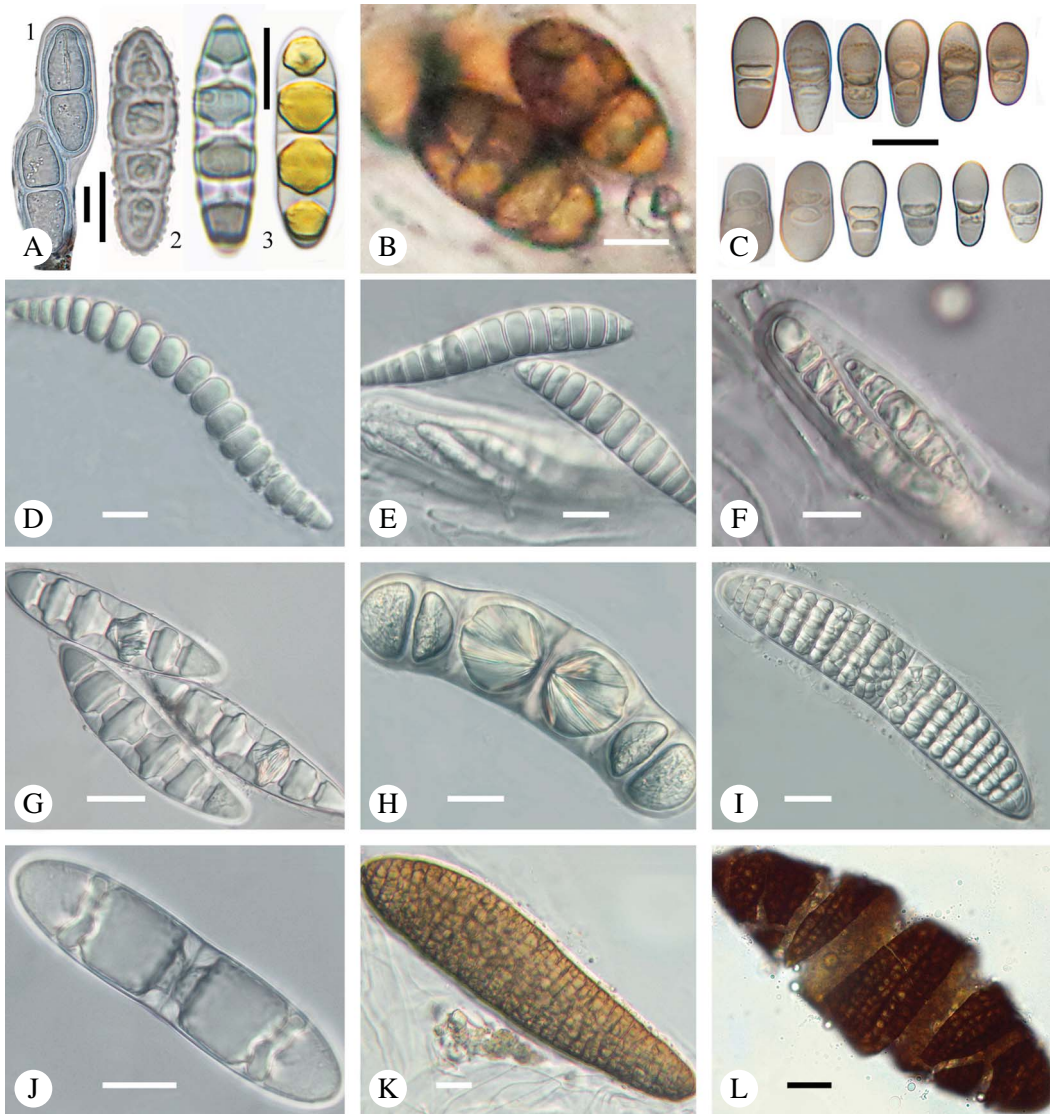


FIG. 9. Ascospores in *Trypetheliaceae*. A1, *Constrictolumina malaccitula*; A2, *C. majuscula*, with ornamented wall; A3, *Pseudopyrenula diluta*, in part with yellow content in lumina; B, *Bogoriella decipiens*; C, *Distothelia angulata*, with thick terminal walls; D, *Polymeridium pleurothecium*, thin-walled; E, *Trypethelium subeluteriae*, thin-walled; F, *Bathelium nigroporum*, thin-walled; G, *Astrothelium diplocarpoides*, with diamond-shaped lumina; H, *Architrypethelium nitens*, with crystal-like structures; I, *Astrothelium megaspermum*, muriform with rounded to diamond-shaped lumina; J & K, *Aptrootia terricola*, muriform, brown; in J young, still hyaline ascospore showing astrothelioid stage; L, *A. robusta*, muriform, brown; outer wall breaking apart. Scales: A–F = 10  $\mu\text{m}$ ; G–L = 20  $\mu\text{m}$ . (Images A & C by F. Schumm).

on the thallus (Fig. 10A), rarely in the medulla. The taxonomic value of the presence of lichexanthone has been disputed; species were traditionally separated based on

this feature, in others it was considered infraspecific variation (e.g. Harris 1995). Based on evidence from phylogenetic data (Nelsen *et al.* 2014; Lücking *et al.* 2016a), we



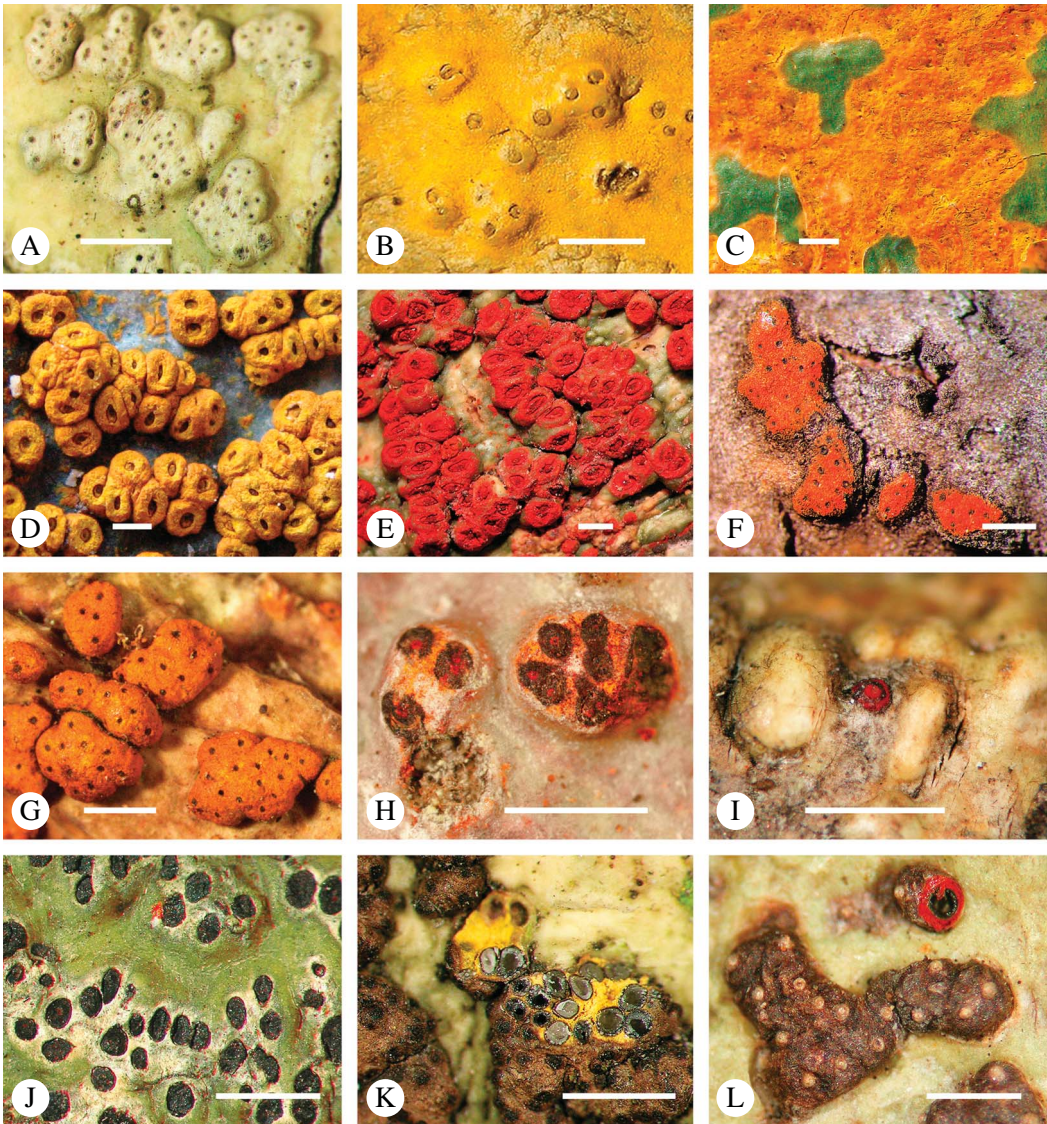


FIG. 10. Secondary chemistry and pigments in *Trypetheliaceae*. A, lichexanthone, *Astrothelium phlyctaena*. B–G, yellow-orange to red anthraquinones on ascomata and pseudostromata; B, *A. croceum*; C, *A. kunzei*; D, *Marcelaria cumingii*; E, *M. purpurina*; F, *Astrothelium aurantiacocinereum*; G, *Trypethelium eluteriae*. H, pseudostromata with yellow internal and orange and red external anthraquinone pigments, *T. astroideum*; I, fused ostiole with red quinone isohypocrellin, *Astrothelium purpurascens*; J, ascomata with pockets of red pigment, *A. sierraleonense*. K & L, pseudostromata with internal yellow and red pigment; K, *A. degenerans*; L, *A. sanguinarium* with isohypocrellin. Scales = 1 mm.

consider the presence and location of lichexanthone species-specific. 1,8-dihydroxy-3,6-dimethoxyxanthone (coronatone) is less often present; it reacts UV+ orange but might

be masked by the present of lichexanthone. The presence and proportion of both substances in UV+ taxa needs to be studied further.

Various quinones, mostly anthraquinones, are regularly present on or in the ascomata or pseudostromata, and/or the ostioles and/or on or in the thallus (Fig. 10B–L), sometimes even in the ascoma wall, the hamathecium, or inside the ascospores (Fig. 9A). Many anthraquinones have not yet been identified, especially when quantities are low (e.g. when restricted to the ostiole or ascospore). However, the following substances have been classified (Mathey & Hoder 1978; Mathey 1979; Mathey *et al.* 1980):

Parietin (= physcione) is the most common yellow-orange pigment, for example in *Astrothelium aeneum*, *A. croceum* (Fig. 10B), *Marcelaria cumingii* (Fig. 10D), and *Trypethelium eluteriae* (Fig. 10G); it reacts K+ purple.

Teloschistin (= fallacinol) is also yellow and is found in *Marcelaria benguelensis*; it reacts K+ purple.

Xanthorin (= lauropurpurone) is red and reacts K+ purple; it is found, for example, in *Marcelaria purpurina* (Fig. 10E).

Secalonic acid derivatives are yellow to orange and react K+ yellow; they occur in *Marcelaria purpurina*.

Emodin and derivatives are orange and react K+ purple; these pigments are found, for example, in *Marcelaria cumingii* (Fig. 10D).

The perylene quinone isohypocrellin is red and reacts with a K+ green efflux: this pigment occurs in *Astrothelium purpurascens* (Fig. 10I), *A. sanguinarium* (Fig. 10L), *A. sanguineoxanthum*, and *Dictyomeridium isohypocrellinum*.

Skyrin, isopigmentosin A and C, and semivioxanthin are also occasionally found; since these substances are detected in low concentration, they have not yet been assigned taxonomic value, since their absence or presence on chromatographic plates might depend on their concentration in the lichen and on analytical conditions. However, it is expected that detailed chemical analyses with sophisticated methods could reveal characteristic, species-specific patterns including these substances.

With regard to UV testing, it should be stressed that only positive UV-reactions that relate to xanthonones and anthraquinones are mentioned in the descriptions. These are yellow or orange for xanthonones and usually red for pigments; whitish or greenish reflections of the thallus or ascoma surface are ignored as these correspond to brightening under the UV lamp of ochraceous (often old) specimens; taxa with such UV reflections only are reported as UV-. Similarly, some specimens with a thick, hyaline cortex show a faint, K+ yellow reaction, which is also ignored as it seems to be caused by a structural change from wetting, not by a secondary substance. When carrying out UV testing, it is therefore recommended to make comparisons with previously identified reference specimens of taxa with a set of known chemical compounds, including lichexanthone and the major pigments.

### Species Delimitation and Nomenclature

Species delimitation within *Trypetheliaceae* has been rather inconsistent in the past and, until recently, sometimes used the same characters to either separate species or include specimens within a single taxon (Harris 1993, 1995). This was also reflected at the genus level, where species with lateral ostioles and transversely septate ascospores were assigned to a single genus, *Astrothelium*, whereas those with lateral ostioles and muriform ascospores were assigned to two separate genera, *Campylothelium* (with solitary ascomata) and *Cryptothelium* (with fused ascomata).

To obtain a more consistent species concept we used two approaches: 1) analysis of morphological, anatomical and chemical variation in phylogenetically defined clades (Lücking *et al.* 2016a); and 2) morphological analysis of a larger number of specimens in larger species complexes. As a result, we found that characters such as thallus and ascoma morphology (e.g. surface structure and emergence), hymenial inspersions, ascospore size, and secondary chemistry



(including lichexanthone) are diagnostic at the species level, much more so than previously believed; hence, a much larger number of species is recognized here based on a revised species concept alone (excluding the many novel taxa described elsewhere in this issue). For example, the rich material available from Rondônia and Sergipe in Brazil (Aptroot & Cáceres 2016; Aptroot *et al.* 2016b), with several hundred collections representing over 70 taxa, and from Venezuela (Komposch & Hafellner 1999; Komposch *et al.* 2002), with *c.* 300 collections belonging to 40 species, allowed us to analyze morphological and anatomical variation in some of the common taxa. As an example, the ascospore width and length of all specimens of the *Astrothelium conicum*-aggregate were analyzed showing that the species recognized within this complex are separated on a combination of UV-reaction and ascospore dimensions.

To obtain a stable nomenclature that reflects this revised species concept, as many collections as possible were studied including most type specimens of published names. Fifty-seven new lectotypes were designated, including in one case an illustration with an additional epitype. To check possibly erroneous nomenclatural citations, including those given in *Index Fungorum* and other similar databases, original protologues of all names were studied. As an extreme example of a revised species concept and nomenclatural treatment, *Astrothelium variolosum sensu* Harris (1993), which in most other treatments corresponds to the four names *Astrothelium confusum*, *A. variolosum* (ostioles lateral, fused, without or with lichexanthone), *Trypethelium nitidiusculum* and *T. ochroleucum* (ostioles apical, separate, without or with lichexanthone), is now considered to encompass at least 34 different species (Table 1) which are not necessarily closely related (Lücking *et al.* 2016a). The fact that all of these names were described in the 19th century underlines the importance of critical analysis of historical literature and type specimens to accurately assess the taxonomy and nomenclature of *Trypetheliaceae*. This situation is similar to

that found in the genus *Ocellularia* where the commonly used names *O. papillata*, *O. perforata* and *O. terebrata* now refer to 69 different taxa, many of them represented by historical names (Lücking 2014).

Keys and short descriptions are presented for the currently accepted species of *Trypetheliaceae* with the exception of those described elsewhere in this issue as new taxa; these are only cross-referenced in the keys. The delimitation of *Astrothelium*, *Bathelium*, and *Trypethelium* is revised so as to be in concordance with the molecular phylogeny, resulting in mostly monophyletic genera that are still morphologically recognizable. Many taxa, including the genera *Campylothelium*, *Cryptothelium* and *Laurera*, are synonymized for the first time (the latter three with *Astrothelium*) whereas others, including the genus *Bogoriella*, have been reinstated.

The revised genus and species concept and the examination of many old type specimens led to the proposal of many new combinations. Numerous species are recorded for the first time from a country or continent. However, there is still a high proportion of species known only from their type material. This also strongly suggests that many species still remain undiscovered, as shown by a statistical prediction exercise (Aptroot *et al.* 2016c). This is corroborated by the fact that a few short field trips in small areas in Brazil yielded many undescribed species (Aptroot & Cáceres 2016; Aptroot *et al.* 2016b; Lücking *et al.* 2016a), and also taxonomic inventories of other understudied areas, such as Panama and Bolivia, unravelled numerous novel taxa (Flakus *et al.* 2016; Lücking *et al.* 2016b).

Some commonly used names are synonymized for the first time, such as *Trypethelium ochroleucum*; many rarely applied names are reinstated, as in the example of the *Astrothelium variolosum* complex above. Inevitably this resulted in new names for some of the most common taxa. We preferred this solution, over the alternative of proposing well-known names for conservation, for two reasons: 1) *Trypetheliaceae* are relatively rarely mentioned in the general literature and mostly known to specialists;

TABLE 1. Revised species concept in the *Trypethelium nitidiusculum*/T. ochroleucum–*Astrothelium variolosum* complex.

Ostiole	Lichexanthone	Inspersion	Species	Ascomata	Thallus	Lichexanthone location*
apical	present	inspersed	<i>grossoides</i>	solitary, thallus cover	bullate	+/-
			<i>punctulatum</i>	solitary, thallus cover	bullate	-/+
			<i>vulcanum</i>	solitary to confluent, whitish	smooth	+/+
		clear	<i>porosum</i>	pseudostromatic, thallus cover	smooth	+/+
			<i>pulcherrimum</i>	solitary, thallus cover	smooth	+/+
			<i>phlyctaena</i>	pseudostromatic, thallus cover	smooth	+/+
			<i>leucosessile</i>	pseudostromatic, whitish	smooth	+/+
			<i>stromatofluorescens</i>	pseudostromatic, thallus cover	smooth	-/+
			<i>subscoria</i>	solitary, whitish	smooth	
	absent	inspersed	<i>scoria</i>	grouped, brown-black	smooth	
			<i>ceratinum</i>	solitary, thallus cover	smooth	
		clear	<i>nitidiusculum</i>	solitary, whitish	smooth	
			<i>meiophorum</i>	solitary to confluent, thallus cover	smooth	
			<i>nigratum</i>	grouped to pseudostromatic, brown-black	smooth	
			<i>bicolor</i>	pseudostromatic, thallus cover	smooth	
			<i>rufescens</i>	pseudostromatic, whitish	smooth	
			<i>scorizum</i>	grouped, brown-black	smooth	
			<i>neovariolosum</i>	pseudostromatic, thallus cover	smooth	+/+
			<i>laevigatum</i>	dispersed, whitish	smooth	+/+
lateral separate lateral fused	absent	clear	<i>subinterjectum</i>	dispersed to confluent, whitish	smooth	+/+
			<i>pseudocyphellatum</i>	pseudostromatic, thallus cover	smooth	+/+
	present	inspersed	<i>variolosum</i>	pseudostromatic, thallus cover	smooth	+/+
			<i>interjectum</i>	pseudostromatic, whitish	smooth	+/+
			<i>straminicolor</i>	pseudostromatic, partially exposed	smooth	+/+
			<i>pyrenastrosulphureum</i>	pseudostromatic, thallus cover	bullate	
		clear	<i>crassum</i>	dispersed-erumpent, thallus cover	smooth	
			<i>subdissocians</i>	dispersed-erumpent, whitish	smooth	
			<i>obscurum</i>	dispersed-erumpent to confluent, exposed	smooth	
			<i>peranceps</i>	dispersed-prominent, thallus cover	smooth	
<i>nigrum</i>	dispersed-prominent, exposed		smooth			
<i>nigricans</i>	dispersed-prominent on whitish lines, exposed		smooth			
absent	inspersed	<i>acrophaeum</i>	dispersed to confluent, partially exposed	smooth		
		<i>obigocarpum</i>	confluent-prominent, partially exposed	bullate		
		<i>subfuscum</i>	pseudostromatic, partially exposed	bullate		

\*Lichexanthone location: +/+ indicates lichexanthone present on both thallus and ascomata (pseudostromata); +/- indicates lichexanthone present on the thallus but not on the ascomata (pseudostromata) and -/+ indicates lichexanthone not present on the thallus but is present on the ascomata (pseudostromata).



2) the new names reflect the revised taxonomy and hence will force future workers to assess morphological, anatomical and chemical characters more critically. For instance, the name *Trypethelium ochroleucum* has been applied in a pantropical context to a number of species now recognized as different: *Astrothelium porosum* (pseudostromatic, inspersed), *A. pulcherrimum* (solitary, clear) and *A. phlyctaena* (pseudostromatic, clear). The fact that the name *ochroleucum* has been subsumed in synonymy will hopefully lead to proper revision and identification of herbarium material and newly collected specimens. Similarly, the taxon formerly known as *Trypethelium nitidiusculum* was split into *Astrothelium bicolor* (pseudostromatic, clear), *A. nitidiusculum* (solitary, clear) and *A. scoria* (grouped, inspersed).

We are very much aware that the present revision is not a thorough monograph of *Trypetheliaceae*. Rather, we present this revisionary synopsis to stimulate further research in this highly diverse and fascinating family, hoping that future workers will pay more attention to morphological, anatomical and chemical features to identify species and that the molecular phylogenetic data will be much expanded. Undoubtedly, further research will lead to additional changes in the classification of *Trypetheliaceae* and many additional new species will be discovered (Aptroot *et al.* 2016c). Notably, we are more confident with the taxonomic concept of the less common and rare species, which often have a unique combination of diagnostic characters different from similar and related taxa, than with the common species, such as *Astrothelium aeneum*, *A. bicolor*, *A. porosum*, *A. phlyctaena*, *A. scoria* and *Trypethelium eluteriae* which have a degree of variation that needs to be assessed by additional molecular phylogenetic studies.

### Distribution and Ecology

*Trypetheliaceae* is almost exclusively tropical and epiphytic, with very few species (e.g. *Viridothelium virens*) found in temperate regions and few species growing on other substrata. In general terms, the distribution

and ecology of *Trypetheliaceae* is very similar to that of *Graphidaceae* although the latter has more taxa in extra-tropical regions and on substrata other than bark (Rivas Plata *et al.* 2008; Lücking *et al.* 2014). More commonly than *Graphidaceae*, *Trypetheliaceae* are found in (semi-) exposed microhabitats and habitats, such as the forest canopy and open savannahs and dry forest, often forming colourful crustose lichen communities with dominant taxa producing yellow to orange pigments (Komposch & Hafellner 2000, 2002, 2003; Cáceres 2007; Aptroot *et al.* 2008; Cáceres *et al.* 2008; Rivas Plata *et al.* 2008). It appears that species with green thalli and partially immersed or covered ascomata are more frequently found in the rainforest understorey, but this has not been tested quantitatively. However, the observation that many taxa are typical of the more exposed canopy, a microhabitat that has not been well studied, indicates that this microhabitat might harbour many yet unknown species.

Following this revisionary synopsis, the list of accepted species known from the various countries has changed considerably, especially for countries in which much previous work was carried out, such as India and Brazil. A table with the currently accepted species and their updated, confirmed world distribution is available as supplementary material in Aptroot *et al.* (2016c).

Some species are much more widespread and common than others. In order to facilitate identification, lists are given here of the most common species. These are only a fraction of those known. Half of what remains are known only from the type location; the chance of finding any of these elsewhere is probably not much higher than that of finding an undescribed species, as demonstrated by the papers on Bolivian and Rondónian *Trypetheliaceae* in this issue (Aptroot & Cáceres 2016; Flakus *et al.* 2016).

Species with over 100 specimens seen include: *Astrothelium macrocarpum*, *A. phlyctaena*, *A. scoria*, *A. scorioides*, *A. versicolor*, *Constrictolumina cinchonae*, *Nigrovothelium tropicum* and *Trypethelium eluteriae*.

Species with between 20 and 100 specimens seen include: *Astrothelium aeneum*, *A. bicolor*, *A. cinnamomeum*, *A. degenerans*, *A. eustomum*, *A. feei*, *A. inspersaeneum*, *A. megaspermum*, *A. obscurum*, *A. ochrothelium*, *A. porosum*, *A. variolosum*, *Bathelium madreporiforme*, *Bogoriella hemisphaerica*, *B. punctata*, *B. subfallens*, *Dictyomeridium proponens*, *Marcelaria benguelensis*, *M. purpurina*, *Polymeridium albocinereum*, *P. catapastum*, *P. pleiomerellum*, *P. subcinereum*, *Pseudopyrenula diluta*, *P. subgregaria*, *P. subnudata*, *Trypethelium subeluteriae* and *Viridothelium virens*.

### Taxonomic Treatment

#### Trypetheliales Lücking, Aptroot & Sipman

In Aptroot *et al.*, *Biblioth. Lichenol.* 97: 13 (2008); type: *Trypetheliaceae* Eschw.

Ascomycetes, usually lichenized with trentepohlioid algae, more rarely bark saprobes or lichenicolous fungi.

*Ascomata* perithecia, solitary or grouped and fused (with separate or fused ostioles), round, immersed to sessile. *Wall* dark brown to carbonized. *Interascal hyphae* thin, richly branched and anastomosing, forming a net-like structure. *Asci* fissitunicate, I–. *Ascospores* ellipsoid-fusiform, with variously developed endospore thickenings giving the lumina a diamond-shaped or more rarely a round outline, colourless or rarely (dark) brown.

*Discussion.* This order encompasses a phylogenetically quite distinct group, now containing two families, viz. the lichenicolous *Polycoccaceae* and the lichenized *Trypetheliaceae* (Aptroot *et al.* 2008; Hyde *et al.* 2013; Ertz *et al.* 2015).

The order *Trypetheliales*, based on *Trypetheliaceae* Eschw., was introduced by Aptroot *et al.* (2008) to reflect the phylogenetic distinctiveness of the *Trypetheliaceae* within Dothideomycetes (Del Prado *et al.* 2006; Nelsen *et al.* 2009, 2011). The name *Trypetheliaceae* Eschw. itself (Eschweiler 1824) has been considered invalidly published in *Index Fungorum* (IF 81884) and

*Mycobank* (MB 81884), with the argument that it was associated with the rank term “*cohors*”; the same applies to the family names *Parmeliaceae* Eschw., *Usneaceae* Eschw., and *Verrucariaceae* Eschw. However, this interpretation appears to be incorrect, since an inappropriate rank term does not invalidate a name. Rather, ICN Art. 17.2 and 18.2 specify that if there is conflict between the intended rank (based on context and/or Latin termination) and the associated rank term, a name is presumed to be validly published at the intended rank, but not invalid. According to Art. 17.2, one might then conclude that *Trypetheliaceae* Eschw. (Eschweiler 1824) is to be accepted as a valid name at the order level (i.e. *Trypetheliales* Eschw.) because of the associated rank term “*cohors*”. In that case, because the principles of priority and homonymy do not apply to names above the rank of family, the names *Trypetheliales* Lücking *et al.* and *Trypetheliales* Eschw. would both be legitimate and could be used interchangeably. However, the opposite is the case, since Art. 17.2 states: “Names intended as names of orders, but published with their rank denoted by a term such as ‘*cohors*’, ‘*nixus*’, ‘*alliance*’, or ‘*Reihe*’ instead of ‘*order*’, are treated as having been published as names of orders.” This means that a name is to be treated at the order level, if the *intention* was to designate a name as an order, *in spite* (not because) of having used a rank term such as “*cohors*” (i.e. ‘*cohors*’ is *not* a rank term that *automatically* designates the rank of order). There is no further definition of the term ‘*cohors*’ in the *Code*, but its best Latin translation would be ‘*group*’, and there is no provision in the *Code* that the use of the term ‘*cohors*’ would preclude the meaning of family (as a group of genera). Correspondingly, the correct interpretation of the analogous Art. 18.2 is that a name is to be treated as family if the *intention* was to designate a family, *in spite* of using the rank term ‘*ordo*’. Eschweiler’s (1824) intention undoubtedly was to establish a family, as he used the term “*familia*” in the Latin description, defined *Trypetheliaceae* as a group of genera (the next higher, principal hierarchical level above genus is family), and used the correct Latin



termination “-aceae” (Art. 18.1); technically, the termination is not relevant as the *Code* was not in place at the time, but the termination ‘-aceae’ has been widely accepted since the late 18th century as denoting taxa at the family level in botanical nomenclature. As a consequence, neither Art. 17.2 nor Art. 18.2 apply in this case, since *Trypetheliaceae* Eschw. was not intended as a name of an order (required for Art. 17.2) and it was not associated with the rank term ‘ordo’ (required for Art. 18.2). On the other hand, by extension of the meaning of both articles, which imply that 1) ‘cohors’ is not a rank term naturally corresponding to order level, 2) a name is to be accepted at the level of family if intended so, and 3) there is no conflict between the use of the rank term ‘cohors’ and the family rank defined in either article or the *Code* as a whole, the name *Trypetheliaceae* Eschw. (Eschweiler 1824) is valid at the family rank and is not to be treated at the order level or to be considered invalid. Similar considerations would apply to the names *Parmeliaceae* Eschw., *Usneaceae* Eschw., and *Verrucariaceae* Eschw.

### **Trypetheliaceae Eschw.**

Eschweiler, *Syst. Lich.*: 17 (1824); Fée, *Essai Crypt. Écorc.*: xxvi (1824; as “Trypetheliées”), *nom. inval.* [ICN Art. 18.4, 32.1(b)]; *Trypetheliaceae* Zenker, in Goebel & Kunze, *Pharmaceutische Waarenkunde* 1(3): 123 (1827; as “Trypethelia”). *nom. illeg.* [ICN Art. 52.1]; type: *Trypethelium* Spreng.

*Thallus* crustose, corticate or not, without pseudocyphellae, sometimes surrounded by a black hypothallus. *Algae* trentepohlioid.

*Ascomata* perithecioid, mostly simple, but sometimes with fused ostioles, or the ascomata fused and having shared ostioles, with or without pseudostromatic tissues of a different structure and colour. *Ostioles* apical or eccentric. *Wall* usually completely carbonized, rarely only partly carbonized, with or usually without a clypeus, with or without crystals. *Hamathecium* usually colourless, rarely yellow, IKI–, clear or interspersed with oil droplets. Hamathecial filaments branched and usually anastomosing paraphysoids of 0.5–2.0 µm thick, rarely almost unbranched

paraphysoids that are much wider at the base than at the tips; paraphyses absent; short paraphysoids rarely present. *Asci* bitunicate, cylindrical, IKI–, usually with a broad ocular chamber that is especially distinct in immature asci. *Ascospores* 1–8 per ascus, distoseptate, usually IKI–, rarely IKI+ violet, with rounded or angular lumina, without additional eusepta, colourless, rarely becoming brown, rarely constricted at the septa, with or without a gelatinous sheath.

*Conidiomata* pycnidia. *Conidia* colourless, rod-shaped. Conidiogenesis acrogenous.

*Chemistry.* Lichexanthone (or the closely related 1,8-dihydroxy-3,6-dimethoxyxanthone or coronatone) or quinones, mostly anthraquinones, often present. Non-specific substances such as skyrin, isopigmentosin A and C and semivioxanthin sometimes detected.

*Discussion.* This family currently comprises 16 genera. Most were traditionally assigned to this family, but some have been erected here to accommodate species aggregates traditionally assigned to other groups (e.g. *Arthopyrenia*, *Mycomicrothelia*) that were found to belong here based on phylogenetic studies (Nelsen *et al.* 2009, 2011, 2014; Lücking *et al.* 2016a). The new genus *Constrictolumina* is used for species formerly placed in *Arthopyrenia*, which in its strict sense remains a small, non-lichenized, extratropical genus (Hyde *et al.* 2013), and *Novomicrothelia* for several species previously classified in *Mycomicrothelia*, while *Bogoriella* is reinstated to accommodate most of the former *Mycomicrothelia* species. Most genera accepted here are supported by molecular data, whereas the inclusion of the reinstated *Distothelia* is based on morphological similarities. The circumscription of *Astrothelium*, *Bathelium*, and *Trypethelium* had to be changed so as to be in concordance with the phylogeny (Nelsen *et al.* 2014; Lücking *et al.* 2016a). *Bathelium* and *Trypethelium* are restricted here to small, morphologically recognizable groups of species related to their respective types; some species included in *Bathelium sensu*

Harris (1995), with astrothelioid ascospores, were found to belong in *Astrothelium* (Nelsen *et al.* 2014; Lücking *et al.* 2016a). The new genus *Viridothelium* encompasses a clade with species morphologically similar to *Astrothelium* but with ascospores reminiscent of those of *Trypethelium*, whereas *Marcelaria*

was recently established for a small group of species with very conspicuous ascomata and muriform ascospores (Aptroot *et al.* 2013a).

For the correct nomenclature and authorship of the name *Trypetheliaceae*, see discussion under *Trypetheliales* above.

### Key to the genera of *Trypetheliaceae*

While this key does not explicitly include similar, lichenized or non-lichenized ascomycetes from other orders, cross-references are given where appropriate. When in doubt about the family to which a specimen belongs, check general keys for pyrenocarpous lichens, such as Aptroot *et al.* (2008). Most similar taxa are found in the families *Massariaceae* (non-lichenized), *Monoblastiaceae*, *Pyrenulaceae*, and *Strigulaceae*. Members of *Trypetheliaceae* can mostly be recognized by the following character combinations:

Ascospores hyaline, transversely 1(–3)-septate, with slightly thickened walls and often with additional invaginations (pinched), combined with basally broadened hamathecium filaments (versus *Anisomeridium* in *Monoblastiaceae* and *Strigula* in *Strigulaceae* with thin-walled ascospores and thin hamathecium filaments).

Ascospores hyaline, transversely 3- to multiseptate, astrothelioid and lichenized (versus non-lichenized *Massariaceae*).

Ascospores hyaline, large, transversely 3-septate (versus *Megalotremis* and *Trypetheliopsis* in *Monoblastiaceae* with large but mostly 1-septate ascospores).

Ascospores hyaline, muriform with young stages astrothelioid and hamathecium net-like (versus *Phyllobathelium* in *Strigulaceae* with hamathecium not net-like and filaments broad).

Ascospores brown, small, transversely 1(–3)-septate with thin to slightly thickened walls and septa, often ornamented walls and anastomosing hamathecium filaments (versus certain species of *Pyrenula* in *Pyrenulaceae* with a thickened endospore and unbranched hamathecium filaments).

Ascospores brown, large, transversely at least 3-septate and hamathecium net-like (versus certain species of *Pyrenula* in *Pyrenulaceae* with unbranched hamathecium filaments).

Ascospores brown, large, muriform and hamathecium net-like (versus species of *Anthracotheicum* and *Pyrenula* in *Pyrenulaceae* with unbranched hamathecium filaments).

1 Ascospores brown when mature . . . . . 2  
Ascospores remaining hyaline . . . . . 5

2(1) Ascospores small, under 20 × 15 µm; thallus ecorticate, whitish; ascomata usually exposed and black . . . . . 3

Ascospores large, over 80 × 20 µm; thallus corticate or with cartilaginous, corticiform layer, olive-green to yellowish brown or rarely silvery grey; ascomata at least partly covered by (corticate) thallus . . . . . 4

3(2) Ascospores with strongly thickened terminal walls when mature, sole-shaped; lumina moon- or hourglass-shaped, small in relation to the ascospores . . . . **Distothelia**

Ascospores with thin or slightly but evenly thickened walls; lumina not hourglass-shaped, not small in relation to the ascospores . . . . **Bogoriella, Novomicrothelia**

The morphological distinction of these two latter genera is not yet clear, although they form distinct phylogenetic clades; the single species of *Novomicrothelia* is therefore keyed out under *Bogoriella*.



- 4(2) Ascospores transversely septate. . . . . **Architrypethelium** p.p.  
 Ascospores muriform . . . . . **Aptrootia**
- 5(1) Thallus ecorticate; ascomata more or less exposed, grey-black, mostly erumpent . . . 6  
 Thallus corticate, usually with medulla; ascomata usually at least in part covered by  
 thallus, if exposed and (brown-)black then barrel-shaped or distinctly pseudo-  
 stromatic and prominent to sessile . . . . . 9
- 6(5) Hamathecium filaments at the base much thicker than at the top, not anastomosing;  
 ascospores often with additional wall invaginations besides the (sub-)median  
 septum . . . . . **Constrictolumina**  
 Hamathecium filaments of uniform width, anastomosing; ascospores without wall  
 invaginations, either with thin septa and rectangular lumina or astrothelioid with  
 diamond-shaped lumina . . . . . 7
- 7(6) Ascospores muriform; ascomata with lateral ostioles. . . . . **Dictyomeridium**  
 Ascospores transversely septate or submuriform, rarely muriform and then with  
 apical ostioles . . . . . 8
- 8(7) Lumina angular, ascospores with reduced endospore . . . . . **Polymeridium**  
 Lumina diamond-shaped when mature, ascospores with thickened endospore . . . . .  
 . . . . . **Pseudopyrenula**
- 9(5) Ascospores transversely 3- to multiseptate with rectangular (to oval) lumina. . . . 10  
 Ascospores either muriform or transversely septate, but in the latter case with  
 diamond-shaped lumina or else ascospores very large (over 90 µm long) and with  
 few (3(-5)) septa . . . . . 12
- 10(9) Ascomata confluent in brown-black, sessile pseudostromata; ascospores with few  
 (3-9), thin septa, usually up to 40 µm long . . . . . **Bathelium** p.p.  
 Ascomata in variously coloured pseudostromata or solitary and immersed; asco-  
 spores with numerous ((5-)9-19), usually slightly thickened septa, longer than  
 40 µm . . . . . 11
- 11(10) Ascomata immersed-erumpent, solitary to aggregate, rarely pseudostromatic;  
 pigments usually absent . . . . . **Viridothelium** p.p.  
 Ascomata in erumpent to prominent pseudostromata; pigments often present . . . .  
 . . . . . **Trypethelium**
- 12(9) Ascospores transversely septate. . . . . 13  
 Ascospores muriform . . . . . 15
- 13(12) Ascospores very large with few (3(-5)) septa, with reduced endospore and not  
 distinctly astrothelioid when mature . . . . . **Architrypethelium** p.p.  
 Ascospores usually small to medium-sized, if large and with few septa, then with  
 thickened endospore and astrothelioid (i.e. with diamond-shaped lumina) . . . 14
- 14(13) Ascomata prominent to sessile, fully exposed and black, solitary but usually crowded,  
 lacking pigments; ascospores 3-septate . . . . . **Nigrovothelium**  
 Ascomata immersed to prominent or in immersed to sessile pseudostromata, at least  
 partly covered by thallus or in exposed, brown-black pseudostromata filled with  
 yellow-orange pigment; ascospores 3- to multiseptate. . . . . **Astrothelium** p.p.

- 15(12) Ascomata in prominent to sessile, brown-black pseudostromata filled with yellow-orange pigments . . . . . **Bathelium** p.p.  
 Ascomata immersed to sessile or in immersed to sessile pseudostromata, at least partly covered by thallus and/or with thick pigment layer . . . . . 16
- 16(15) Ascomata in large, prominent to sessile, red or yellow-orange warts, usually with a split between the inner wall and the surrounding covering tissue, usually with thick, yellow-orange or red pigment layer . . . . . **Marcelaria**  
 Ascomata immersed to prominent or in immersed to sessile pseudostromata, lacking pigment or with a thin pigment layer, lacking a split between inner wall and covering tissue . . . . . **Astrothelium** p.p., **Viridothelium** p.p.  
 The morphological distinction between the single, muriform-spored species of *Viridothelium* and muriform-spored species of *Astrothelium* is not yet clear, although they belong to distinct phylogenetic clades; *Viridothelium* is therefore cross-referenced in the *Astrothelium* key.

**Aptrootia Lücking & Sipman**

In Lücking *et al.*, *Lichenologist* **39**: 188 (2007); type: *Aptrootia terricola* (Aptroot) Lücking, Umaña & Chaves (holotype).

*Thallus* either corticate and green and bullate or verrucose, or not corticate and grey, ± smooth and cartilaginous.

*Ascomata* solitary, black, globose to ampulliform, immersed in thalline warts or in the substratum. *Ostioles* apical. *Hamathecium* colourless, clear or interspersed with large irregular oil droplets near the ostiole, filaments thin, anastomosing paraphysoids. *Ascospores* 1(–2) per ascus, IKI+ violet, with scarcely rounded lumina, initially colourless, becoming dark brown but wall internally remaining hyaline (only outer layer brown), ornamented with brown warts or not, fusiform or

usually elongate-ellipsoidal to bacilliform with subacute or rounded ends, densely irregularly muriform, not constricted at the septa, surrounded by a gelatinous sheath.

*Pycnidia* unknown.

*Chemistry*. No substances detected.

*Discussion*. This recently established genus (Lücking *et al.* 2007) differs from other *Trypetheliaceae* in the combination of immersed ascomata and dark brown, muriform ascospores, as well as in its peculiar ecology growing often over bryophytes, a feature otherwise unknown in the family. The genus was erected for a terricolous lichen known from mountains in Papua New Guinea and Costa Rica. Two additional Australasian species have been transferred to *Aptrootia* (Aptroot 2009a).

**Key to the species of *Aptrootia***

- 1 Thallus on bark, corticate, green, bullate; ascospores ornamented (this synopsis; Fig. 11A) . . . . . **Aptrootia elatior**  
 Thallus on soil and bryophytes, not corticate, grey, cartilaginous, smooth; ascospores smooth . . . . . 2
- 2(1) Ascospores 170–230 × 40–70 µm (this synopsis; Fig. 11B) . . . . **Aptrootia terricola**  
 Ascospores 150–360(–400) × 65–140 µm (this synopsis; Fig. 11C) . . . . . **Aptrootia robusta**

***Aptrootia elatior* (Stirt.) Aptroot**

*Fl. Australia* **57**: 600 (2009).—*Ascidium elatius* Stirt., *J. Linn. Soc., Bot.* **14**: 466 (Feb. 1875).—*Leptotrema elatius* (Stirt.) Müll. Arg., *Bull. Herb. Boissier* **2** (App. 1):

75 (1894).—*Thelotrema elatius* (Stirt.) Hellb., *K. Svenska Vetensk.-Akad. Handl.* **21**(3, 13): 79 (1896).—*Laurera elatior* (Stirt.) D. J. Galloway, *New Zealand J. Bot.* **21**: 193 (1983); type: New Zealand, near Wellington, *Buchanan* (BM!—lectotype; Galloway, *Fl. New Zealand Lichens*: 205, 1985).



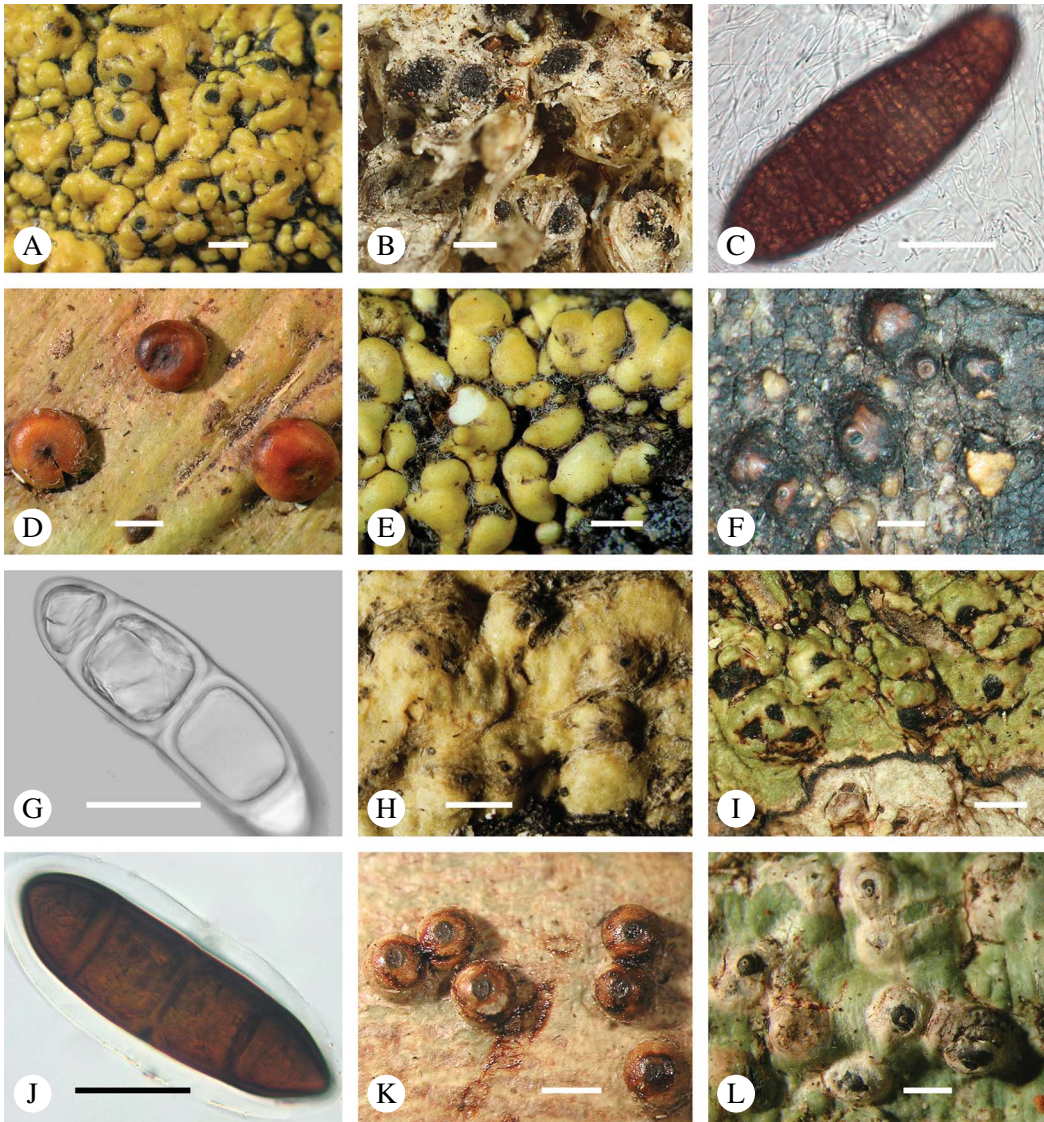


FIG. 11. Habitus, anatomy and ascospore of *Aptrootia* (A–C) and *Archityrpethelium* species (D–L). A, *Aptrootia elatior* (New Zealand, lectotype); B, *A. terricola* (Papua New Guinea, *Aptroot* 37658); C, *A. robusta* (Tasmania, *Lumbsch* 20012n); D, *Archityrpethelium grande* (Brazil, lectotype); E, *A. lauropaluanum* (Brazil, holotype); F & G, *A. hyalinum* (Venezuela, *Sipman & van der Werff* 10902); H, *A. penuriixanthum* (Bolivia, holotype); I & J, *A. nitens* (I, Venezuela, holotype of *Pleurothelium ernstianum*; J, Costa Rica, *Lücking* 15212b); K, *A. columbianum* (Colombia, lectotype); L, *A. uberinum* (Costa Rica, *Lücking* s. n.). Scales: A, B, D–F, H, I, K & L = 1 mm; C = 100  $\mu$ m; G & J = 50  $\mu$ m.

*Ascidium melanosporum* C. Knight, *Trans. Proc. N. Z. Inst.* 7: 363 (Jul. 1875); type: New Zealand, Knight s. n. (NSW!).

*Anthracothecium monosporum* Müll. Arg., *Bull. Herb. Boissier* 3: 327 (1895).—*Polyblastiopsis monosporum* (Müll. Arg.) Upreti & A. Singh, *Brunonia* 10: 226 (1987).—*Julella monospora* (Müll. Arg.) D. D. Awasthi,

*Lichenology in Indian Continent*: 15 (2000); type: Australia, Victoria, *Knight* 214 (G!—holotype).

*Verrucaria luteonitens* Nyl., *Ann. Soc. Sci. Fenn.* 26(10): 24 (1900).—*Anthracothecium luteonitens* (Nyl.) Zahlbr., *Catal. Lich. Univ.* 1: 464 (1922); type: Sri Lanka, Pedretalagalla, *Almquist* (H-Nyl 1061!—holotype).

(Fig. 11A)

*Thallus* corticolous, corticate, pale yellow-brown to green, verrucose-bullate.

*Ascomata* trypethelioid, with apical ostioles, ampulliform, oval or subglobose (in section), 0.7–1.7 mm diam., erumpent, covered by thallus except the rather broad, black ostiolar area, with copious hyaline crystals and a conspicuous black ring around the ostiole free of crystals. *Wall* to 150 µm thick. *Hamathecium* clear except for large irregular oil droplets near the ostiole. *Ascospores* 1(–2) per ascus, 200–330 × 60–90 µm, oblong-ellipsoid, richly muriform, becoming dark brown and ornamented (verruculose), with ascospore wall distinctly bi-layered: outer layer dark brown, inner layer hyaline.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (previously reported from Australia and New Zealand, now also from Sri Lanka and Sabah).

*Discussion.* This species differs from the other two by the ornamented ascospores and bark as substratum. We suspected that it may represent an undescribed genus, but it is phylogenetically nested between the other two species. The ascospore surface with the irregular brown warts is unique in the family. In a thin hand-section, this outer wall appears to be brittle, and a section through the ascospores reveals the subhyaline internal parts.

*New country record. Malaysia:* Sabah, Kota Belud, Kinabalu Park, 2800 m, 1989, *Sipman & Tan* 31305 (B).

### ***Aptrootia robusta* (P. M. McCarthy & Kantvilas) Aptroot**

*Fl. Australia* 57: 661 (2009).—*Laurera robusta* P. M. McCarthy & Kantvilas, *Lichenologist* 25: 51 (1993); type: Australia, Tasmania, Crater Peak, *Kantvilas & James* (HO—holotype, not seen; BM!—isotype).

(Fig. 11C)

*Thallus* muscicolous, with thin, cartilaginous cortex, grey, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, globose (in section), 0.9–1.5 mm diam., immersed, partially covered by thallus except the rather broad, black ostiolar area. *Wall* to 120 µm thick. *Hamathecium* clear. *Ascospores* 1 per ascus, 150–360(–400) × 65–140 µm, ellipsoid, richly muriform, becoming dark brown.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Australia.

*Discussion.* This species differs from *Aptrootia terricola* principally by the larger ascospores (170–230 × 40–70 µm in the latter).

### ***Aptrootia terricola* (Aptroot) Lücking *et al.***

In Lücking *et al.*, *Lichenologist* 39: 188 (2007).—*Thelenella terricola* Aptroot, *Fungal Diversity* 2: 45 (1999); type: Papua New Guinea, Simbu Prov., Mount Wilhelm, Pindaunde Valley, near the hut on the S-shore of Lake Piunde, *Aptroot* 32649 (CBS!—holotype; ABL!—isotype).

(Fig. 11B)

*Thallus* terricolous, with thin, cartilaginous cortex, grey, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, globose (in section), 0.9–1.5 mm diam., immersed, partially covered by thallus except the rather broad, black ostiolar area. *Wall* to 120 µm thick. *Hamathecium* clear. *Ascospores* 1 per ascus, 170–230 × 40–70 µm, ellipsoid, richly muriform, becoming dark brown late during maturity, I+ violet when hyaline.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Amphi-Pacific, known from tropical mountains in Costa Rica and Papua New Guinea, now also reported from the Solomon Islands.

*Discussion.* This species differs from *Aptrootia robusta* principally by the smaller



ascospores (150–360(–400) × 65–140 µm in the latter).

*New country record. Solomon Islands: Guadalcanal Island: Central part, Mount Popomansiu, summit, c. 2200 m, 1965, Hill 9400 (BM, ABL).*

### **Architrypethelium Aptroot**

*Biblioth. Lichenol.* 44: 120 (1991); type: *Architrypethelium uberinum* (Fée) Aptroot (holotype).

*Thallus* corticate.

*Ascomata* solitary or aggregated. *Ostioles* apical or eccentric. *Wall* hyphal (textura intricata), carbonized. *Hamathecium* clear or interspersed with oil droplets, filaments thin, anastomosing paraphysoids. *Ascospores* distoseptate, usually also with euseptate walls, mostly brown, 3–5-septate, large, often with longitudinal folds in the wall, rarely colourless.

*Pycnidia* unknown.

*Chemistry.* Lichexanthone rarely present.

*Discussion.* *Architrypethelium* externally resembles species of *Astrothelium*, including those previously placed in the genera *Laurera*, *Cryptothelium*, and *Trypethelium*, but differs anatomically by its 3-septate, extremely large ascospores, which are hyaline to dark brown when mature and do not have the diamond-shaped lumina typical of *Astrothelium* when mature (Aptroot 1991). Phylogenetically it can be considered the sister clade to *Astrothelium*. Species of *Pyrenula* with large, 3-septate ascospores can be confused with *Architrypethelium* but, in addition to the differences in hamathecium structure, are distinguished as follows: *Pyrenula subpraelucida* has ascospores with small terminal lumina against the endospore, while in *P. laii* and *P. montocensis*, the ascospores have angular lumina with very thick septa and lateral walls. In addition, 3-septate ascospores in *Pyrenula* are less than 90 µm long while in *Architrypethelium* they are usually longer than 90 µm (up to 160 µm).

### **Key to the species of *Architrypethelium***

- 1 Ascospores remaining hyaline. . . . . 2  
Ascospores soon becoming brown . . . . . 5
- 2(1) *Ascomata* sessile, very large (up to 3 mm diam.) (this synopsis; Fig. 11D) . . . . .  
. . . . . ***Architrypethelium grande***  
*Ascomata* immersed or in erumpent prominent thallus warts, smaller (usually not exceeding 1 mm diam.) . . . . . 3
- 3(2) *Ascomata* completely immersed between bullate thallus warts, not visible except for ascospores accumulating around ostiole (Lücking *et al.* 2016b; Fig. 11E) . . . . .  
. . . . . ***Architrypethelium lauropaluanum***  
*Ascomata* erumpent to prominent but at least partly covered by thallus; thallus otherwise smooth to uneven . . . . . 4
- 4(3) Thallus with lichexanthone (this synopsis; Fig. 11F & G) . . . . .  
. . . . . ***Architrypethelium hyalinum***  
Thallus without lichexanthone (Flakus *et al.* 2016; Fig. 11H) . . . . .  
. . . . . ***Architrypethelium penuriixanthum***
- 5(1) Ostiole eccentric; *ascomata* sometimes with fused ostioles (this synopsis; Fig. 11I & J) . . . . .  
. . . . . ***Architrypethelium nitens***  
Ostiole apical; *ascomata* solitary . . . . . 6
- 6(5) Hamathecium interspersed (this synopsis; Fig. 11K) . . . . . ***Architrypethelium columbianum***  
Hamathecium clear (this synopsis; Fig. 11L) . . . . . ***Architrypethelium uberinum***

**Architrypethelium columbianum (Nyl.)  
Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816650

*Trypethelium columbianum* Nyl., *Ann. Sci. Nat. Bot. sér. 5*, **3**: 347 (1867); type: Colombia, Rio Negro, *Lindig* 35 (H-Nyl 321!—lectotype, designated here; BM!, BR—isolectotypes).

(Fig. 11K)

*Thallus* corticate, light olive-grey, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.7–1.2 mm diam., sessile, covered by a brownish thallus layer. *Wall* thick, fully carbonized. *Hamathecium* inspersed. *Ascospores* 2–4 per ascus, 120–155 × 35–50 µm, oblong-ellipsoid, 3-septate, outer lumina much smaller than inner lumina, lumina rounded in the corners, often with needle-like crystals, wall 3–5 µm thick, surrounded by a gelatinous sheath 7–10 µm wide, becoming dark brown, I–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Colombia).

*Discussion.* This species differs from *Architrypethelium uberinum* mainly in the inspersed hamathecium.

**Architrypethelium grande (Kremp.)  
Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816651

*Ascidium grande* Kremp., *Flora* **59**: 249 (1876); *Phaeotrema grande* (Kremp.) Zahlbr., *Catal. Lich. Univ.* **2**: 607 (1923); type: Brazil, Rio de Janeiro, *Glaziou* 6271 (M!—lectotype, designated here; BM!, C!—isolectotypes).

(Fig. 11D)

*Thallus* corticate, olive-green to yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 1–3 mm diam., sessile, covered by a light, orange-brown layer. *Wall* thick, fully carbonized, with thick, gelatinous

cortex composed of anastomosing hyphae. *Hamathecium* clear. *Ascospores* 2–4 per ascus, 120–165 × 40–50 µm, oblong-ellipsoid, 3-septate, lumina angular to almost rounded in the corners, often with needle-like crystals, wall 3–5 µm thick, surrounded by a gelatinous sheath 3–5 µm wide, hyaline (although given as becoming pale olive-brown in the protologue), I–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Brazil).

*Discussion.* This species differs from the other two species with hyaline ascospores, *Architrypethelium hyalinum* and *A. penuriixanthum*, in the sessile ascomata, and from *A. hyalinum* also in the absence of lichexanthone. Krempelhuber (1876) described the ascospores as becoming pale olive-brown, but we observed only hyaline ascospores in the type material. The only species with brown ascospores, an apical ostiole and clear hymenium is *A. uberinum*, from which *A. grande* also differs markedly in the sessile, orange-brown perithecial warts.

**Architrypethelium hyalinum Aptroot**

In Aptroot *et al.*, *Biblioth. Lichenol.* **98**: 37 (2008); type: Costa Rica, Puntarenas, Las Cruces Biological Station, trail to Rio Java, *Sipman* 53229 (B!—holotype; INB-3993295!—isotype).

(Fig. 11F & G)

*Thallus* corticate, olive-green, smooth to uneven, sometimes gall-like.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.7–1.5 mm diam., prominent, irregularly covered by thallus except for the black ostioles which are sometimes surrounded by an ochraceous zone. *Wall* 200–400 µm thick, fully carbonized. *Hamathecium* clear. *Ascospores* 4–8 per ascus, 100–150 × 30–50 µm, oblong-ellipsoid, often curved, 3-septate, outer lumina much smaller than inner lumina, lumina rounded in the corners, often with needle-like crystals, constricted at the median septum, wall 3–5 µm thick,

surrounded by a gelatinous sheath 7–15 µm wide, hyaline, I–.

*Chemistry.* Thallus and ascomata UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropical (previously reported from Costa Rica and Brazil).

*Discussion.* This *Architrypethelium* has among the largest 3-septate ascospores in the family. It is also the only species in the genus with lichexanthone. The species could be mistaken for a *Trypethelium* except for the extremely large ascospores.

*New country records.* **Puerto Rico:** Distr. Mayagüez: Reserva Forestal Maricao, 1989, Aptroot & Aptroot 24960, 25322 (ABL).—**Venezuela:** Falcon: Miranda, 1979, Sipman & van der Werff 10902 (B).—**Colombia:** Santuario, 1989, Wolf et al. 5992 (ABL, COL).—**Guyana:** Demerara-Berbice District: Mabura Hill, 1988, Bleij & Biesmeijer s. n. (ABL).

### **Architrypethelium nitens (Fée) Aptroot**

In Aptroot et al., *Biblioth. Lichenol.* **98**: 38 (2008).—*Verrucaria nitens* Fée, *Essai Crypt. Écorc.*: 88 (1824); type: South America, on “cinchona” (L!—lectotype; Aptroot et al., *Biblioth. Lichenol.* **98**: 38 (2008)).

*Pyrenastrum seminudum* Mont., *Ann. Sci. Nat. Bot. sér. 2*, **19**: 64 (1843).—*Architrypethelium seminudum* (Montagne) Aptroot, *Biblioth. Lichenol.* **44**: 120 (1991); type: French Guiana, Leprieur 588 (PC!—holotype).

*Pleurothelium ernstianum* Müll. Arg., *Flora* **60**: 475 (1877).—*Parathelium ernstianum* (Müll. Arg.) Müll. Arg., *Hedwigia* **34**: 36 (1895); type: Venezuela, Caracas, Ernst 130 (G!—holotype).

*Parathelium superans* Müll. Arg., *Bull. Soc. Roy. Bot. Belg.* **32**(1): 165 (1893).—*Splanchnonema superans* (Müll. Arg.) O. Erikss., *Opera Bot.* **60**: 133 (1981); type: Costa Rica, Puntarenas, Boruca, Tonduz s. n. (G!—lectotype, designated here; BR!, G!—isolectotypes; Pitier, *Pl. Costaric. Exs.* 6253).

(Fig. 11I & J)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* pleuro- to astrothelioid, solitary with eccentric ostioles or few chambers joined with eccentric, fused ostioles, 1.0–1.5 mm diam., erumpent to prominent, covered by thallus except for the blackish ostiolar area. *Wall* thick, fully carbonized.

*Hamathecium* clear. *Ascospores* 8 per ascus, 90–150 × 25–50 µm, oblong-ellipsoid, 3-septate, outer lumina much smaller than inner lumina, lumina rounded in the corners, often with needle-like crystals, wall 3–5 µm thick, surrounded by a gelatinous sheath 7–10 µm wide, becoming dark brown, I–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Costa Rica, Venezuela, Guyana, French Guiana and Brazil).

*New country records.* **Puerto Rico:** Mayagüez: Reserva Forestal Maricao, 1989, Aptroot & Aptroot 24930, 25420, 25040, 25002 (ABL).—**Panamá:** Panamá: Alto de Campana, 2001, Etayo 18782 (ABL).

### **Architrypethelium uberinum (Fée) Aptroot**

*Biblioth. Lichenol.* **44**: 122 (1991).—*Porina uberina* Fée, *Essai Crypt. Écorc.*: 83 (1824).—*Porophora uberina* (Fée) Spreng., *Syst. Orb. Veget.* **4**(1): 242 (1827).—*Pyrenula uberina* (Fée) Fée, *Essai Crypt. Écorc. Suppl.*: 84 (1837).—*Pertusaria uberina* (Fée) A. Massal., *Ric. Auton. Lich. Crost.*: 190 (1852).—*Trypethelium uberinum* (Fée) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* **5**: 141 (1857).—*Verrucaria uberina* (Fée) Trevis., *Consp. Verruc.*: 8 (1860).—*Stromatothelium uberinum* (Fée) Trevis., *Flora* **44**: 20 (1861).—*Pseudopyrenula uberina* (Fée) Vain., *Ann. Acad. Sci. Fem., ser. A* **15**(6): 353 (1921); type: Peru, “cort. cinchonae” (G!—holotype).

*Trypethelium uberinoides* Nyl., *Flora* **41**: 381 (1858); type: Mexico, Orizaba, Müller (PC—lectotype, designated here).

*Verrucaria megalospora* Kremp., *Flora* **59**: 525 (1861).—*Parathelium megalosporum* (Kremp.) Müll. Arg., *Hedwigia* **32**: 134 (1893); type: Brazil, Rio de Janeiro, Glaziou 6276 (M!—holotype; BM!, UPS!—isotypes).

(Fig. 11L)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, 1.0–1.7 mm diam., erumpent to prominent, covered by thallus except for the blackish ostiolar area surrounded by a whitish rim. *Wall* thick, fully carbonized. *Hamathecium* clear. *Ascospores* 2–4 per ascus, 120–155 × 35–50 µm, oblong-ellipsoid, 3-septate, outer lumina much smaller than inner lumina,



lumina rounded in the corners, often with needle-like crystals, wall 3–5 µm thick, surrounded by a gelatinous sheath 7–10 µm wide, becoming dark brown, I–.

**Chemistry.** Thallus and ascomata UV–, K–. TLC: no substances detected.

**Distribution.** Possibly pantropical; previously reported from Costa Rica, Peru, and Brazil. Incorrectly reported from Sri Lanka but now found in Oceania.

**New country records. American Samoa:** Tutuila: Pago Pago, 1970, *Degelius* P-279 (UPS).—**French Polynesia:** Tahiti: Taravao, 1970, *Degelius* P-371 (UPS).

### **Astrothelium** Eschw.

**Syst. Lich.:** 18 (1824); type: *Astrothelium conicum* Eschw. [= *A. cinnamomeum* (Eschw.) Müll. Arg., lectotype; Mas-salongo, *Atti I. R. Istitut. Veneto, Ser. 3, 5:* 335, 1860].

*Meissneria* Fée, *Essai Crypt. Écorc. Suppl.:* 66 (1837), *nom. illeg., non Meissneria* DC. (1828); type: *Trypethelium deforme* Fée (as *Meissneria varia* Fée, holotype).

*Laurera* Reichenb., *Deutsch. Bot. Herb.-Buch:* 15 (1841), *nom. cons., nom. nov. pro Meissneria* Fée; type: *Trypethelium deforme* Fée (as *Meissneria varia* Fée, holotype).

*Heufleria* Trevis., *Spighe e Paglie:* 19 (1853); type: *Heufleria conica* (Eschw.) Trevis. (= cf. *Astrothelium cinnamomeum*, holotype).

*Meristosporum* A. Massal., *Atti I. R. Istitut. Veneto, Ser. 3, 5:* 327 (1860); type: *Meristosporum javanicum* A. Massal. (holotype).

*Cryptothelium* A. Massal., *Atti I. R. Istitut. Veneto, Ser. 3, 5:* 335 (1860); type: *Cryptothelium sepulchrum* (Mont.) A. Massal. (holotype).

*Leightonia* Trevis., *Flora* 44: 19 (1861), *nom. illeg., non. Trevis.* (1853); type: *Leightonia porosa* (Ach.) Trevis. (holotype).

*Campylothelium* Müll. Arg., *Flora* 66: 245 (1883); type: *Campylothelium puiggarii* Müll. Arg. (holotype).

*Thallus* corticate, mostly olive-green.

**Ascomata** simple or aggregated or forming pseudostromata, immersed to prominent, with the pseudostromata often of a different structure and colour than the thallus. **Ostioles** apical or eccentric, simple or fused. **Wall** hyphal (textura intricata), usually carbonized. **Hamathecium** clear or interspersed with oil droplets, filaments thin, anastomosing paraphysoids. **Ascospores** distoseptate, hyaline, transversely septate or muriform.

**Pycnidia** occasionally present.

**Chemistry.** Lichexanthone, red crystals and/or anthraquinones regularly present, in or on the thallus, pseudostromata and/or ostioles.

**Discussion.** The type species, *Astrothelium conicum*, was not validly published when the genus *Astrothelium* was published (Eschweiler 1824), but only later by Eschweiler (in Martius 1833); however, this does not render the description of the genus invalid. Several other species were described in the genus prior to *A. conicum*, which makes the lectotypification with the latter slightly unusual, but not invalid either. The synonymy of *A. conicum* (the type species of the genus) with *A. cinnamomeum* was confirmed by combining the observations of Müller (1884: 270), who observed the ascospores, and Harris (1986: 59), who observed no ascospores but saw the negative reaction with UV.

### **Key to species of *Astrothelium* (including cross-references to species of *Bathelium*, *Nigrothelium*, and *Viridothelium*)**

#### **Main key to groups**

- 1 Ascospores transversely septate. . . . . 2
  - Ascospores (sub-)muriform . . . . . 5
- 2(1) Ascomata each with a separate, consistently apical ostiole (previously classified in *Trypethelium sensu* Harris 1986). . . . . 3
  - Ascomata either with a separate, eccentric to lateral ostiole or several ascomata with a fused ostiole which is then positioned apically relative to the ascomatal cluster but with individual channels originating eccentric or lateral from each individual ascoma or chamber (previously classified in *Astrothelium sensu* Harris 1986) . . . 4

- 3(2) Thallus and/or ascomata with external or internal, yellow to red pigment(s) (usually K+ red to purple) and/or with lichexanthone (then UV+ yellow) . . . . . **Group 1**  
Pigments and lichexanthone absent . . . . . **Group 2**
- 4(2) Thallus and/or ascomata with external or internal, yellow to red pigment(s) (usually K+ red to purple) and/or with lichexanthone (then UV+ yellow) . . . . . **Group 3**  
Pigments and lichexanthone absent . . . . . **Group 4**
- 5(1) Ascumata each with a separate, consistently apical ostiole (previously classified in *Laurera sensu* Harris 1986) . . . . . 6  
Ascumata either with a separate, eccentric to lateral ostiole or several ascumata with a fused ostiole which is then positioned apically relative to the ascumatal cluster but with individual channels originating eccentrically or laterally from each individual ascumata or chamber (previously classified in *Campylothelium sensu* Harris 1986 and *Cryptothelium sensu* Harris 1986) . . . . . 7
- 6(5) Thallus and/or ascumata with external or internal, yellow to red pigment(s) (usually K+ red to purple) and/or with lichexanthone (then UV+ yellow) . . . . . **Group 5**  
Pigments and lichexanthone absent . . . . . **Group 6**
- 7(5) Thallus and/or ascumata with external or internal, yellow to red pigment(s) (usually K+ red to purple) and/or with lichexanthone (then UV+ yellow) . . . . . **Group 7**  
Pigments and lichexanthone absent . . . . . **Group 8**

**Group 1: Ascospores transversely septate, ostiole apical, secondary substances present**

- 1 Lichexanthone present, thallus and/or ascumata UV+ yellow; pigment(s) present or absent. . . . . 2  
Lichexanthone absent, thallus and ascumata UV–; pigment(s) always present. . . . . 15
- 2(1) Pigments present in thallus and/or ascumata; lichexanthone on thallus; ascumata pseudostromatic, in irregular black lines . . . . . 3  
Pigments absent; lichexanthone on thallus and/or ascumata; ascumata variable . . . . . 4
- 3(2) Ascospores 3-septate, small (18–26 µm long); ascumata with external orange pigment, scattered laterally along pseudostromata (this synopsis; Fig. 12A & B) . . . . . **Astrothelium neogalbineum**  
Ascospores (3–)5-septate, large (90–115 µm long); ascumata with external purplish red pigment, scattered laterally along pseudostromata (Aptroot *et al.* 2016b; Fig. 12C) . . . . . **Astrothelium pictum**
- 4(2) Ascospores (5–)7(–9)-septate; hamathecium interspersed . . . . . 5  
Ascospores 3-septate; hamathecium clear or interspersed . . . . . 6
- 5(4) Lichexanthone on ascumata; ascumata solitary to irregularly confluent, erumpent, covered by thallus (this synopsis; Fig. 12D & E) . . . **Astrothelium cinereorosellum**  
Lichexanthone on pseudostromata; ascumata distinctly pseudostromatic (Lücking *et al.* 2016b; Fig. 12F). . . . . **Astrothelium fijiense**

- 6(4) Hamathecium inspersed; ascospores small (15–30 µm long) . . . . . 7  
 Hamathecium clear; ascospores small to medium-sized (15–70 µm long) . . . . . 10
- 7(6) Lichexanthone on ascomata only, absent from thallus; ascomata solitary to irregularly  
 confluent, largely immersed and covered by thallus (this synopsis; Fig. 12G & H) . . .  
 . . . . . **Astrothelium punctulatum**  
 Lichexanthone on thallus and ascomata or on thallus only . . . . . 8
- 8(7) Lichexanthone on thallus only, absent from ascomata; ascomata solitary but dense;  
 thallus gall-like (this synopsis; Fig. 12I) . . . . . **Astrothelium grossoides**  
 Lichexanthone on thallus and ascomata; thallus not gall-like . . . . . 9
- 9(8) Ascomata solitary, erumpent, whitish (Aptroot *et al.* 2016a; Fig. 12J) . . . . .  
 . . . . . **Astrothelium vulcanum**  
 Ascomata pseudostromatic, immersed in prominent pseudostromata that are often  
 partly covered by thallus (this synopsis; Fig. 12K & L) . . . **Astrothelium porosum**
- 10(6) Ascospores small (15–30 µm long) . . . . . 11  
 Ascospores (small to) medium-sized ((25–)30–70 µm long) . . . . . 14
- 11(10) Lichexanthone on ascomata only, absent from thallus; ascomata pseudostromatic,  
 immersed in prominent pseudostromata covered by thallus (Aptroot & Cáceres  
 2016; Fig. 13A) . . . . . **Astrothelium stromatofluorescens**  
 Lichexanthone on thallus and ascomata . . . . . 12
- 12(11) Ascomata solitary to irregularly confluent, erumpent, covered by thallus (this  
 synopsis; Fig. 13B–D) . . . . . **Astrothelium pulcherrimum**  
 Ascomata pseudostromatic, immersed in pseudostromata that are often partly covered  
 by thallus . . . . . 13
- 13(12) Pseudostromata well delimited, whitish, prominent to sessile (Lücking *et al.* 2016b;  
 Fig. 13E) . . . . . **Astrothelium leucosessile**  
 Pseudostromata not well delimited, covered by thallus, erumpent to prominent (this  
 synopsis; Fig. 13F–L) . . . . . **Astrothelium phlyctaena**
- 14(10) Ascospores 25–40 × 8–13 µm; ascomata solitary to irregularly confluent, erumpent to  
 prominent, covered by thallus (this synopsis; Fig. 14A & B) . . . . .  
 . . . . . **Astrothelium pupula**  
 Ascospores 60–70 × 16–18 µm; ascomata pseudostromatic, pseudostromata prominent,  
 whitish (Aptroot *et al.* 2016a; Fig. 14C) . . . . .  
 . . . . . **Astrothelium megochroleucum**
- 15(1) Ascospores 3-septate . . . . . 16  
 Ascospores 5–19-septate . . . . . 36
- 16(15) Ascospores medium-sized (50–65 µm long); medulla (ascomata) with internal, red  
 pigment; ascomata solitary to irregularly confluent, erumpent, covered by thallus  
 (this synopsis; Fig. 14D & E) . . . . . **Astrothelium thelotremoides**  
 Ascospores small to medium-sized (15–50 µm long); pigment external or internal,  
 yellow to red . . . . . 17



- 17(16) Hamathecium interspersed . . . . . 18  
 Hamathecium clear . . . . . 22
- 18(17) Ascomata with external, yellow to orange pigment mostly developed around the  
 ostiolar area; ascomata solitary to irregularly confluent, erumpent, covered by  
 thallus except for black ostiolar area . . . . . 19  
 Medulla (ascomata) with internal, red pigment; ascomata variable . . . . . 21
- 19(18) Ascomata with yellow pigment; ascomata diffusely pseudostromatic, pseudostromata  
 forming irregular lines (Aptroot *et al.* 2016a; Fig. 14F) . . . . .  
 . . . . . **Astrothelium neoinpersum**  
 Thallus and/or ascomata with orange pigment; ascomata solitary to irregularly  
 confluent . . . . . 20
- 20(19) Both thallus and ascomata with abundant orange pigment (this synopsis; Fig. 14G)  
 . . . . . **Astrothelium inspersaeneum**  
 Only ascomata with sparse orange pigment (Aptroot *et al.* 2016a; Fig. 14H) . . . . .  
 . . . . . **Astrothelium aenascens**
- 21(18) Ascospores 20–30 × 7–9 µm (Aptroot *et al.* 2016b; Fig. 14I) . . . . .  
 . . . . . **Astrothelium rubrocrystallinum**  
 Ascospores 30–50 × 14–16 µm (this synopsis; Fig. 14J) . . . . . **Astrothelium buckii**
- 22(17) Thallus and/or ascomata with external pigment(s) . . . . . 23  
 Medulla (ascomata) with internal pigment(s) . . . . . 31
- 23(22) Ascomata with external, red pigment(s) (this synopsis; Fig. 14K) . . . . .  
 . . . . . **Astrothelium coccineum**  
 Ascomata with external, yellow to orange pigment(s) . . . . . 24
- 24(23) Thallus grey, barely lichenized; ascomata distinctly pseudostromatic, pseudo-  
 stromata prominent to sessile, with orange cover strongly contrasting with thallus  
 (Lücking *et al.* 2016b; Fig. 14L) . . . . . **Astrothelium aurantiacocinereum**  
 Thallus olive-green, distinctly lichenized; ascomata solitary or pseudostromatic, if  
 pseudostromatic, then pseudostromata immersed to erumpent and in irregular,  
 often reticulate lines . . . . . 25
- 25(24) Ascospores very small (16–18 µm long); ascomata pseudostromatic, immersed,  
 pseudostromata in irregular, often reticulate lines, covered with pigment and  
 contrasting with olive-green thallus (Aptroot & Cáceres 2016; Fig. 15A) . . . . .  
 . . . . . **Astrothelium flavum**  
 Ascospores small (20–35 µm long) . . . . . 26
- 26(25) Ascospores 20–25(–27) × 6–10 µm; ascomata solitary or pseudostromatic . . . . . 27  
 Ascospores 25–35 × 10–12 µm; ascomata solitary to irregularly confluent, erumpent,  
 covered by thallus . . . . . 29
- 27(26) Ascomata solitary to irregularly confluent; pigment on thallus and ascomata (this  
 synopsis; Fig. 15B–F) . . . . . **Astrothelium aeneum**  
 Ascomata pseudostromatic, pseudostromata in irregular lines, covered with pigment  
 and contrasting with olive-green thallus . . . . . 28  
 If ascospores with reduced endospore, and thin septa and pigment, see *Viridothelium leptoseptatum*  
 (Aptroot *et al.* 2016b)

- 28(27) Thallus strongly bullate (Aptroot & Cáceres 2016; Fig. 15G) . . . . . **Astrothelium flavostromatum**  
 Thallus smooth to uneven (this synopsis; Fig. 15H & I) . . . . **Astrothelium kunzei**
- 29(26) Pigment orange, abundant (Flakus *et al.* 2016; Fig. 15J) . . . **Astrothelium megaenum**  
 Pigment yellow, sparse . . . . . 30
- 30(29) Ostioles partly lateral and fused; pigment K+ purple (Flakus *et al.* 2016; Fig. 15K) . . . .  
 . . . . . **Astrothelium pallidoflavum**  
 Ostioles consistently apical; pigment K+ red (this synopsis; Fig. 15L) . . . . .  
 . . . . . **Astrothelium subcatervarium**
- 31(22) Ascospores medium-sized (30–50 × 10–16 µm) . . . . . 32  
 Ascospores small (15–30 × 5–9 µm) . . . . . 34
- 32(31) Medullary pigment red (this synopsis) . . . . . **Astrothelium cartilagineum**  
 Medullary pigment yellow . . . . . 33
- 33(32) Thallus bullate (this synopsis; Fig. 16A & B) . . . . . **Astrothelium endochryseum**  
 Thallus smooth (Lücking *et al.* 2016b; Fig. 16C & D) . . **Astrothelium laevithalinum**
- 34(31) Ascomata solitary to irregularly confluent, erumpent, covered by thallus; medullary  
 pigment orange (Aptroot *et al.* 2016b; Fig. 16E) . . . . **Astrothelium aeneoides**  
 Ascomata pseudostromatic; pseudostromata blackish brown; medullary pigment  
 (pale) yellow . . . . . 35
- 35(34) Medullary pigment K+ red (this synopsis; Fig. 16F–I) . . . **Astrothelium degenerans**  
 Medullary pigment K– (this synopsis; Fig. 16J–L) . . . . . **Astrothelium feei**  
 If ascospores with reduced endospore and thin septa, see *Bathelium austroafricanum* (this synopsis;  
 ascospores 18–21 µm long, medullary pigment K+ purple) and *B. porinosporum* (Lücking *et al.* 2016b;  
 ascospores 20–30 µm long, medullary pigment K+ orange to cinnabar red)
- 36(15) Ascospores small to medium-sized (15–45 × 6–9 µm) . . . . . 37  
 Ascospores medium-sized to large (50–150 × 10–40 µm) . . . . . 39
- 37(36) Medulla (ascomata) with internal, red pigment; ascospores 9–13-septate; ascomata  
 pseudostromatic, exposed, forming irregular, reticulate lines or groups (this  
 synopsis; Fig. 17A) . . . . . **Astrothelium nigrorufum**  
 Medulla (ascomata) with internal, yellow to orange pigment; ascospores 5–9-  
 septate . . . . . 38
- 38(37) Hamathecium interspersed; medullary pigment K+ red; ascomata pseudostromatic,  
 pseudostromata erumpent to prominent, whitish (Aptroot *et al.* 2016a; Fig. 17B)  
 . . . . . **Astrothelium pseudodissimilum**  
 Hamathecium clear; medullary pigment K+ purple; ascomata pseudostromatic,  
 exposed, forming irregular, reticulate lines or groups (this synopsis;  
 Fig. 17C & D) . . . . . **Astrothelium dissimilum**  
 If ascospores with reduced endospore and thin septa, see *Bathelium albidoporum* (this synopsis; ascospores  
 5–7-septate), *B. nigroporum* (this synopsis; ascospores 5–9-septate), and *B. porinosporum* (Lücking  
*et al.* 2016b; ascospores 3–5-septate)

39(36) Ascospores medium-sized (50–90 µm long) ..... 40  
 Ascospores large (110–150 µm long)..... 41

40(39) Ascomata with scattered, external, pink pigment, solitary to irregularly confluent, immersed in large thallus verrucae; hamathecium inspersed; ascospores 50–65 × 10–17 µm (Aptroot & Cáceres 2016; Fig. 17E) .....  
 ..... **Astrothelium decemseptatum**  
 Medulla (ascomata) with internal, yellow pigment; ascomata pseudostromatic, pseudostromata prominent, covered by thallus except black ostiolar areas; hamathecium clear; ascospores 55–90 × 13–28 µm (this synopsis; Fig. 17F–H) .....  
 ..... **Astrothelium luridum**

41(39) Ascomata with scattered, external, pink pigment, solitary, immersed; ascospores 17–22 µm broad, 13–19-septate (this synopsis; Fig. 17I).....  
 ..... **Astrothelium calosporum**  
 Ascomata with external and internal yellow pigment; ascospores 30–37µm broad, 7–11-septate (Aptroot *et al.* 2016a; Fig. 17J–L) ..... **Astrothelium rimosum**

**Group 2: Ascospores transversely septate, ostiole apical, secondary substances absent**

1 Ascospores 3-septate ..... 2  
 Ascospores (3–)5–15-septate ..... 25

2(1) Ascospores small to medium-sized (15–45(–50) × 6–16 µm) ..... 3  
 Ascospores medium-sized to large ((45–)50–120 × 15–35 µm) ..... 19

3(2) Hamathecium inspersed ..... 4  
 Hamathecium clear ..... 6

4(3) Ascospores (25–)30–40 µm long; ascomata in irregular groups to pseudostromatic, pseudostromata erumpent, white, contrasting with olive-green thallus (Aptroot *et al.* 2016a; Fig. 18A) ..... **Astrothelium perspersum**  
 Ascospores 15–25(–30) µm long ..... 5

5(4) Ascomata solitary, erumpent, with white cover (Flakus *et al.* 2016; Fig. 18B) .....  
 ..... **Astrothelium subscoria**  
 Ascomata irregularly grouped to pseudostromatic, immersed to erumpent, mostly exposed, brown-black (this synopsis; Fig. 18C–E) ..... **Astrothelium scoria**

6(3) Ascospores I+ violet ..... 7  
 Ascospores I– ..... 8

7(6) Ascomata solitary, immersed, covered by thallus except dark ostiolar area (this synopsis; Fig. 18G) ..... **Astrothelium infossum**  
 Ascomata distinctly pseudostromatic, pseudostromata erumpent, brown-black, with pale ostiolar areas (this synopsis; Fig. 18H & I) . . . **Astrothelium infuscatulum**



- 8(6) Ascospores  $15\text{--}28 \times 7\text{--}10\text{--}(12) \mu\text{m}$  (*Astrothelium nitidiusculum* complex) . . . . . 9  
 Ascospores  $26\text{--}46 \times (7\text{--})10\text{--}16 \mu\text{m}$  . . . . . 15
- 9(8) Ascomata pseudostromatic; pseudostromata either prominent or contrasting with thallus in colour . . . . . 10  
 Ascomata solitary to irregularly confluent or grouped but not prominent or contrasting with thallus . . . . . 13  
 If ascomata solitary to irregularly confluent (dense), prominent to sessile and completely exposed and black, see *Nigrovothelium tropicum* (this synopsis; thallus smooth to uneven) and *N. bullatum* (Lücking *et al.* 2016*b*; thallus verrucose-bullate)
- 10(9) Pseudostromata prominent, partly covered by thallus and hence not strongly contrasting with thallus in colour (this synopsis; Fig. 18J) . . . **Astrothelium bicolor**  
 Pseudostromata immersed to erumpent and more or less levelled with thallus, often forming irregular to reticulate lines or groups, contrasting with thallus in colour (either dark or whitish) . . . . . 11
- 11(10) Pseudostromata whitish (this synopsis; Fig. 18K & L) . . . . **Astrothelium rufescens**  
 Pseudostromata exposed, brown-black . . . . . 12
- 12(11) Pseudostromata forming distinct, compact groups laterally covered by thallus (Lücking *et al.* 2016*b*; Fig. 19A) . . . . . **Astrothelium subendochryseum**  
 Pseudostromata diffuse, exposed (this synopsis; Fig. 19B) . . . **Astrothelium nigratum**
- 13(9) Ascomata forming irregular groups, with rather broad, brown-black ostiolar area (this synopsis; Fig. 19C & D) . . . . . **Astrothelium meiothorum**  
 Ostiolar areas not broad . . . . . 14
- 14(13) Ascomata covered by olive-green thallus (this synopsis; Fig. 19E) . . . . .  
 . . . . . **Astrothelium ceratinum**  
 Ascomata with broad white area surrounding the ostiole or entirely white (this synopsis; Fig. 19F–L) . . . . . **Astrothelium nitidiusculum**
- 15(8) Ascospores  $36\text{--}46 \times 14\text{--}16 \mu\text{m}$ ; ascomata solitary, erumpent, covered by thallus and with pale ring surrounding the dark ostiolar spot (this synopsis; Fig. 20A & B) . . . . .  
 . . . . . **Astrothelium floridanum**  
 Ascospores  $26\text{--}39 \times 7\text{--}14 \mu\text{m}$ ; ascomata variable . . . . . 16
- 16(15) Ascomata pseudostromatic, pseudostromata exposed, immersed and levelled with thallus, forming irregular to reticulate lines or groups . . . . . 17  
 Ascomata solitary, covered by thallus . . . . . 18
- 17(16) Thallus verrucose-papillate (this synopsis; Fig. 20C) . . . . **Astrothelium scoriiothelium**  
 Thallus smooth to coarsely uneven (Aptroot & Cáceres 2016; Fig. 20D) . . . . .  
 . . . . . **Astrothelium disjunctum**
- 18(16) Thallus and ascomata finely verrucose; ascomata immersed to erumpent, numerous and dense (this synopsis; Fig. 20E) . . . . . **Astrothelium papulosum**  
 Thallus and ascomata smooth to uneven; ascomata erumpent to prominent, scattered (Aptroot & Cáceres 2016; Fig. 20F) . . . . . **Astrothelium solitarium**

- 19(2) Hamathecium inspersed . . . . . 20  
 Hamathecium clear . . . . . 22
- 20(19) Ascospores 45–62 × 15–22 μm; thallus uneven-bullate; ascomata solitary, erumpent, covered by thallus, with pale ring surrounding the dark ostiolar spot (Flakus *et al.* 2016; Fig. 20G) . . . . . **Astrothelium inspersotuberculosis**  
 Ascospores 85–120 × 22–35 μm; thallus and ascomata variable . . . . . 21
- 21(20) Ascospores 85–95 × 22–25 μm; thallus uneven-verrucose; ascomata solitary, prominent, exposed, with gently sloping sides (Aptroot *et al.* 2016a; Fig. 20H) . . . . .  
 . . . . . **Astrothelium clypeatum**  
 Ascospores 100–120 × 30–35 μm; thallus uneven-verrucose; ascomata confluent, erumpent to prominent, exposed, with gently to steeply sloping sides (Aptroot *et al.* 2016a; Fig. 20I) . . . . . **Astrothelium megatropicum**
- 22(19) Ascomata prominent, completely exposed (this synopsis; Fig. 20J) . . . . .  
 . . . . . **Astrothelium phaeothelium**  
 Ascomata immersed to erumpent, covered by thallus, with pale ring surrounding the dark ostiolar spot . . . . . 23
- 23(22) Thallus verrucose-papillose; ascomata solitary to irregularly confluent, prominent to sessile (Aptroot *et al.* 2016a; Fig. 20K) . . . . . **Astrothelium pseudannulare**  
 Thallus uneven to shallowly bullate . . . . . 24
- 24(23) Thallus coarsely uneven to shallowly bullate; ascomata solitary to irregularly grouped in large verrucae (this synopsis; Fig. 20L) . . . . . **Astrothelium tuberculosum**  
 Thallus smooth to uneven; ascomata solitary (this synopsis; Fig. 21A) . . . . .  
 . . . . . **Astrothelium annulare**
- 25(1) Ascospores medium-sized (29–59(–80) × 8–17 μm) . . . . . 26  
 Ascospores large (85–220 × (8–)20–45 μm) . . . . . 30  
 If ascospores with reduced endospore and weakly I+ blue-violet, see *Viridothelium cinereooglaucescens* (this synopsis; ascospores 50–80 × 8–15 μm), *V. induum* (this synopsis; ascospores 90–105 × 12–16 μm), *V. inspersum* (Aptroot *et al.* 2016a; hamathecium inspersed, ascospores 60–75 × 12–17 μm), *V. kimabaluense* (Aptroot *et al.* 2016a; ascospores 100–150 × 18–23 μm), and *V. virens* (this synopsis; ascospores 38–52 × 7–10 μm)
- 26(25) Hamathecium inspersed; ascospores 50–59 μm long, with thickened median septum; thallus verrucose-bullate; ascomata solitary to irregularly confluent, erumpent, whitish around ostiole (this synopsis; Fig. 21B) . . . . **Astrothelium galligenum**  
 Hamathecium clear; ascospores 29–52 μm long, without thickened median septum . . . .  
 . . . . . 27
- 27(26) Ascomata in irregular groups to pseudostromatic, groups or pseudostromata erumpent to prominent . . . . . 28  
 Ascomata solitary to irregularly confluent, immersed to erumpent . . . . . 29
- 28(27) Pseudostromata whitish (this synopsis; Fig. 21C) . . . . . **Astrothelium ubianense**  
 Pseudostromata brownish (this synopsis) . . . **Astrothelium pseudoplatystomum**

- 29(27) Ascomata with erumpent part exposed, blackish (this synopsis; Fig. 21D) . . . . .  
 . . . . . **Astrothelium trypethelizans**  
 Ascomata covered by thallus except dark ostiole (this synopsis; Fig. 21E) . . . . .  
 . . . . . **Astrothelium nitidulum**
- 30(25) Hamathecium inspersed . . . . . 31  
 Hamathecium clear . . . . . 35
- 31(30) Ascospores 9–13-septate, occasionally with a longitudinal septum in one or several  
 cells, 17–22 µm broad; ascomata solitary to irregularly confluent, immersed to  
 erumpent, covered by thallus with broad whitish area around the dark ostiolar spot  
 (this synopsis; Fig. 21F) . . . . . **Astrothelium macrosporum**  
 Ascospores 5–9-septate, lacking longitudinal septa, 29–45 µm broad; ascomata  
 variable. . . . . 32
- 32(31) Ascospores 180–220 × 40–45 µm, 5–9-septate; ascomata grouped in large thallus  
 verrucae (this synopsis; Fig. 21G) . . . . . **Astrothelium pustulatum**  
 Ascospores 100–170 × 29–40 µm, 5-septate; ascomata variable . . . . . 33
- 33(32) Ascospores curved; ascomata grouped (Aptroot & Cáceres 2016; Fig. 21H) . . . . .  
 . . . . . **Astrothelium curvisporum**  
 Ascospores straight; ascomata solitary to irregularly confluent . . . . . 34
- 34(33) Ascomata solitary, prominent to sessile, covered by thallus except dark ostiolar area  
 (Aptroot *et al.* 2016a; Fig. 21I) . . . . . **Astrothelium sipmanii**  
 Ascomata solitary to irregularly confluent, erumpent, upper part exposed (Aptroot  
*et al.* 2016a; Fig. 21J) . . . . . **Astrothelium pseudomegalophthalmum**
- 35(30) Ascospores 140–190 µm long, 11–19-septate; ascomata solitary to irregularly  
 confluent . . . . . 36  
 Ascospores 85–120 µm long, 3–17-septate; ascomata irregularly grouped to  
 pseudostromatic . . . . . 37
- 36(35) Thallus verrucose-bullate; ascomata erumpent to prominent, covered by thallus  
 except broad, blackened ostiolar area (this synopsis; Fig. 21K) . . . . .  
 . . . . . **Astrothelium basilicum**  
 Thallus smooth; ascomata immersed, completely covered by thallus (this synopsis;  
 Fig. 21L) . . . . . **Astrothelium spectabile**
- 37(35) Ascospores 20–32 µm broad, 3–7-septate; thallus verrucose-bullate; ascomata  
 exposed, brown-black, groups or pseudostromata levelled with thallus (this  
 synopsis; Fig. 22A & B) . . . . . **Astrothelium megalophthalmum**  
 Ascospores 8–16 µm broad, 9–17-septate; thallus smooth to uneven; ascomata  
 covered by thallus, groups or pseudostromata erumpent to prominent (this  
 synopsis; Fig. 22C & D) . . . . . **Astrothelium olivaceofuscum**



**Group 3: Ascospores transversely septate, ostiole lateral, secondary substances present**

- 1 Lichexanthone present, thallus and/or ascomata UV+ yellow; pigment(s) present or absent. . . . . 2  
 Lichexanthone absent, thallus and ascomata UV–; pigment(s) always present . . 34
- 2(1) Pigments present on/in thallus and/or ascomata; lichexanthone on thallus only. . . 3  
 Pigments absent; lichexanthone on thallus and/or ascomata . . . . . 10
- 3(2) Ascospores 9–11-septate, 50–75 × 12–22 µm; thallus with external, orange pigment (absent on ascomata); ascomata solitary to irregularly confluent, erumpent, covered by thallus except dark ostiolar area (Aptroot *et al.* 2016a; Fig. 22E). . . . . **Astrothelium dicoloratum**  
 Ascospores 3-septate, 21–55 × 7–23 µm; ascomata with external, yellow-orange pigment (absent on thallus) . . . . . 4
- 4(3) Hamathecium inspersed; ascospores 20–25 × 9–11 µm; groups of fused ascomata dispersed to irregularly confluent (Aptroot *et al.* 2016a; Fig. 22F) . . . . . **Astrothelium inspersogalbineum**  
 Hamathecium clear; ascospores variable in size . . . . . 5
- 5(4) Ascospores 21–28 × 7–11 µm . . . . . 6  
 Ascospores 28–55 × 10–23 µm . . . . . 7
- 6(5) Ascomata pseudostromatic; pseudostromata prominent, containing one or several groups of fused ascomata, covered with orange pigment (this synopsis; Fig. 22G–K). . . . . **Astrothelium macrocarpum**  
 Ascomata solitary to irregularly confluent, erumpent, containing a single group of fused ascomata (Luangsaphabool *et al.* 2016; Fig. 22L) . . . . . **Astrothelium flavocoronatum**
- 7(5) Ascospores 37–55 × 15–23 µm; ascomata pseudostromatic, pseudostromata erumpent, containing several groups of fused ascomata, covered with orange pigment (this synopsis; Fig. 23A & B) . . . . . **Astrothelium ochrothelium**  
 Ascospores 28–35 × 10–15 µm . . . . . 8
- 8(7) Thallus strongly folded-bullate, whitish; groups of fused ascomata dispersed, immersed, with yellow-orange pigment around ostiolar area (this synopsis; Fig. 23C) . . . . . **Astrothelium versicolor**  
 Thallus smooth to uneven, light olive-brown to olive-green; ascomata pseudostromatic . . . . . 9
- 9(8) Pseudostromata immersed to erumpent, containing several groups of fused ascomata, forming irregular to reticulate lines covered with yellow-orange pigment (this synopsis; Fig. 23D). . . . . **Astrothelium aureomaculatum**  
 Pseudostromata erumpent to prominent, each containing one group of fused ascomata, covered by orange pigment (this synopsis; Fig. 23E). . . . . **Astrothelium grossum**
- 10(2) Ascospores 3-septate, rarely 3(–5)-septate . . . . . 11  
 Ascospores (3–)5–11-septate . . . . . 24

- 11(10) Ascospores small to medium-sized ( $20\text{--}52 \times 6\text{--}17 \mu\text{m}$ ) . . . . . 12  
 Ascospores medium-sized to large ( $50\text{--}120 \times 17\text{--}40 \mu\text{m}$ ) . . . . . 20
- 12(11) Ascospores  $30\text{--}52 \times 10\text{--}17 \mu\text{m}$  . . . . . 13  
 Ascospores  $20\text{--}30 \times 6\text{--}11 \mu\text{m}$  . . . . . 15
- 13(12) Hamathecium inspersion, inspersion dirty yellow-brown; lichexanthone on ascomata only; ascomata pseudostromatic, pseudostromata prominent, containing one or several groups of fused ascomata (Lücking *et al.* 2016b; Fig. 23F) . . . . .  
 . . . . . **Astrothelium sordithecium**  
 Hamathecium clear; lichexanthone on thallus and ascomata; ascomata crowded or indistinctly pseudostromatic, pseudostromata immersed to erumpent, containing one or several groups of fused ascomata . . . . . 14
- 14(13) Ascomata solitary or in dispersed, diffuse pseudostromata, conical with flattened top, whitish (this synopsis; Fig. 23G) . . . . . **Astrothelium leucothelium**  
 Ascomata crowded, hemispherical to wart-shaped, covered by thallus (this synopsis; Fig. 23H & I) . . . . . **Astrothelium chrysostomum**
- 15(12) Lichexanthone on thallus and ascomata; hamathecium inspersion or clear; ascospores  $20\text{--}26 \mu\text{m}$  long . . . . . 16  
 Lichexanthone on ascomata only; hamathecium clear; ascospores ( $20\text{--}$ ) $23\text{--}30 \mu\text{m}$  long . . . . . 18
- 16(15) Hamathecium inspersion; ascomata diffusely pseudostromatic, erumpent, with whitish cover (Luangsaphabool *et al.* 2016; Fig. 23J) . . . . **Astrothelium neovariolosum**  
 Hamathecium clear . . . . . 17
- 17(16) Groups of fused ascomata dispersed, immersed to erumpent (this synopsis; Fig. 23K & L) . . . . . **Astrothelium laevigatum**  
 Ascomata pseudostromatic, pseudostromata prominent, often whitish, containing one or several groups of fused ascomata (this synopsis; Fig. 24A–D) . . . . .  
 . . . . . **Astrothelium variolosum**
- 18(15) Ascomata diffusely pseudostromatic, pseudostromata erumpent, covered by thallus, containing one or several groups of fused ascomata; ascospores  $20\text{--}25 \mu\text{m}$  (Lücking *et al.* 2016b; Fig. 24E) . . . . . **Astrothelium subinterjectum**  
 Ascomata distinctly pseudostromatic, pseudostromata prominent, with white or grey cover contrasting with the olive-green thallus, containing one or several groups of fused ascomata . . . . . 19
- 19(18) Thallus with pseudocyphellae; pseudostromata grey (this synopsis; Fig. 24F & G) . . . .  
 . . . . . **Astrothelium pseudocyphellatum**  
 Thallus lacking pseudocyphellae; pseudostromata whitish (this synopsis; Fig. 24H & I) . . . . .  
 . . . . . **Astrothelium interjectum**
- 20(11) Ascospores  $100\text{--}130 \times 35\text{--}45 \mu\text{m}$ ; groups of fused ascomata dispersed to aggregate, immersed–erumpent, covered by thallus except for whitish ostiolar area (Aptroot *et al.* 2016a; Fig. 24J) . . . . . **Astrothelium ultralucens**  
 Ascospores  $50\text{--}75 \times 14\text{--}26 \mu\text{m}$  . . . . . 21

- 21(20) Hamathecium interspersed; ascomata diffusely pseudostromatic, pseudostromata erumpent, whitish, containing one or several groups of fused ascomata (this synopsis; Fig. 24K & L) . . . . . **Astrothelium leucoconicum**  
Hamathecium clear; ascomata variable . . . . . 22
- 22(21) Lichexanthone on thallus and ascomata; groups of fused ascomata dispersed, immersed to erumpent, with broad, dark ostiolar area (Flakus *et al.* 2016; Fig. 25A) . . . . . **Astrothelium nigrocacuminum**  
Lichexanthone on ascomata only; ascomata variable . . . . . 23
- 23(22) Ascomata distinctly pseudostromatic, pseudostromata erumpent, with white cover contrasting with the olive-green thallus, containing one or several groups of fused ascomata; ascospores 60–70 × 17–20 µm (Aptroot *et al.* 2016b; Fig. 25B) . . . . . **Astrothelium sinuosum**  
Groups of fused ascomata dispersed, immersed, with broad, dark ostiolar area; ascospores 50–60 × 14–17 µm (Lücking *et al.* 2016b; Fig. 25C) . . . . . **Astrothelium obtectum**
- 24(10) Ascospores small (20–30 × 6–11 µm), 3–5-septate . . . . . 25  
Ascospores medium-sized to large (30–110 × 11–25 µm), 5–11-septate . . . . . 27
- 25(24) Lichexanthone on ascomata only; ascomata distinctly pseudostromatic, pseudostromata erumpent, with white cover contrasting with the olive-green thallus, containing one or several groups of fused ascomata (this synopsis; Fig. 25D) . . . . . **Astrothelium eustomum**  
Lichexanthone on thallus and ascomata; ascomata variable . . . . . 26
- 26(25) Ascomata distinctly pseudostromatic, pseudostromata erumpent, with white cover contrasting with the olive-green thallus (Luangsaphabool *et al.* 2016; Fig. 25E) . . . . . **Astrothelium neglectum**  
Ascomata indistinctly pseudostromatic, pseudostromata erumpent to prominent, covered by thallus (Aptroot *et al.* 2016a; Fig. 25F) **Astrothelium sexloculatum**
- 27(24) Ascospores 30–55 µm long; ascomata with white cover contrasting with the olive-green thallus, erumpent . . . . . 28  
Ascospores 65–110 µm long; ascomata variable . . . . . 30
- 28(27) Hamathecium interspersed; ascomata dispersed to irregularly confluent (Luangsaphabool *et al.* 2016; Fig. 25G) . . . . . **Astrothelium siamense**  
Hamathecium clear; ascomata distinctly pseudostromatic, containing several groups of fused ascomata . . . . . 29
- 29(28) Lichexanthone on ascomata only (Aptroot & Cáceres 2016; Fig. 25H) . . . . . **Astrothelium octoseptatum**  
Lichexanthone on thallus and ascomata (Aptroot *et al.* 2016a; Fig. 25I) . . . . . **Astrothelium septemseptatum**



- 30(27) Hamathecium interspersed; lichexanthone on thallus and ascomata; ascomata distinctly pseudostromatic, pseudostromata erumpent, with white cover contrasting with the olive-green thallus, each containing a single group of fused ascomata (this synopsis; Fig. 25J) . . . . . **Astrothelium diplocarpoides**  
 Hamathecium clear; lichexanthone on ascomata only; ascomata variable . . . . . 31
- 31(30) Ascospores  $80\text{--}110 \times 17\text{--}25 \mu\text{m}$ , 5–7-septate; ascomata diffusely pseudostromatic, pseudostromata erumpent, covered by thallus, each containing a single group of fused ascomata (Lücking *et al.* 2016b; Fig. 25K). . . . . **Astrothelium macrostomoides**  
 Ascospores when transversely septate  $65\text{--}85 \times 14\text{--}18 \mu\text{m}$ , 5–11-septate, submuriform when longer; ascomata variable. . . . . 32
- 32(31) Ascospores 5–7-septate; ascomata diffusely pseudostromatic, pseudostromata erumpent to prominent, covered by thallus, uneven-verrucose, each containing a single group of fused ascomata (Aptroot *et al.* 2016b; Fig. 25L) . . . . . **Astrothelium macrostomum**  
 Ascospores 9–11-septate; ascomata distinctly pseudostromatic, pseudostromata immersed, with white cover contrasting with the olive-green thallus, containing one to several groups of fused ascomata . . . . . 33
- 33(32) Ascospores  $65\text{--}70 \times 15\text{--}17 \mu\text{m}$ , transversely septate only (Aptroot & Cáceres 2016; Fig. 26A) . . . . . **Astrothelium eumultiseptatum**  
 Ascospores  $90\text{--}110 \times 22\text{--}28 \mu\text{m}$ , in part with longitudinal septa and becoming submuriform (this synopsis; Fig. 26B & C) . . . . . **Astrothelium diplocarpum**
- 34(1) Ascospores 5-septate; ascomata diffusely pseudostromatic, pseudostromata erumpent, covered by thallus and with external pink pigment, each containing a single group of fused ascomata (Aptroot & Cáceres 2016; Fig. 26D) . . . . . **Astrothelium bivelum**  
 Ascospores 8 per ascus, 3-septate; ascomata variable, with external, yellow to orange pigment . . . . . 35
- 35(34) Ascospores small ( $20\text{--}30 \times 6\text{--}12 \mu\text{m}$ ) . . . . . 36  
 Ascospores small to medium-sized ( $30\text{--}65 \times 10\text{--}25 \mu\text{m}$ ) . . . . . 39
- 36(35) Thallus and ascomata with orange pigment . . . . . 37  
 Pigment on ascomata only, yellow to orange. . . . . 38
- 37(36) Pseudostromata immersed to erumpent, whitish (Aptroot *et al.* 2016a; Fig. 26E) . . . . . **Astrothelium pseudoferrugineum**  
 Pseudostromata erumpent to prominent, covered by thallus (this synopsis; Fig. 26F & G). . . . . **Astrothelium ferrugineum**
- 38(36) Pigment yellow, sparse; ostioles partly apical; ascomata solitary to irregularly confluent and fused, erumpent, covered by thallus (Flakus *et al.* 2016; Fig. 26H). . . . . **Astrothelium pallidoflavum**  
 Pigment orange, distinct; ostioles consistently lateral and fused; ascomata pseudostromatic, erumpent to prominent, with orange cover, containing one to several groups of fused ascomata (this synopsis; Fig. 26I–L) . . . . . **Astrothelium cinnamomeum**

- 39(35) Thallus cracked; ascospores  $30\text{--}35 \times 10\text{--}12 \mu\text{m}$  (this synopsis; Fig. 27A–C) . . . . .  
 . . . . . **Astrothelium croceum**  
 Thallus not cracked; ascospores  $(30\text{--})35\text{--}65 \times (10\text{--})12\text{--}25 \mu\text{m}$  . . . . . 40
- 40(39) Ascospores  $55\text{--}65 \times 15\text{--}25 \mu\text{m}$ ; ascomata diffusely pseudostromatic, pseudostromata immersed to erumpent, covered by thallus and with thin orange rim around broad, dark ostiolar area, each containing a single group of fused ascomata (this synopsis; Fig. 27D & E) . . . . . **Astrothelium ocellatum**  
 Ascospores  $30\text{--}45 \times 10\text{--}17 \mu\text{m}$ ; ascomata diffusely pseudostromatic, pseudostromata erumpent, covered by orange pigment, containing one or several groups of fused ascomata (this synopsis; Fig. 27F & G). . . . . **Astrothelium scorioides**

**Group 4: Ascospores transversely septate, ostiole lateral, secondary substances absent**

- 1 Ascospores 3-septate . . . . . 2  
 Ascospores  $(3\text{--})5\text{--}23$ -septate . . . . . 20
- 2(1) Ascospores medium-sized ( $55\text{--}80 \times 15\text{--}25 \mu\text{m}$ ); thallus distinctly verrucose-papillose . . . . . 3  
 Ascospores small to medium-sized ( $(12\text{--})20\text{--}45 \times (4\text{--})7\text{--}15 \mu\text{m}$ ); thallus variable. . . . . 4
- 3(2) Ascospores  $55\text{--}65 \times 15\text{--}19 \mu\text{m}$ ; ascomata immersed (Aptroot *et al.* 2016b; Fig. 27H) . . . . . **Astrothelium simplex**  
 Ascospores  $62\text{--}80 \times 20\text{--}25 \mu\text{m}$ ; ascomata prominent to sessile (Aptroot *et al.* 2016a; Fig. 27I). . . . . **Astrothelium pseudannulare**
- 4(2) Hamathecium inspersed . . . . . 5  
 Hamathecium clear . . . . . 6
- 5(4) Ascospores  $20\text{--}25 \mu\text{m}$  long; ascomata diffusely pseudostromatic, pseudostromata prominent, laterally covered by thallus, with one to several groups of fused ascospores forming broad, flat, dark ostiolar areas often fused in lobate pattern (this synopsis; Fig. 27J–L) . . . . . **Astrothelium straminicolor**  
 Ascospores  $25\text{--}30 \mu\text{m}$  long; ascomata diffusely pseudostromatic, pseudostromata prominent, covered by thallus, with one to several groups of fused ascospores with dark, papilliform, always separate ostiolar areas (this synopsis; Fig. 28A) . . . . .  
 . . . . . **Astrothelium pyrenastrosulphureum**
- 6(4) Ascospores  $(12\text{--})20\text{--}27 \times (4\text{--})7\text{--}10 \mu\text{m}$  . . . . . 7  
 Ascospores  $28\text{--}45 \times 10\text{--}15 \mu\text{m}$  . . . . . 16
- 7(6) Ascospores  $12\text{--}15 \times 4\text{--}5 \mu\text{m}$ ; ascomata diffusely pseudostromatic, pseudostromata prominent, laterally covered by thallus, with one to several groups of fused ascospores forming broad, flat, dark ostiolar areas often fused in lobate pattern (this synopsis; Fig. 28B). . . . . **Astrothelium acrophaeum**  
 Ascospores  $19\text{--}27 \times 7\text{--}10 \mu\text{m}$ ; thallus and ascospores variable (*Astrothelium crassum* complex) . . . . . 8
- 8(7) Ostioles separate; ascospores aggregate in irregular groups or lines, immersed (this synopsis; Fig. 28C & D) . . . . . **Astrothelium scorizum**  
 Ostioles fused; fused ascospores dispersed to aggregate . . . . . 9

- 9(8) Thallus mottled olive-whitish, with irregular whitish areas or lines; ascomata usually developed on the whitish areas (but not covered by them) . . . . . 10  
 Thallus uniformly olive-brown to olive-green, without whitish areas except when covering the ascomata. . . . . 12
- 10(9) Ascomata dispersed, conical, partially or fully covered by thallus (this synopsis; Fig. 28E) . . . . . **Astrothelium peranceps**  
 Ascomata dispersed to irregularly confluent, completely exposed . . . . . 11
- 11(10) Ascomata black, developed on distinct, white, irregular to reticulate lines (this synopsis; Fig. 28F) . . . . . **Astrothelium nigricans**  
 Ascomata dark brown, emerging from thallus (Aptroot & Cáceres 2016; Fig. 28G) . . . . . **Astrothelium nigrum**
- 12(9) Ascomata aggregate in irregular groups bordered by a thin whitish line; thallus rather thick, uneven to irregularly folded (this synopsis; Fig. 28H & I) . . . . . **Astrothelium subfuscum**  
 Ascomata dispersed to irregularly confluent, exposed and brown or with whitish or (partial) thallus cover; thallus thin to thick but not folded . . . . . 13
- 13(12) Ascomata exposed and brown-black, conical (this synopsis; Fig. 28J) . . . . . **Astrothelium obscurum**  
 Ascomata at least with lateral thallus cover or with whitish rim or cover, lens-shaped to hemispherical . . . . . 14
- 14(13) Ascomata prominent, with basal thallus cover and upper part exposed; individual ascomata clearly discernible (this synopsis; Fig. 28K) . . . . . **Astrothelium oligocarpum**  
 Ascomata erumpent to prominent, whitish or whitish rim; individual ascomata only visible as immersed chambers . . . . . 15
- 15(14) Ascomata with complete whitish cover including ostiolar area; thallus thin (this synopsis; Fig. 28L) . . . . . **Astrothelium subdissocians**  
 Ascomata with whitish rim bordering a wide, dark ostiolar area; thallus thickened (this synopsis; Fig. 29A & B) . . . . . **Astrothelium crassum**
- 16(6) Thallus strongly verrucose-bullate; groups of fused ascomata dispersed, immersed, visible only by their dark, narrow ostiolar area (Aptroot *et al.* 2016*b*; Fig. 29C) . . . . . **Astrothelium globosum**  
 Thallus smooth to uneven; ascomata distinct, diffusely to distinctly pseudostromatic, pseudostromata covered with thallus . . . . . 17
- 17(16) Ascomata distinctly pseudostromatic, pseudostromata strongly prominent to sessile, uneven-verrucose, covered with thallus, with whitish ring around dark ostiolar zone, containing one or several groups of fused ascomata (this synopsis; Fig. 29D & E) . . . . . **Astrothelium fallax**  
 Ascomata diffusely pseudostromatic, pseudostromata erumpent to prominent, smooth to uneven, covered with thallus, containing several to many groups of fused ascomata . . . . . 18



- 18(17) Ascospores 35–45 × 14–16 μm (this synopsis; Fig. 29F) **Astrothelium marcidum**  
 Ascospores 28–33 × 8–15 μm ..... 19
- 19(18) Pseudostromata with distinctly separate, whitish ostiolar areas; ascospores 12–15 μm  
 broad (this synopsis; Fig. 29G & H) ..... **Astrothelium intermedium**  
 Pseudostromata with upper part entirely whitish; ascospores 8–10 μm broad (this  
 synopsis; Fig. 29I & J) ..... **Astrothelium pleiostomum**
- 20(1) Ascospores medium-sized (45–80 × 12–28 μm) ..... 21  
 Ascospores large (80–130 × 17–30 μm) ..... 27
- 21(20) Hamathecium inspersed ..... 22  
 Hamathecium clear ..... 23
- 22(21) Ascospores 45–55 × 13–16 μm, 7–9-septate; ascomata indistinctly pseudostromatic,  
 pseudostromata erumpent to prominent, brownish (Aptroot *et al.* 2016a;  
 Fig. 29K) ..... **Astrothelium trypethelioides**  
 Ascospores 50–75 × 14–22 μm, 5-septate; ascomata diffusely pseudostromatic,  
 pseudostromata erumpent, covered by thallus, containing one to several groups of  
 fused ascomata (this synopsis; Fig. 29L) ..... **Astrothelium subclandestinum**
- 23(21) Ascospores 4–5-septate; groups of fused ascomata dispersed, erumpent, with whitish  
 ring around dark ostiolar zone ..... 24  
 Ascospores 7–19-septate; ascomata variable ..... 25
- 24(23) Ascospores predominantly 4-septate, 45–55 × 15–18 μm (Aptroot & Cáceres 2016;  
 Fig. 30A) ..... **Astrothelium quatuorseptatum**  
 Ascospores 5-septate, 50–75 × 14–22 μm (Aptroot & Cáceres 2016; Fig. 30B) .....  
 ..... **Astrothelium supraclandestinum**
- 25(23) Ascospores 7-septate, 14–28 μm broad; ascomata pseudostromatic, pseudostromata  
 immersed-erumpent, whitish (Aptroot *et al.* 2016a; Fig. 30C) .....  
 ..... **Astrothelium zebrinum**  
 Ascospores 9–19-septate, 12–17 μm broad ..... 26
- 26(25) Ascospores 45–55 μm long, consistently 9-septate; ascomata pseudostromatic,  
 pseudostromata erumpent, with white cover contrasting with olive-green thallus,  
 with several to many groups of fused ascomata (Aptroot & Cáceres 2016;  
 Fig. 30D) ..... **Astrothelium novemseptatum**  
 Ascospores 60–80 μm long, 9–19-septate; groups of fused ascomata dispersed, erumpent,  
 brown-black with whitish ring around base (this synopsis; Fig. 30E) .....  
 ..... **Astrothelium heterophorum**
- 27(20) Ascospores I+ violet, occasionally with a longitudinal septum in one or several cells;  
 thallus bullate-folded; groups of ascomata dispersed to irregularly confluent, immersed  
 to erumpent, exposed and brown-black (Flakus *et al.* 2016; Fig. 30F) .....  
 ..... **Astrothelium neodiplocarpum**  
 Ascospores I–, lacking longitudinal septa; groups of fused ascomata dispersed  
 (or ostioles separate), mostly covered by thallus ..... 28

- 28(27) Hamathecium inspersed; groups of fused ascomata prominent, with broad white ostiolar area; ascospores 9–11-septate, 80–100 µm long (Luangsuphabool *et al.* 2016; Fig. 30G) . . . . . **Astrothelium macrostiolum**  
Hamathecium clear; ascomata variable; ascospore septa variable, ascospores (90–) 100–130 µm long . . . . . 29
- 29(28) Ascospores 5–7(–9)-septate, median septum not thickened; groups of fused ascomata erumpent (this synopsis; Fig. 30H & I) . . . . . **Astrothelium robustum**  
Ascospores 11–23-septate, median septum thickened or not; ascomata variable . . . . . 30
- 30(29) Ascospores 11–15-septate; solitary ascomata erumpent (Aptroot & Cáceres 2016; Fig. 30J) . . . . . **Astrothelium robustosporum**  
Ascospores 19–23-septate; groups of fused ascomata strongly prominent to sessile, with protruding, irregular ostioles (this synopsis; Fig. 30K & L) . . . . .  
. . . . . **Astrothelium gigasporum**  
If ostioles separate, see *Viridothelium megaspermum* (this synopsis), *V. solomonense* (Aptroot *et al.* 2016a) and *V. vonkonratii* (Lücking *et al.* 2016b)

### Group 5: Ascospores muriform, ostiole apical, secondary substances present

- 1 Lichexanthone present, thallus and/or ascomata UV+ yellow; pigment(s) present or absent. . . . . 2  
Lichexanthone absent, thallus and ascomata UV–; pigment(s) always present . . 11
- 2(1) Pigments present on/in thallus and/or ascomata; ascospores large, 70–160 × 15–32 µm . . . . . 3  
Pigments absent; ascospores medium-sized to large, 40–160 × 15–40 µm . . . . . 5
- 3(2) Thallus and ascomata with external, yellow-orange, K+ purple pigment(s); lichexanthone on thallus only; ascomata distinctly pseudostromatic, pseudostromata erumpent to prominent, covered with orange pigment, sharply delimited and contrasting with thallus (Aptroot & Cáceres 2016; Fig. 31A) . . . . .  
. . . . . **Astrothelium flavoduplex**  
Ascomata or medulla with internal, red, K+ yellow-green pigment(s); lichexanthone on thallus and ascomata . . . . . 4  
If internal pigment yellow to orange, ascomata pseudostromatic and pseudostromata prominent to sessile and pruinose, see *Bathelium pruinosucens* (this synopsis)
- 4(3) Ascospores I+ violet; ascomata solitary to irregularly confluent, erumpent to prominent, whitish around ostiole(s) (Aptroot *et al.* 2016a; Fig. 31B) . . . . .  
. . . . . **Astrothelium sanguineoxanthum**  
Ascospores I–; ascomata distinctly pseudostromatic, pseudostromata erumpent to prominent, whitish, sharply delimited and contrasting with thallus (Flakus *et al.* 2016; Fig. 31C) . . . . . **Astrothelium elixii**
- 5(2) Hamathecium inspersed; ascospores with or without thickened median septum . . . . . 6  
Hamathecium clear; ascospores without thickened median septum . . . . . 8
- 6(5) Ascospores 40–80 µm long, (2–)4(–6) per ascus, without thickened median septum; lichexanthone on thallus only (this synopsis; Fig. 31D) . . . . .  
. . . . . **Astrothelium stramineum**  
Ascospores 70–220 µm long, 8 per ascus, with thickened median septum; lichexanthone on thallus and/or ascomata; ascomata solitary, in large, prominent thalline warts . . . . . 7

- 7(6) Ascospores 70–120 × 18–24 μm (this synopsis; Fig. 31E) .....  
 ..... **Astrothelium meristosporoides**  
 Ascospores 120–220 × 25–40 μm (this synopsis; Fig. 31F–H) .....  
 ..... **Astrothelium meristosporum**
- 8(5) Ascospores 70–115 × 15–24 μm ..... 9  
 Ascospores 110–170 × 20–35 μm ..... 10
- 9(8) Ascospores 70–90 × 18–20 μm, 8 per ascus; lichexanthone on thallus only; ascomata indistinctly pseudostromatic, pseudostromata erumpent, whitish, not sharply delimited (Aptroot *et al.* 2016a; Fig. 31I) ..... **Astrothelium lucidothallinum**  
 Ascospores 80–115 × 15–24 μm, 4 per ascus; lichexanthone on thallus and ascomata; ascomata distinctly pseudostromatic, pseudostromata erumpent to prominent, brown-black, sharply delimited (Aptroot & Cáceres 2016; Fig. 31J) .....  
 ..... **Astrothelium ochroleucoides**
- 10(8) Ascomata pseudostromatic; pseudostromata erumpent, whitish (Flakus *et al.* 2016; Fig. 31K) ..... **Astrothelium variabile**  
 Ascomata pseudostromatic; pseudostromata erumpent, brown-black (Aptroot & Cáceres 2016; Fig. 31L) ..... **Astrothelium xanthosuperbum**
- 11(1) Ascospores medium-sized, 45–80 μm long ..... 12  
 Ascospores large, 80–200 μm long ..... 17
- 12(11) Ascospores 40–55 μm long ..... 13  
 Ascospores 60–80 μm long ..... 14
- 13(12) Thallus and ascomata with external, orange pigment and medulla (ascomata) additionally with internal, purple pigment; ascospores about twice as long as broad (Aptroot *et al.* 2016a; Fig. 32A) ..... **Astrothelium condoricum**  
 Ascomata with internal, yellow pigment; ascospores about 3–4 times as long as broad (Aptroot & Cáceres 2016; Fig. 32B) ..... **Astrothelium duplicatum**  
 If ascomata pseudostromatic and pseudostromata prominent to sessile, see *Bathelium madreporiforme* (this synopsis; thallus smooth to uneven) and *B. tuberosum* (this synopsis; thallus verrucose-bullate)
- 14(12) Ascomata with internal red pigment crystals; ostiolar area very broad and flat, black (this synopsis; Fig. 32C) ..... **Astrothelium sierraleonense**  
 If ascomata with internal yellow to orange pigment, pseudostromatic and pseudostromata prominent to sessile, see *Bathelium mastoideum* (this synopsis)  
 Pigment external; ostiolar area narrow, whitish ..... 15
- 15(14) Hamathecium inspersed; pigment on ascomata only; ascospores 20–30 μm broad; ascomata pseudostromatic, pseudostromata prominent, covered with orange pigment, sharply delimited from thallus (this synopsis; Fig. 32D) .....  
 ..... **Astrothelium auratum**  
 Hamathecium clear; pigment on thallus and ascomata; ascospores 12–25 μm broad; ascomata variable ..... 16
- 16(15) Ascomata pseudostromatic; pseudostromata erumpent, covered with orange pigment, sharply delimited (Aptroot *et al.* 2016b; Fig. 32E) .....  
 ..... **Astrothelium graphicum**  
 Ascomata pseudostromatic; pseudostromata immersed, whitish, not sharply delimited (Aptroot *et al.* 2016a; Fig. 32F) ..... **Astrothelium flavomaculatum**



- 17(11) Ascomata with internal, red, K+ yellow-green pigment; ascospores I+ violet; ascomata pseudostromatic, pseudostromata erumpent to prominent, brown-black, sharply delimited (this synopsis; Fig. 32G) . . . . . **Astrothelium sanguinarium**  
Thallus and/or ascomata with external or internal, yellow to orange, K+ purple pigment; ascospores I-; ascomata variable . . . . . 18
- 18(17) Pigment in medulla of pseudostromata only . . . . . 19  
Pigment external on thallus and/or ascomata . . . . . 20
- 19(18) Ascomata erumpent to prominent, covered by thallus; ascospores 8 per ascus, 90–105 × 26–36 µm (this synopsis; Fig. 32H) . . . . . **Astrothelium deforme**  
Ascomata immersed-erumpent, with exposed blackish ostiolar area; ascospores 2 per ascus, ascospores 110–130 × 30–35 µm (Aptroot *et al.* 2016a; Fig. 32I) . . . . .  
. . . . . **Astrothelium laurerospaerioides**  
If ascomata pseudostromatic and pseudostromata prominent to sessile, see *Bathelium lineare* (this synopsis; ascospores 100–120 µm long) and *B. sphaericum* (this synopsis; ascospores 130–200 µm long)
- 20(18) Ascospores 8 per ascus, 20–25 µm broad; ascomata pseudostromatic, immersed to erumpent, covered with orange pigment, sharply delimited (Aptroot & Cáceres 2016; Fig. 32J) . . . . . **Astrothelium mesoduplex**  
Ascospores 2–4 per ascus, 25–50 µm broad; ascomata variable . . . . . 21
- 21(20) Pigment on ascomata only, absent from thallus; ostiole in part lateral (this synopsis; Fig. 32K) . . . . . **Astrothelium vezdae**  
Pigment on thallus only, absent from ascomata; ostiole consistently apical (this synopsis; Fig. 32L) . . . . . **Astrothelium chrysoglyphum**

#### Group 6: Ascospores muriform, ostiole apical, secondary substances absent

- 1 Hamathecium interspersed . . . . . 2  
Hamathecium clear . . . . . 19
- 2(1) Ascospores small to medium-sized (30–70 × 11–20 µm) . . . . . 3  
Ascospores large (80–300 × 20–75 µm) . . . . . 6
- 3(2) Ascomata aggregate in irregular groups or lines, immersed to erumpent, exposed, blackish; ascospores 35–50 × 12–18 µm (this synopsis; Fig. 33A–E) . . . . .  
. . . . . **Astrothelium subdiscretum**  
Ascomata solitary or few aggregate, at least partly covered by thallus; ascospores variable. . . . . 4
- 4(3) Ascospores 32–45 × 11–13 µm; ascomata aggregate to pseudostromatic, pseudostromata prominent to sessile, covered by thallus (this synopsis) . . . . .  
. . . . . **Astrothelium pseudovariatum**  
Ascospores 45–70 × 13–20 µm; ascomata solitary to aggregate, if aggregate then whitish . . . . . 5
- 5(4) Ascomata solitary, prominent, mostly exposed and brown-black (this synopsis; Fig. 33F) . . . . . **Astrothelium ambiguum**  
Ascomata solitary, erumpent, mostly covered by thallus except for dark ostiolar area (this synopsis; Fig. 33G) . . . . . **Astrothelium indicum**

- 6(2) Ascospores 1–2 per ascus, 210–300  $\mu\text{m}$  long . . . . . 7  
 Ascospores 4–8 per ascus, 80–200(–230)  $\mu\text{m}$  long . . . . . 8
- 7(6) Ascospores 1 per ascus, 240–300  $\times$  45–50  $\mu\text{m}$ , with thickened median septum; ascomata confluent to irregularly pseudostromatic, immersed–erumpent, with whitish cover around the blackish ostiole (Aptroot *et al.* 2016a; Fig. 33H) . . . . .  
 . . . . . **Astrothelium colombiense**  
 Ascospores 2 per ascus, 210–225  $\times$  30–35  $\mu\text{m}$ , without thickened median septum; ascomata solitary, prominent, mostly exposed and brown-black (this synopsis; Fig. 33I) . . . . . **Astrothelium megaleium**
- 8(6) Ascospores submuriform, with few longitudinal septa, 17–22  $\mu\text{m}$  broad; ascomata solitary to irregularly confluent, immersed to erumpent, covered by thallus with broad whitish area around the dark ostiolar spot (this synopsis; Fig. 33J) . . . . .  
 . . . . . **Astrothelium macrosporum**  
 Ascospores distinctly muriform, 20–75  $\mu\text{m}$  broad; ascomata variable . . . . . 9
- 9(8) Ascospores 80–140  $\mu\text{m}$  long . . . . . 10  
 Ascospores (125–)140–230  $\mu\text{m}$  long, most ascospores distinctly exceeding 140  $\mu\text{m}$  . . . 12
- 10(9) Ascospores 2–3 times as long as broad (80–100(–125)  $\times$  28–48  $\mu\text{m}$ ), without thickened median septum; ascomata solitary, erumpent, laterally covered by thallus with ostiolar area exposed, black (this synopsis) . . . . . **Astrothelium effusum**  
 Ascospores 4–5 times as long as broad (115–140  $\times$  25–33  $\mu\text{m}$ ), with thickened median septum; ascomata variable . . . . . 11
- 11(10) Ascomata solitary, strongly prominent, completely covered by thallus (this synopsis; Fig. 33K) . . . . . **Astrothelium aurantiacum**  
 Ascomata solitary to irregularly confluent, immersed to erumpent, covered by thallus but with exposed, dark ostiolar area bordered by whitish rim (this synopsis; Fig. 33L) . . . . . **Astrothelium sikkimense**
- 12(9) Ascospores with thickened median septum . . . . . 13  
 Ascospores without thickened median septum . . . . . 17
- 13(12) Ascomata distinctly pseudostromatic, pseudostromata prominent to sessile, with whitish cover; thallus smooth to uneven (Aptroot *et al.* 2016a; Fig. 34A) . . . . .  
 . . . . . **Astrothelium alboverrucoides**  
 Ascomata solitary; thallus variable . . . . . 14
- 14(13) Thallus smooth to uneven; ascomata prominent, exposed and blackish (Aptroot *et al.* 2016a; Fig. 34B) . . . . . **Astrothelium flavomeristosporum**  
 Thallus verrucose-papillose or bullate; ascomata immersed, covered by thallus . . . . . 15
- 15(14) Thallus coarsely bullate, gall-like; ascomata immersed in large thallus verrucae, completely covered by thallus (Aptroot *et al.* 2016a; Fig. 34C) . . . . .  
 . . . . . **Astrothelium philippinense**  
 Thallus verrucose-papillose; ascomata variable but ostioles partly lateral. . . . . 16

- 16(15) Hamathecium orange; ascospores 26–34 µm broad (this synopsis; Fig. 34D) . . . . .  
 . . . . . **Astrothelium papillosum**  
 Hamathecium uncoloured; ascospores 35–45 µm broad (Aptroot *et al.* 2016a;  
 Fig. 34E) . . . . . **Astrothelium komposchii**
- 17(12) Ascospores 135–165 µm long; thallus uneven-verrucose; ascomata solitary to irre-  
 regularly confluent, erumpent, covered by thallus, uneven-verrucose (this synopsis;  
 Fig. 34F) . . . . . **Astrothelium irregulare**  
 Ascospores (140–)165–230 µm long; thallus and ascomata variable. . . . . 18
- 18(17) Thallus bullate; ascomata solitary to confluent, immersed in coarse thallus verrucae,  
 covered by thallus, with yellowish ostiolar rim (Aptroot *et al.* 2016a; Fig. 34G) . . . . .  
 . . . . . **Astrothelium flavostiolatum**  
 Thallus smooth to uneven; ascomata solitary, prominent, covered by thallus except  
 for dark ostiolar area usually bordered by a whitish rim (this synopsis; Fig. 34H–L)  
 . . . . . **Astrothelium megaspernum**
- 19(1) Ascospores small (30–60 × 11–20 µm) . . . . . 20  
 Ascospores medium-sized to large (60–280 × (15–)20–65 µm) . . . . . 21
- 20(19) Ascospores 30–45 × 11–13 µm; ascomata pseudostromatic, pseudostromata  
 (strongly) prominent, covered by thallus except for ostioles (this synopsis; Fig. 35A  
 & B) . . . . . **Astrothelium variatum**  
 Ascospores 50–60 × 15–20 µm; ascomata solitary, prominent, covered by thallus (this  
 synopsis) . . . . . **Astrothelium keralense**
- 21(19) Ascospores 200–280 × 50–65 µm, 2 per ascus; ascomata irregularly grouped to dif-  
 fusely pseudostromatic, pseudostromata erumpent, completely covered by thallus  
 (this synopsis; Fig. 35C & D) . . . . . **Astrothelium gigantosporum**  
 Ascospores 70–195 × 14–50(–60) µm, (1–)4–8 per ascus; ascomata variable . . . . . 22
- 22(21) Ascospores I+ violet-blue, 125–170 × 27–40 µm, 8 per ascus; ascomata solitary to  
 confluent, prominent, completely exposed and brown-black (Flakus *et al.* 2016;  
 Fig. 35E) . . . . . **Astrothelium amylosporum**  
 Ascospores I–, variously sized and numbered; ascomata variable . . . . . 23
- 23(22) Ascospores with thickened median septum . . . . . 24  
 Ascospores without thickened median septum . . . . . 25
- 24(23) Ascospores 4 per ascus, 145–175 × 30–35 µm; thallus strongly bullate; ascomata solitary  
 to irregularly confluent, immersed in bullate thallus warts and completely covered by  
 thallus except for protruding ostiole (Aptroot *et al.* 2016b; Fig. 35F) . . . . .  
 . . . . . **Astrothelium tetrasporum**  
 Ascospores (6–)8 per ascus, (85–)100–170 × 23–33 µm; thallus smooth to uneven;  
 ascomata solitary to diffusely pseudostromatic, prominent, whitish surrounding the  
 black ostiolar area (this synopsis; Fig. 35G) . . . . . **Astrothelium alboverrucum**
- 25(23) Ascospores (1–)2–4 per ascus . . . . . 26  
 Ascospores 8 per ascus . . . . . 28



- 26(25) Ascomata distinctly pseudostromatic, pseudostromata erumpent to prominent, with white cover, sharply delimited from thallus; ascospores  $80\text{--}140 \times 25\text{--}35 \mu\text{m}$  (this synopsis; Fig. 35H). . . . . **Astrothelium sphaerioides**  
 Ascomata irregularly confluent to diffusely pseudostromatic, erumpent to prominent, either fully exposed and brown-black or covered by olive-green thallus; ascospores  $120\text{--}180(\text{--}200) \times 30\text{--}50(\text{--}60) \mu\text{m}$  . . . . . 27
- 27(26) Ascomata erumpent, fully exposed and brown-black; ascospores  $120\text{--}175 \times 30\text{--}45 \mu\text{m}$  (this synopsis; Fig. 35I & J) . . . . . **Astrothelium subdisjunctum**  
 Ascomata prominent, covered by thallus except dark ostiole bordered by a white rim, with one to several ascomata per thallus wart and ostioles often pointing in different directions; ascospores  $160\text{--}180(\text{--}200) \times 40\text{--}50(\text{--}60) \mu\text{m}$  (Lücking *et al.* 2016b; Fig. 35K) . . . . . **Astrothelium nicaraguense**
- 28(25) Ascospores  $150\text{--}190 \times 40\text{--}45 \mu\text{m}$ ; ascomata solitary or few grouped, covered by thallus (this synopsis) . . . . . **Astrothelium octosporoides**  
 Ascospores  $60\text{--}150 \times 15\text{--}30 \mu\text{m}$ ; ascomata variable . . . . . 29
- 29(28) Ascomata solitary, immersed to erumpent, covered by thallus except for dark ostiolar area surrounded by irregular whitish rim; ascospores not exceeding  $80 \mu\text{m}$  in length (this synopsis; Fig. 35L). . . . . **Astrothelium exostemmatis**  
 Ascomata irregularly confluent to pseudostromatic, erumpent to prominent, fully exposed or covered by thallus; ascospores usually exceeding  $80 \mu\text{m}$  in length . . . 30
- 30(29) Ascomata fully exposed and dark brown (this synopsis; Fig. 36A). . . . .  
 . . . . . **Astrothelium chapadense**  
 Ascomata covered by thallus except for dark ostiolar area (Aptroot *et al.* 2016a; Fig. 36B) . . . . . **Astrothelium corallinum**
- Group 7: Ascospores muriform, ostiole lateral, secondary substances present**
- 1 Lichexanthone present, thallus and/or ascomata UV+ yellow; pigment(s) present or absent. . . . . 2  
 Lichexanthone absent, thallus and ascomata UV-; pigment(s) always present . . . 14
- 2(1) Hamathecium inspersed; ascomata with separate or fused ostioles . . . . . 3  
 Hamathecium clear; ascomata with fused ostioles. . . . . 5
- 3(2) Ascospores  $80\text{--}115 \times 25\text{--}35 \mu\text{m}$ , 4 per ascus; lichexanthone in medulla; ascomata with separate ostioles, immersed, covered by thallus (Aptroot *et al.* 2016a; Fig. 36C) . . . . . **Astrothelium lucidomedullatum**  
 Ascospores  $150\text{--}220 \times 40\text{--}65 \mu\text{m}$ , 2 or 8 per ascus; lichexanthone external on thallus and/or ascomata . . . . . 4
- 4(3) Ascospores 8 per ascus,  $40\text{--}50 \mu\text{m}$  broad; ascomata with separate ostioles, prominent, covered by thallus except for broad black ostiolar area; lichexanthone on thallus and ascomata (Flakus *et al.* 2016; Fig. 36D) . . . . . **Astrothelium carrascoense**  
 Ascospores 2 per ascus,  $50\text{--}65 \mu\text{m}$  broad; ascomata with fused ostioles, groups of fused ascomata dispersed, covered by thallus except ostioles; lichexanthone on ascomata only (this synopsis; Fig. 36E). . . . . **Astrothelium megalostomum**

- 5(2) Ascospores small (35–45 × 15–19 µm) . . . . . 6  
 Ascospores large (85–250 × 19–65 µm) . . . . . 7
- 6(5) Only ostiole UV+ yellow; fused ascomata pseudostromatic, pseudostromata erumpent, with white cover contrasting with olive-green thallus (Aptroot & Cáceres 2016; Fig. 36F) . . . . . **Astrothelium eustomurale**  
 Entire pseudostroma UV+ yellow; fused ascomata pseudostromatic, pseudostroma immersed, with white cover contrasting with olive-brown thallus (Aptroot *et al.* 2016a; Fig. 36G) . . . . . **Astrothelium lucidostromum**
- 7(5) Ascospores 150–250 × 30–65 µm, (1–)2 per ascus; ascomata with fused ostioles . . . . 8  
 Ascospores 85–150 × 19–45 µm, 2 or 8 per ascus; ascomata variable . . . . . 10
- 8(7) Fused ascomata solitary, immersed and covered by thallus; thallus smooth to uneven; lichexanthone on thallus and ascomata (this synopsis; Fig. 36H) . . . . .  
 . . . . . **Astrothelium sepultum**  
 Fused ascomata pseudostromatic, pseudostromata immersed, whitish and contrasting with olive-green thallus; thallus bullate-bumpy; lichexanthone on pseudostromata only . . . . . 9
- 9(8) Thallus dominated by finely and densely cracked pseudostromata, with thallus bumps dispersed; ascomata completely immersed in pseudostromata, hardly visible (Lücking *et al.* 2016b; Fig. 36I) . . . . . **Astrothelium cryptolucens**  
 Thallus dominated by vegetative part forming large bumps separating the smooth pseudostromata; ascomata immersed to erumpent with the ostiolar area broadly exposed and black (Lücking *et al.* 2016b; Fig. 36J & K) . . . . .  
 . . . . . **Astrothelium norisianum**
- 10(7) Ascospores 85–130 µm long, 2 per ascus; lichexanthone internal in medulla; fused ascomata solitary to irregularly confluent, immersed to erumpent, covered by thallus except dark ostiolar area surrounded by irregular whitish rim (this synopsis; Fig. 36L) . . . . . **Astrothelium consimile**  
 Ascospores 100–150 µm long, 8 per ascus; lichexanthone external on ascomata; ascomata variable . . . . . 11
- 11(10) Ascospores 30–45 µm broad; ascomata solitary, erumpent to prominent, covered by thallus except broad whitish ostiolar area (this synopsis; Fig. 37A–C) . . . . .  
 . . . . . **Astrothelium defossum**  
 Ascospores 17–23 µm broad; ascomata variable . . . . . 12
- 12(11) Ascomata solitary, immersed to erumpent, covered by thallus except dark ostiolar area; thallus shallowly folded (this synopsis; Fig. 37D) . . . . .  
 . . . . . **Astrothelium octosporum**  
 Ascomata irregularly confluent to grouped, erumpent to prominent, completely covered by thallus; thallus smooth to uneven . . . . . 13

- 13(12) Ostioles visible as sessile, broad white papillae (Aptroot *et al.* 2016b; Fig. 37E) . . . . . **Astrothelium megeustomum**  
 Ostioles visible as minute, immersed dark pores (this synopsis; Fig. 37F) . . . . . **Astrothelium confluens**
- 14(1) Ascospores (small to) medium-sized ( $35\text{--}80 \times 12\text{--}25 \mu\text{m}$ ) . . . . . 15  
 Ascospores large ( $75\text{--}200 \times 22\text{--}50 \mu\text{m}$ ) . . . . . 16
- 15(14) Ascomata pseudostromatic, pseudostromata immersed, whitish, forming irregular to reticulate lines, well delimited from thallus; pigment external on thallus only, orange (this synopsis; Fig. 37G) . . . . . **Astrothelium praetervisum**  
 Ascomata solitary, immersed to erumpent, covered by thallus except dark ostiolar area surrounded by whitish rim; pigment external on ascomata only, orange (this synopsis; Fig. 37H). . . . . **Astrothelium subaequans**
- 16(14) Pigment orange, external on ascomata or internal in medulla . . . . . 17  
 Pigment red, external on ascomata . . . . . 19
- 17(16) Pigment internal in medulla of ascomata (this synopsis; Fig. 37I) . . . . .  
 Pigment external on ascomata . . . . . **Astrothelium amazonum** 18
- 18(17) Ascospores  $100\text{--}170 \times 30\text{--}40 \mu\text{m}$ , regularly muriform; ascomata pseudostromatic, pseudostromata erumpent, with orange cover (Lücking *et al.* 2016b; Fig. 37J) . . . . . **Astrothelium carassense**  
 Ascospores  $90\text{--}110 \times 22\text{--}28 \mu\text{m}$ , with few longitudinal septa, submuriform; ascomata solitary to irregularly grouped, covered by thallus except ostiole (this synopsis; Fig. 37K) . . . . . **Astrothelium diplocarpum**
- 19(16) Ascospores  $100\text{--}130 \times 25\text{--}30 \mu\text{m}$ , 8 per ascus; ascomata solitary, immersed to erumpent, irregularly bumpy with central red ostiole (this synopsis; Fig. 37L) . . . . . **Astrothelium purpurascens**  
 Ascospores  $150\text{--}200 \times 40\text{--}50 \mu\text{m}$ , 2 per ascus (this synopsis) . . . . . **Astrothelium isabellinum**

#### Group 8: Ascospores muriform, ostiole lateral, secondary substances absent

- 1 Ascomata solitary, with separate ostioles . . . . . 2  
 Ascomata fused, with joint ostioles . . . . . 16
- 2(1) Hamathecium inspersed . . . . . 3  
 Hamathecium clear . . . . . 9
- 3(2) Ascospores  $70\text{--}100 \times 20\text{--}35 \mu\text{m}$ ; thallus lacking pseudocyphellae . . . . . 4  
 Ascospores ( $85\text{--}$ ) $100\text{--}230 \times 25\text{--}55 \mu\text{m}$ , if less than  $100 \mu\text{m}$  then thallus with pseudocyphellae . . . . . 6
- 4(3) Ascospores curved; ascomata dispersed, immersed to erumpent and covered by thallus except ostioles (Aptroot *et al.* 2016b; Fig. 38A) . . . . . **Astrothelium curvatum**  
 Ascospores straight . . . . . 5



- 5(4) Ascospores 8 per ascus; thallus smooth to uneven; ascomata dispersed to irregularly confluent, immersed to erumpent, laterally covered by thallus but otherwise exposed and black, surrounded by irregular whitish rim (this synopsis; Fig. 38B) ..... **Astrothelium santessonii**  
 Ascospores 2 per ascus; thallus verrucose-papillose; ascomata dispersed to irregularly confluent, sessile, covered by thallus except the strongly protruding ostiole (this synopsis; Fig. 38C & D) ..... **Astrothelium puiggarii**
- 6(3) Ascospores  $250\text{--}350 \times 40\text{--}60 \mu\text{m}$ , 1 per ascus; thallus irregularly bullate-bumpy; ascomata solitary, immersed, hardly visible (Lücking *et al.* 2016b; Fig. 38E) . . . . . **Astrothelium megacrypticum**  
 Ascospores  $85\text{--}230 \times 25\text{--}55 \mu\text{m}$ , (1–)2–8 per ascus; ascomata variable . . . . . 7
- 7(6) Ascospores  $200\text{--}230 \times 30\text{--}40 \mu\text{m}$ , about 6–7 times as long as broad, 8 per ascus; thallus verrucose; ascomata prominent, covered by thallus except for dark, flat ostiolar area surrounded by whitish ring (Aptroot *et al.* 2016b; Fig. 38F) . . . . . **Astrothelium longisporum**  
 Ascospores  $85\text{--}175 \times 25\text{--}55 \mu\text{m}$ , about 2.5–4 times as long as broad, 1–2 per ascus; ascomata variable . . . . . 8
- 8(7) Thallus with pseudocyphellae; ascomata laterally covered by thallus, with black ostiolar area surrounded by black rim (Flakus *et al.* 2016; Fig. 38G) . . . . . **Astrothelium pyrenuliforme**  
 Thallus lacking pseudocyphellae; ascomata solitary, exposed and pure black (Aptroot *et al.* 2016a; Fig. 38H) . . . . . **Astrothelium ecuadoriense**
- 9(2) Ascospores 210–230  $\mu\text{m}$  long, 1 per ascus; thallus irregularly verrucose; ascomata dispersed, immersed, hardly visible (this synopsis; Fig. 38I) . . . . . **Astrothelium lugescens**  
 Ascospores 70–200  $\mu\text{m}$  long, (1–)2–8 per ascus; ascomata variable . . . . . 10
- 10(9) Ascospores  $70\text{--}130 \times 20\text{--}36 \mu\text{m}$  . . . . . 11  
 Ascospores  $120\text{--}200 \times 30\text{--}50\text{--}(60) \mu\text{m}$  . . . . . 13
- 11(10) Ascospores 2 per ascus; ascomata irregularly confluent to pseudostromatic, immersed to erumpent, covered by thallus except black ostiolar area surrounded by irregular whitish rim (this synopsis; Fig. 38J) . . . . . **Astrothelium andamanicum**  
 Ascospores 4–8 per ascus; ascomata dispersed . . . . . 12
- 12(11) Ascospores with distinctly thickened median septum, 4–8 per ascus; thallus smooth to uneven; ascomata erumpent (this synopsis; Fig. 38K & L) . . . . . **Astrothelium tenue**  
 Ascospores lacking thickened median septum, 4 per ascus; thallus gall-like, coarsely bullate to folded; ascomata solitary, immersed, visible only by the dark ostiolar area (Aptroot *et al.* 2016a; Fig. 39A) . . . . . **Astrothelium guianense**

- 13(10) Ascospores I+ violet; thallus strongly bullate; ascomata immersed in thallus warts, completely covered by thallus (Flakus *et al.* 2016; Fig. 39B) . . . . . **Astrothelium bullatum**  
 Ascospores I-. . . . . 14
- 14(13) Ascospores 8 per ascus (this synopsis) . . . . . **Astrothelium superbum**  
 Ascospores 2–4 per ascus; ascomata dispersed to irregularly confluent, erumpent to prominent, covered by thallus, with dark ostiolar area. . . . . 15
- 15(14) Ascomata usually single in thalline warts, warts up to 1 mm diam., with broad, diffusely grey-black ostiolar area; ostioles always eccentric (this synopsis; Fig. 39C) . . . . . **Astrothelium campylocartilagineum**  
 Ascomata 1–5 in thalline warts, warts up to 2 mm diam., with narrow, brown-black ostiolar area surrounded by a whitish rim; ostioles pointing in various directions including apical ones (Lücking *et al.* 2016b; Fig. 39D) . . . . . **Astrothelium nicaraguense**  
 If ascospores 2 per ascus and ascomata pseudostromatic, with whitish pseudostromata strongly contrasting with olive-brown thallus and blackish ostiolar area, see *Viridothelium tricolor* (Lücking *et al.* 2016b)
- 16(1) Ascospores small to medium-sized (30–80 × 16–26 µm) . . . . . 17  
 Ascospores large (125–230 × 28–80 µm) . . . . . 20
- 17(16) Hamathecium interspersed; ascospores 50–65 µm long; groups of fused ascomata irregularly confluent to pseudostromatic, immersed to erumpent, covered by thallus except black ostiolar area surrounded by irregular whitish rim (Aptroot & Cáceres 2016; Fig. 39E) . . . . . **Astrothelium testudineum**  
 Hamathecium clear; ascospores 30–52 or 70–80 µm long . . . . . 18
- 18(17) Ascospores medium-sized (70–80 × 20–25 µm); thallus uneven-verrucose; groups of fused ascomata pseudostromatic, pseudostromata prominent, covered by thallus except for dark, papilliform ostiole (Aptroot *et al.* 2016a; Fig. 39F) . . . . . **Astrothelium mediocrassum**  
 Ascospores small (30–52 × 16–22 µm); thallus and ascomata variable . . . . . 19
- 19(18) Groups of fused ascomata pseudostromatic, pseudostromata immersed, with white cover, forming irregular to reticulate lines, contrasting with thallus (this synopsis; Fig. 39G) . . . . . **Astrothelium cinereum**  
 Groups of fused ascomata dispersed, immersed–erumpent, hardly visible (this synopsis; Fig. 39H). . . . . **Astrothelium leioplacum**
- 20(16) Ascospores 215–230 µm long, 1 per ascus; groups of fused ascomata dispersed, erumpent, completely covered by thallus (this synopsis; Fig. 39I) . . . . . **Astrothelium saxicola**  
 Ascospores 125–200 µm long, 8 per ascus. . . . . 21

- 21(20) Ascospores with median thickening; groups of fused ascomata dispersed, immersed, hardly visible (Aptroot & Cáceres 2016; Fig. 39J) . . . . . **Astrothelium flavomurisporum**  
 . . . . . Ascospores lacking thickening; groups of fused ascomata dispersed to irregularly confluent, covered by thallus except whitish ostiolar area (this synopsis; Fig. 39K–L) . . . . . **Astrothelium cecidiogenum**

**Astrothelium acrophaeum**  
**Müll. Arg.**

*Bot. Jahrb. Syst.* **6**: 383 (1885).—*Trypethelium acrophaeum* Nyl. (1876), nom. nud.—*Pleurotrema acrophaeum* (Müll. Arg.) R. C. Harris, *Acta Amazon. (Suppl.)* **14**: 69 ('1984') [1986]; type: Cuba, *Wright* s. n. (G!—holotype; H-Nyl 268!, US!—isotypes; Müller, *Verr. Cub.* 176).

(Fig. 28B)

*Thallus* corticate, light olive-green to yellowish, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to irregularly confluent or diffusely pseudostromatic, 0.7–1.1 mm diam., erumpent to prominent, basally to laterally covered by thallus but upper part and ostiolar area exposed and blackish. *Hamathecium* clear. *Ascospores* 8 per ascus, 2(–3)-septate, fusiform, 12–14 × 4–5 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Cuba).

**Astrothelium aeneum** (Eschw.)  
**Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816652

*Verrucaria aenea* Eschw., in Martius, *Icon. Sel. Pl. Crypt.* **2**: 15, t. 4, fig. 3 (1828).—*Pseudopyrenula aenea* (Eschw.) Vain., *Acta Soc. Fauna Fl. Fenn.* **7**(2): 207 (1890).—*Trypethelium aeneum* (Eschw.) Zahlbr., in Engler & Prantl, *Nat. Pflanzenfam.* **1**(1\*): 70 (1903); type: Brazil, Bahia, Caeté, *Martius* s. n. (M!—holotype).

*Verrucaria tetracerae* var. *crocea* Eschw., in Martius, *Flora Brasil.* **1**: 134 (1833).—*Spermatodium croceum* (Eschw.) Trevis., *Conspect. Verruc.*: 6 (1860); type: Brazil, *Martius* s. n. (M—holotype, not seen).

*Verrucaria myriococca* Spreng., *Syst. Veget.* **4**(1): 245 (1827); type: not found in L, probably lost.

*Verrucaria heterochroa* Mont., *Ann. Sci. Nat., Bot., sér. 2*, **19**: 60 (1843).—*Pyrenula heterochroa* (Mont.) Trevis., *Spighe e Paglie*: 17 (1853).—*Segestria heterochroa* (Mont.) Trevis., *Conspect. Verruc.*: 6 (1860).—*Pseudopyrenula heterochroa* (Mont.) Müll. Arg., *Flora* **66**: 248 (1883); type: French Guiana, *Leprieur* 452 (BM—lectotype, designated here).

(Fig. 15B–F)

*Thallus* corticate, light olive-green to yellowish but largely covered with orange pigment, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent or diffusely pseudostromatic, 0.3–0.7 mm diam., erumpent, covered by thallus and orange pigment except for dark ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 20–27 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV+ red, K+ purple, with anthraquinone.

*Distribution.* Pantropical (previously reported from the USA, Costa Rica, El Salvador, Islas Revillagigedo, Bahamas, Cuba, Jamaica, Colombia, Venezuela, Guyana, Surinam, French Guiana, Galapagos, Bolivia, Brazil, Sri Lanka, Thailand, Malaysia (Sarawak, Sabah), Papua New Guinea, and Australia).

*Discussion.* *Astrothelium aeneum* as defined here might still represent a collective taxon including forms with solitary or almost pseudostromatic, erumpent to sometimes almost prominent ascomata with different size ranges. Due to the lack of sufficient molecular data spanning a wide range of morphodemes, we have not attempted to

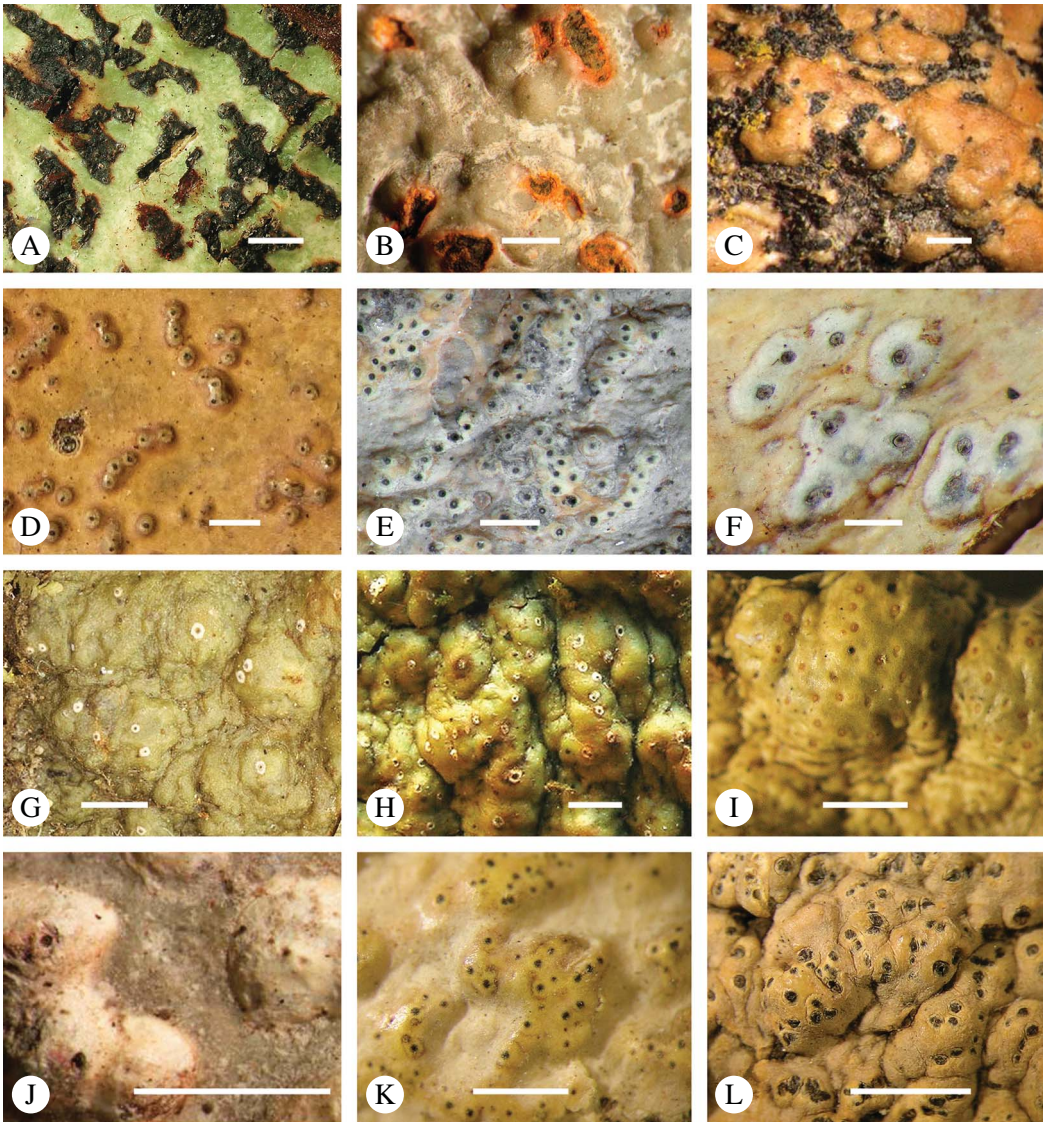


FIG. 12. Habitus of *Astrothelium* species. A & B, *A. neogalbineum* (A, Costa Rica, Lücking 16358a; B, Brazil, Cáceres & Aptroot 11436); C, *A. pictum* (Brazil, holotype); D & E, *A. cinereorosellum* (D, Indonesia, Borneo, lectotype of *Verrucaria antoniae*; E, India, isotype of *Trypethelium flavocinereum*); F, *A. fijiense* (Fiji, holotype); G & H, *A. punctulatum* (Brazil, isotype); I, *A. grossoides* (Papua New Guinea, isotype of *Trypethelium grossum*); J, *A. vulcanum* (Guyana, holotype); K & L, *A. porosum* (K, 'West Indies', isotype; L, Brazil, lectotype of *Trypethelium brachysporum*). Scales = 1 mm.

split this taxon further, after recognizing separate lineages forming flat, linear pseudostromata, such as *A. flavostromatum* (Aptroot & Cáceres 2016) and *A. kunzei* (see

below), with an inspersed hamatecium, such as *A. inspersaeneum* (Lima *et al.* 2013; see below) and *A. neoinspersum* (Aptroot *et al.* 2016a), or with smaller or larger ascospores,



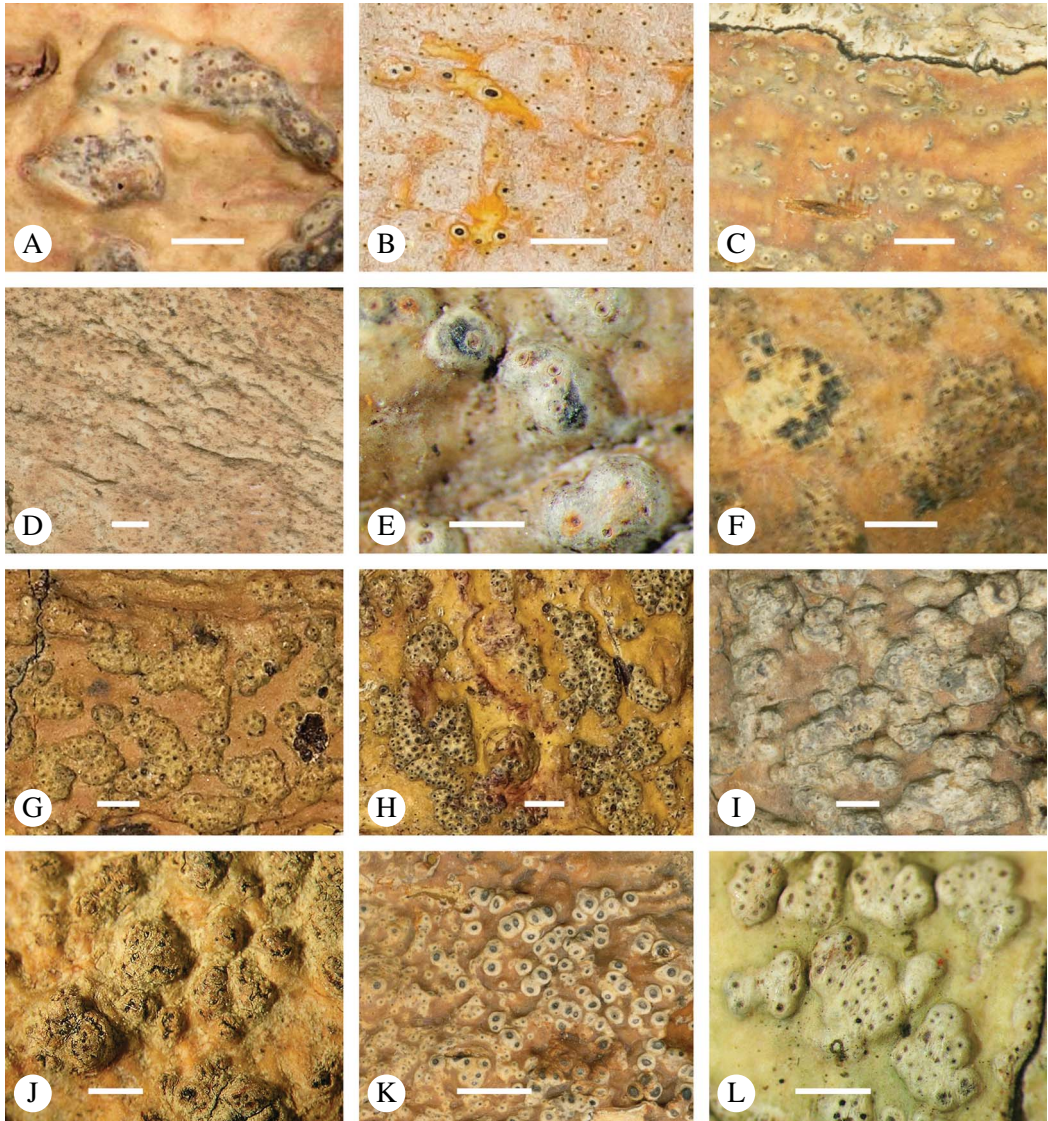


FIG. 13. Habitus of *Astrothelium* species. A, *A. stromatofluorescens* (Brazil, holotype); B–D, *A. pulcherrimum* (B, ‘America’, lectotype; C, Costa Rica, holotype of *Trypethelium tricolor*; D, Colombia, lectotype of *Verrucaria diffluens*); E, *A. leucosessile* (Panama, holotype); F–L, *A. phlyctaena* (F, St. Lucia, lectotype; G, Brazil, lectotype of *Verrucaria ochroleuca*; H, Brazil, holotype of *Trypethelium euporum*; I, French Guiana, lectotype of *T. lepriaurii*; J, Cuba, lectotype of *T. leprosum*; K, São Tomé and Príncipe, lectotype of *T. subalbans*; L, Brazil, Cáceres 2028). Scales = 1 mm.

such as *A. flavum* (Aptroot & Cáceres 2016) and *A. megaeneum* (Flakus *et al.* 2016).

*New country record. Ecuador:* Zamora-Chinchipecordillera Numbala, Reserva Biológica San Francisco, 2004, Sipman & Mandi 53115 (B).

***Astrothelium alboverrucum* (Makhija & Patw.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816653

*Laurera alboverruca* Makhija & Patw., *Mycotaxon* 31: 571 (1988); type: India, Andaman Islands, South Andaman,



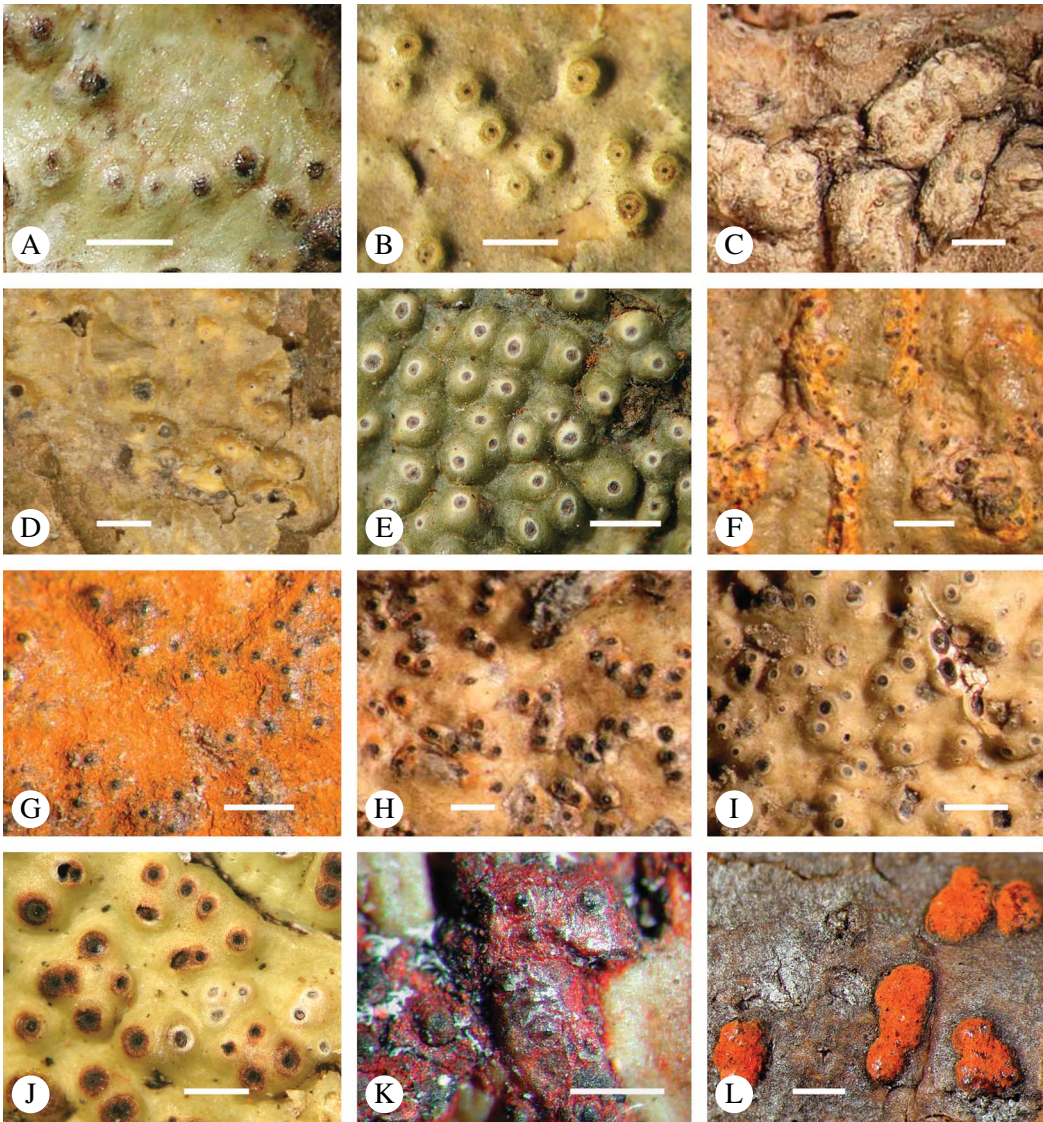


FIG. 14. Habitus of *Astrothelium* species. A & B, *A. pupula* (A, 'West Indies', holotype; B, French Guiana, lectotype of *Pseudopyrenula porinoides*); C, *A. megochroleucum* (El Salvador, holotype); D & E, *A. thelotrenoides* (D, Colombia, lectotype; E, Brazil, van den Boom 1010); F, *A. neoinspersum* (El Salvador, holotype); G, *A. inspersaeneum* (Brazil, holotype); H, *A. aenascens* (Papua New Guinea, isotype); I, *A. rubrocrystallinum* (Brazil, holotype); J, *A. buckii* (Brazil, isotype); K, *A. coccineum* (Mexico, holotype); L, *A. aurantiacocinereum* (New Caledonia, holotype). Scales = 1 mm.

Port Mout, 14 ii 1985, Parwardhan, Nagarkar & Sethy AMH 85.36 (ABL!—isotype).

(Fig. 35G)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypetelioid, with apical ostioles, solitary, 0.9–1.3 mm diam., prominent, hemispherical, basally to laterally covered by thallus but upper part whitish, rough, with narrow, blackish ostiolar spot. *Hamathecium* clear, yellow, IKI–. *Ascospores*



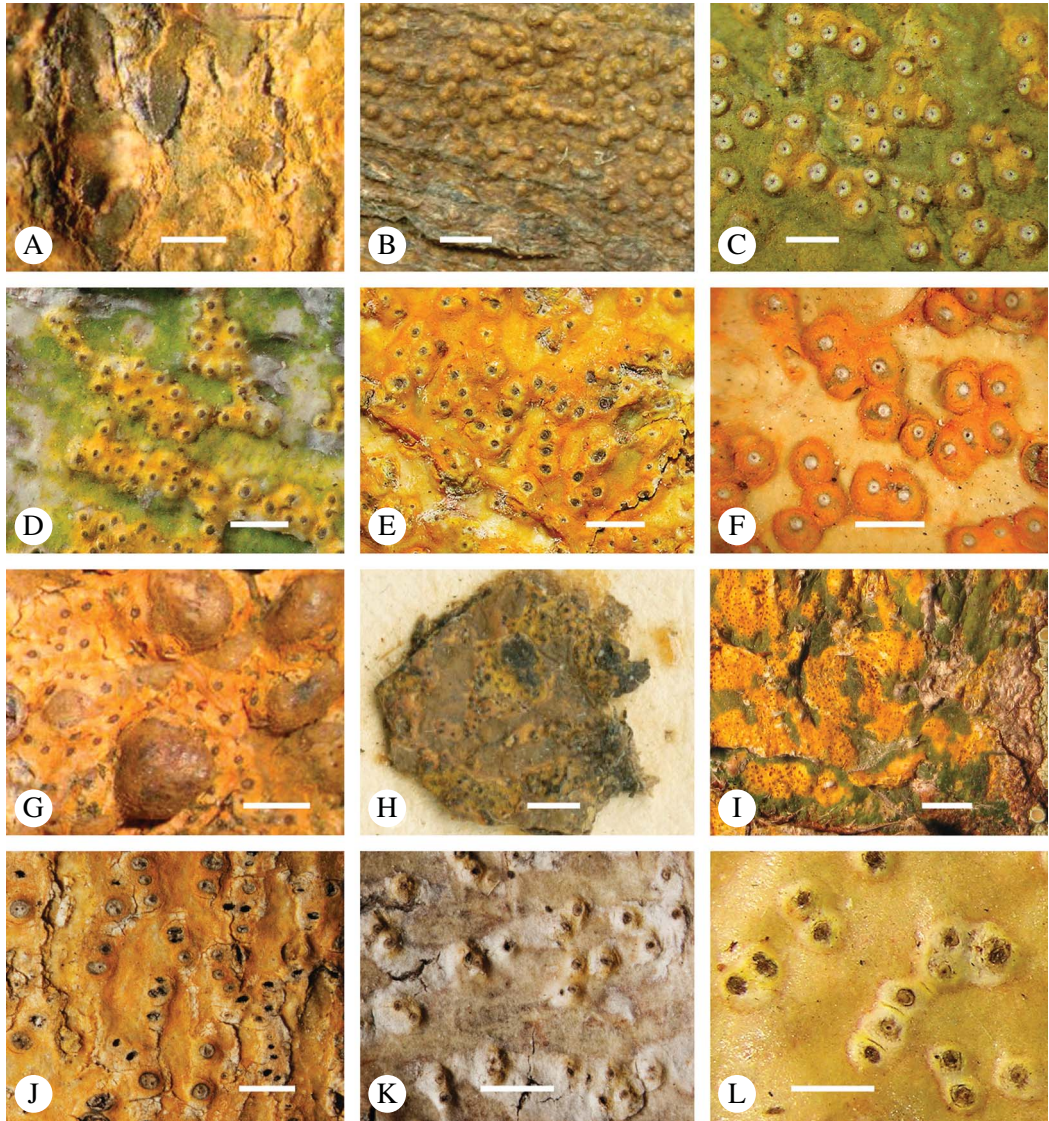


FIG. 15. Habitus of *Astrothelium* species. A, *A. flavum* (Brazil, holotype); B–F, *A. aeneum* (B, French Guiana, isotype of *Verrucaria heterochroa*; C, Brazil, Cáceres 517; D, USA, Florida, Lücking 26814; E, Colombia, *Moncada* 3374; F, Costa Rica, *Dodge* 6486); G, *A. flavostromatum* (Brazil, holotype); H & I, *A. kunzei* (H, Surinam, holotype; I, El Salvador, Lücking 28137); J, *A. megaeneum* (Bolivia, holotype); K, *A. pallidoflavum* (Bolivia, holotype); L, *A. subcatervarium* (Brazil, holotype). Scales = 1 mm.

6–8 per ascus, densely muriform, fusiform, (85–)100–170 × 23–33 μm, with distinctly thickened median septum, yellow, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from India).

***Astrothelium amazonum* (R. C. Harris)  
Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816654



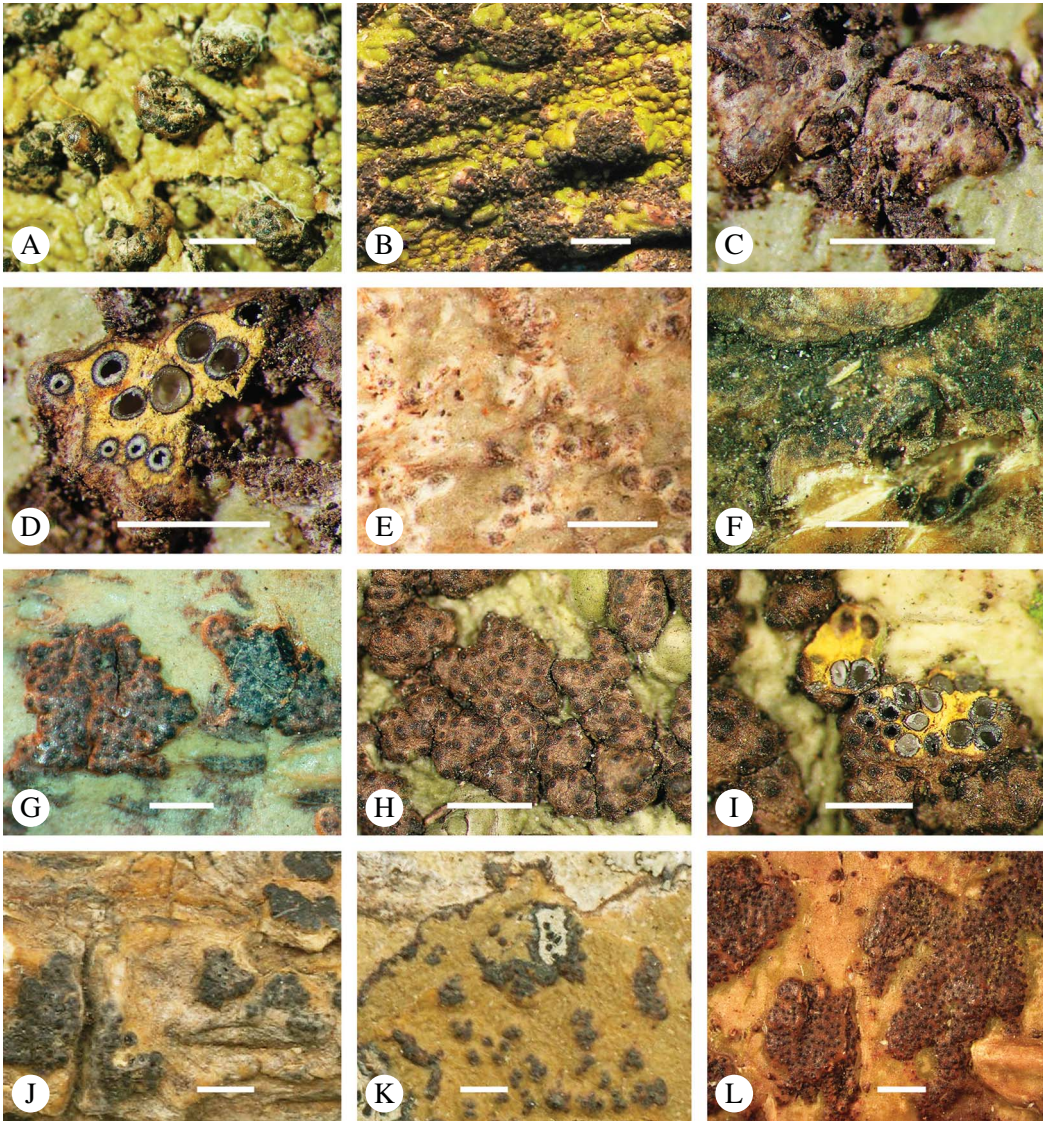


FIG. 16. Habitus of *Astrothelium* species. A & B, *A. endochryseum* (A, Brazil, holotype; B, El Salvador, *Lücking* 28121); C & D, *A. laevithallinum* (Brazil, holotype); E, *A. aeneoides* (Brazil, holotype); F–I, *A. degenerans* (F, Dominica, holotype; G, Puerto Rico, *Aptroot* 25734; H & I, Costa Rica, *Lücking* 16657); J–L, *A. feei* (J, ‘South America’, holotype; K, Cuba, lectotype of *Trypethelium mastoideum* var. *macerum*; L, USA, Florida, *Nelsen* s. n.). Scales = 1 mm.

*Cryptothelium amazonum* R. C. Harris, *Acta Amazon. (Suppl.)* 14: 65 (‘1984’) [1986]; type: Brazil, Amazonas, Reserva Biológica de Campina, *Dumont* 107 (NY!—isotype).

*Verrucaria aurantia* Eschw. in Martius, *Icon. Sel. Pl. Crypt.* 2: 15 (1828) *nom. illeg., non* (Pers.) Wibel (1799); type: Brazil, *Martius* s. n. (M—holotype, not seen).

(Fig. 37I)

*Thallus* corticate, light olive-green to yellowish, uneven to somewhat bullate and often pseudogall-inducing.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, not pseudostromatic, 0.8–1.2 mm diam., erumpent to



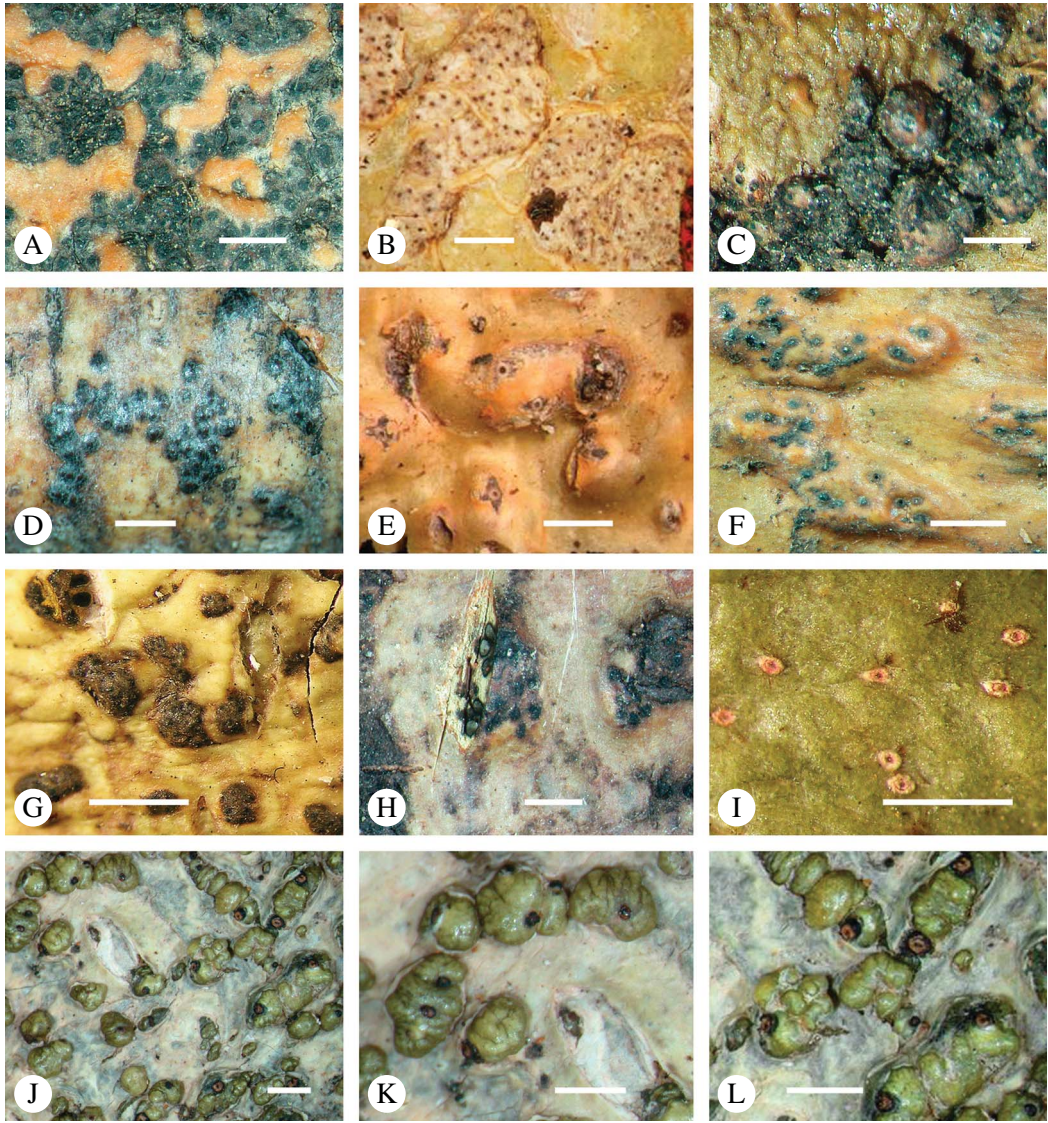


FIG. 17. Habitus of *Astrothelium* species. A, *A. nigrorufum* (India, isotype); B, *A. pseudodissimilum* (Papua New Guinea, holotype); C, *A. dissimilum* (India, isotype); D, *A. aff. dissimilum* (South Korea, Aptroot 67444); E, *A. decemseptatum* (Brazil, holotype); F–H, *A. luridum* (F, India, isotype of *Trypethelium endosulphureum*; G, Malaysia, Labuan, isotype of *T. endochraceum*; H, Japan, *Kashiwadani* 19781); I, *A. calosporum* (Cuba, holotype); J–L, *A. rimosum* (Guyana, holotype). Scales = 1 mm.

prominent, wart-shaped to conical, covered by thallus except for papilliform, reddish to brown-black ostiole, internally with yellow-orange, K+ purple, UV+ red pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, oblong-fusiform,

75–95 × 23–28 μm, median septum thickened, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–, ascomata internally with yellow-orange, K+ purple, UV+ red anthraquinone.



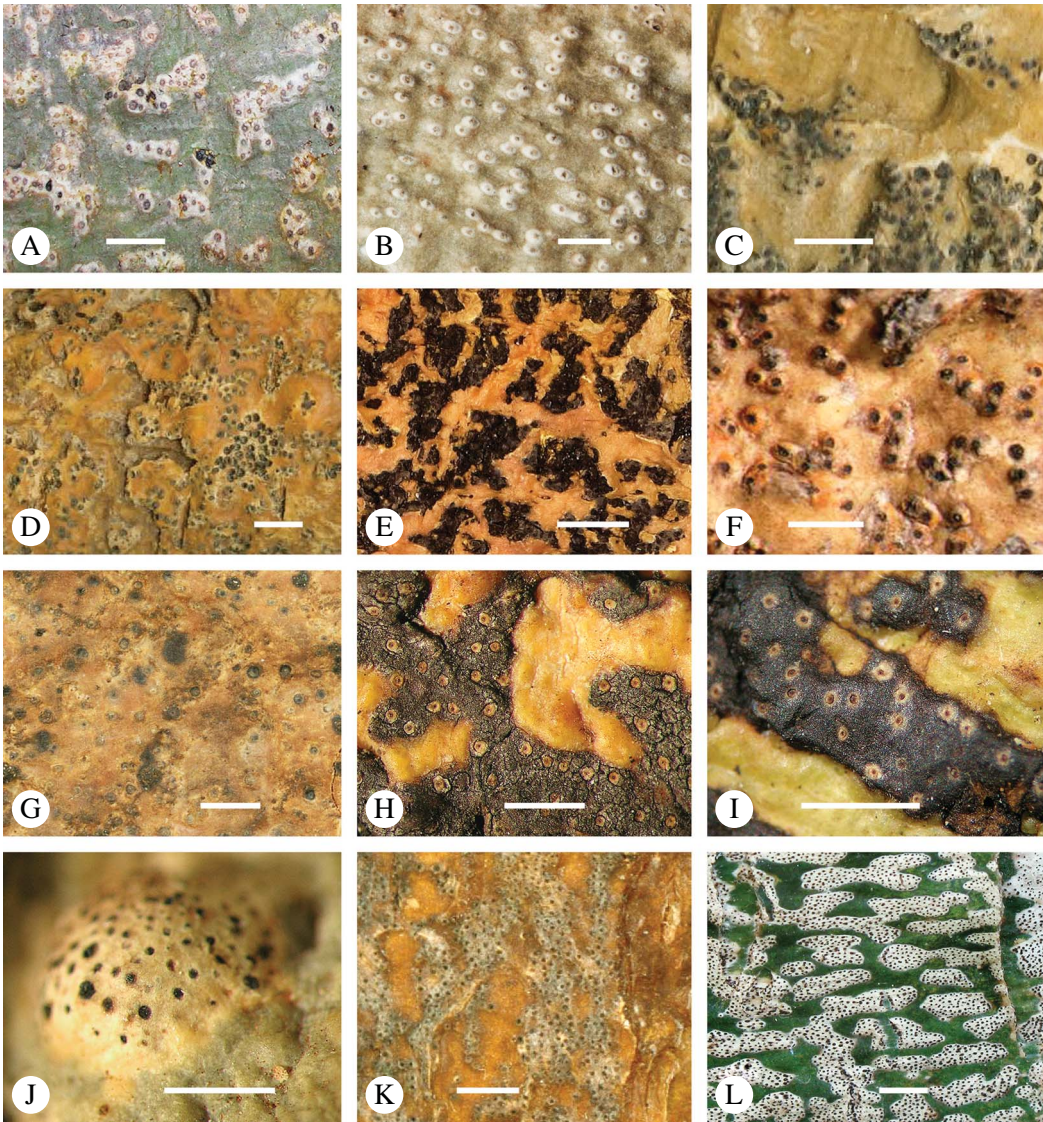


FIG. 18. Habitus of *Astrothelium* species. A, *A. perspersum* (Gabon, holotype); B, *A. subscoria* (Bolivia, holotype); C–E, *A. scoria* (C, ‘America’, lectotype; D, ‘South America’, holotype of *Pyrenula myriocarpa*; E, Brazil, isotype of *Trypethelium scoria* var. *sordidius*); F, *A. aenascens* (Papua New Guinea, holotype); G, *A. infossum* (São Tomé and Príncipe, holotype); H & I, *A. infuscatulum* (H, Cuba, lectotype; I, Venezuela, *Buck* 11586); J, *A. bicolor* (Cuba, lectotype of *Trypethelium polychroum*); K & L, *A. rufescens* (K, Cuba, lectotype; L, Peru, *Lücking* s. n.). Scales = 1 mm.

**Distribution.** Neotropical (previously reported from Guyana and Brazil).

**New country record. Venezuela:** Amazonas: Alto Orinoco, 15 km W of Esmeralda, 110 m, 1997, *Hafellner & Komposch* 178-3-16 (GZU).

***Astrothelium ambiguum* (Malme)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816655

*Laurera ambigu* Malme, *Ark. Bot.* 19(1): 24 (1924).—  
*Meristosporum ambiguum* Malme (1924) nom. inval.;



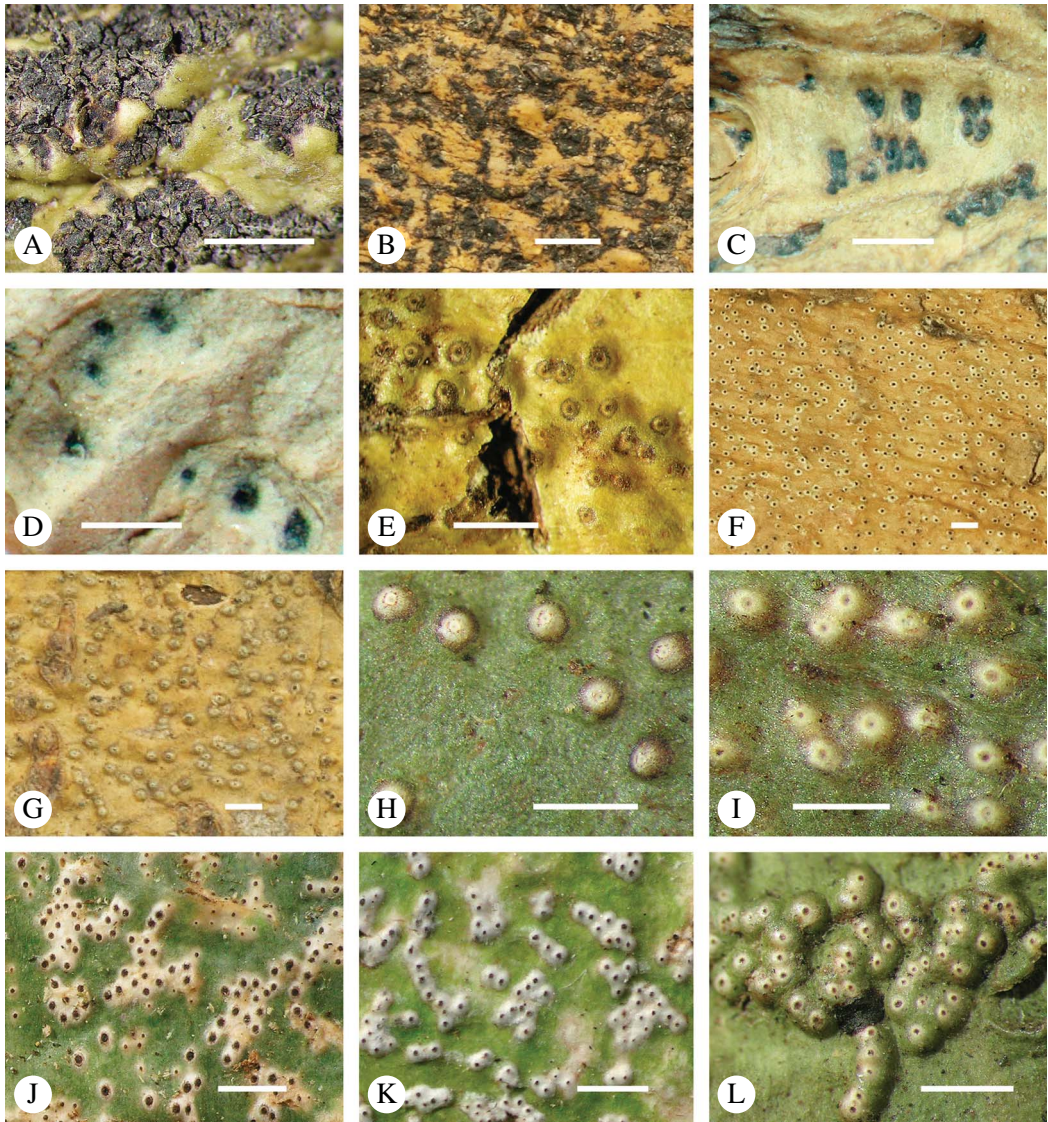


FIG. 19. Habitus of *Astrothelium* species. A, *A. subendochryseum* (Brazil, holotype); B, *A. nigratum* (Cuba, holotype); C & D, *A. meiophorum* (C, India, isotype of *Trypethelium parvicarpum*; D, India, isotype of *T. flavoalbum*); E, *A. ceratinum* (Peru, lectotype); F–L, *A. nitidiusculum* (F, Colombia, isotype; G, French Guiana, holotype of *Pseudopyrenula neglecta*; H, Brazil, Cáceres 438; I, Brazil, Cáceres 437; J, USA, Florida, Lücking 26821; K, USA, Florida, Lücking 26816; L, Brazil, Cáceres 178). Scales = 1 mm.

type: Brazil, Matto Grosso, Cuyabá, *Malmé* 2009 (S!—lectotype, designated here; BM!—isotype).

(Fig. 33F)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.4–0.5 mm diam., erumpent to prominent, hemispherical, mostly exposed, brown-black. *Hamathecium* interspersed, IKI–. *Ascospores* 8 per ascus, muriform, fusiform, 45–60 × 14–20 μm, without distinctly thickened median septum, hyaline, IKI–.



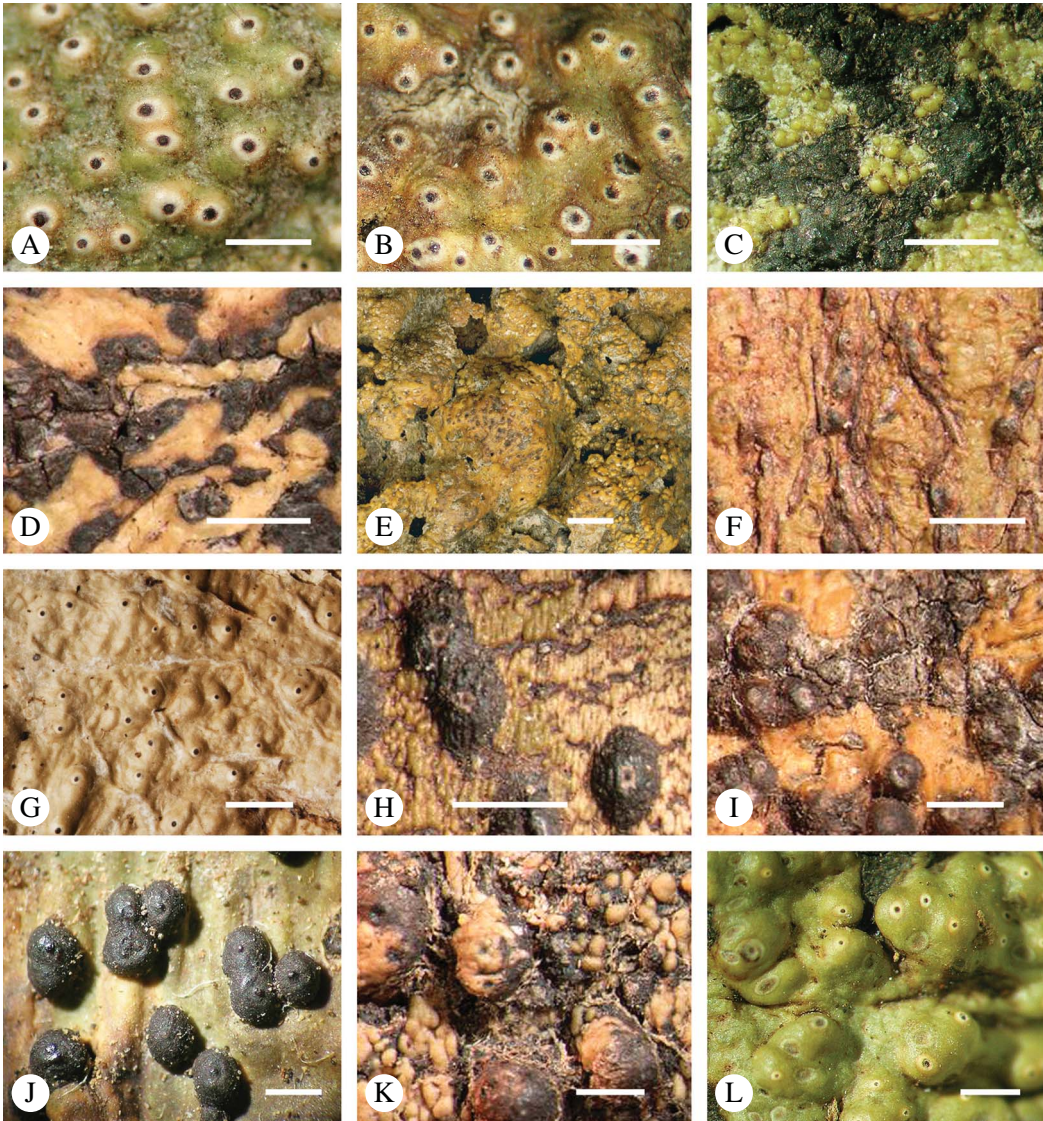


FIG. 20. Habitus of *Astrothelium* species. A & B, *A. floridanum* (A, USA, Florida, Harris 30095; B, USA, Florida, Plitt s. n.); C, *A. scoriothelium* (Guadeloupe; holotype of *Pseudopyrenula infuscatula* var. *tecomae*); D, *A. disjunctum* (Brazil, holotype); E, *A. papulosum* (Colombia, lectotype); F, *A. solitarium* (Brazil, holotype); G, *A. inspersotuberculosum* (Bolivia, holotype); H, *A. clypeatum* (Vietnam, holotype); I, *A. megatropicum* (Guyana, holotype); J, *A. phaeothelium* (Colombia, holotype); K, *A. pseudamulare* (Ecuador, holotype); L, *A. tuberculosum* (Guadeloupe, holotype). Scales = 1 mm.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

***Astrothelium andamanicum* (Makhija & Patw.) Aptroot comb. nov.**

*Distribution.* Neotropical (Brazil).

Mycobank No.: MB 816656



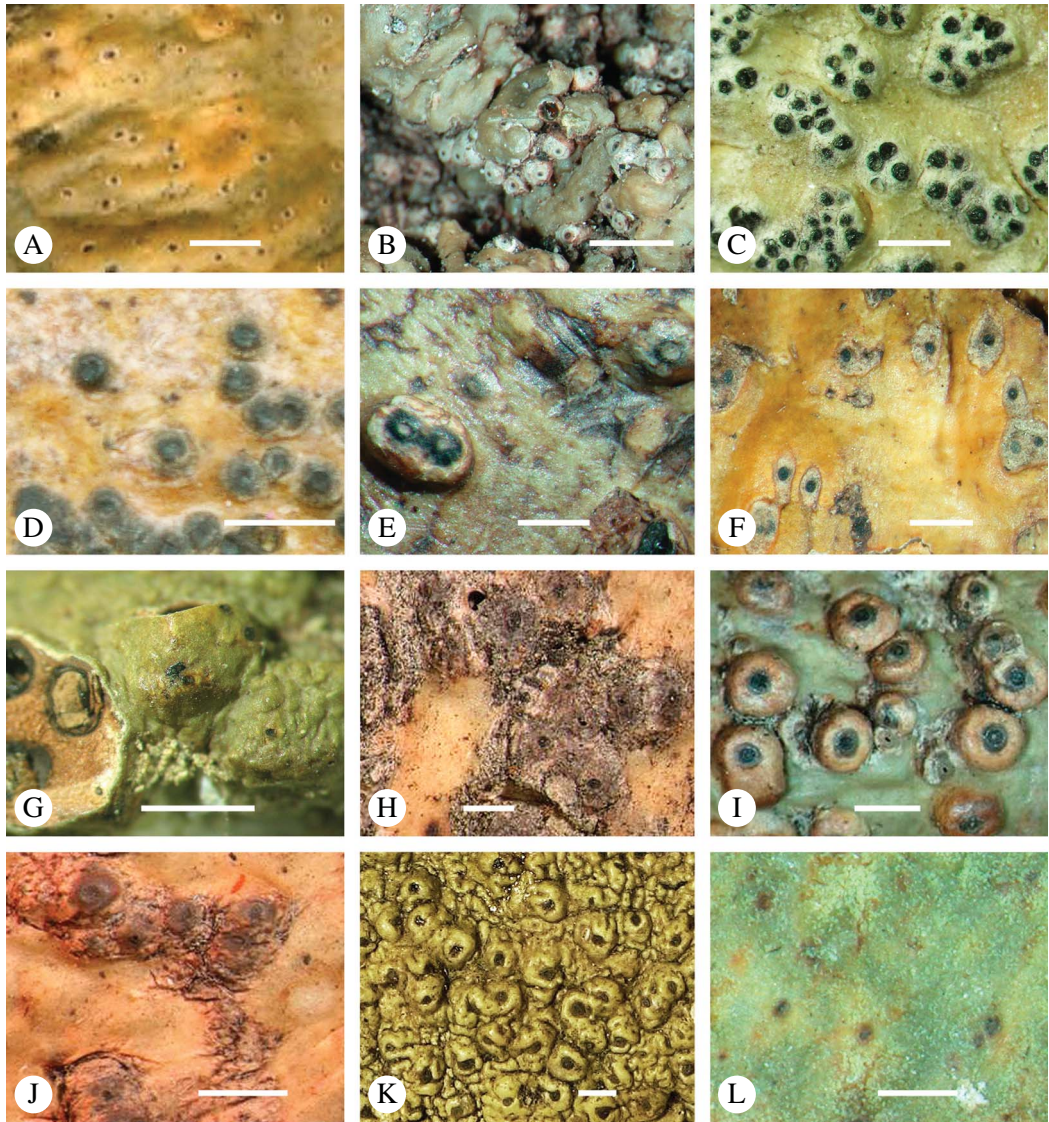


FIG. 21. Habitus of *Astrothelium* species. A, *A. annulare* (Colombia, holotype of *Verrucaria myriomma*); B, *A. galligenum* (Papua New Guinea, isotype); C, *A. ubianense* (Philippines, lectotype); D, *A. trypethelizans* (Malaysia, lectotype); E, *A. nitidulum* (Sri Lanka, holotype); F, *A. macrosporum* (India, isotype); G, *A. pustulatum* (Angola, holotype); H, *A. curvisporum* (Brazil, holotype); I, *A. sipmanii* (Guyana, holotype); J, *A. pseudomegalophthalmum* (Colombia, holotype); K, *A. basilicum* (Uruguay, holotype); L, *A. spectabile* (Argentina, isotype). Scales = 1 mm.

*Cryptothelium andamanicum* Makhija & Patw., *J. Econ. Tax. Bot.* 10: 498 ('1987') [1988].—*Laurera bispora* D. D. Awasthi, *Lichenology in Indian Subcontinent*: 15 (2000) non *Laurera andamanica* D. D. Awasthi (1991); type: India, Andaman Islands, North Andaman, Tugapur Range, Pathat Tikri, 19 xii 1985, Nagarkar & Sethy AMH 85.2323 (ABL)—isotype).

(Fig. 38J)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* pleurothelioid, with eccentric, separate ostioles, solitary, 0.6–1.0 mm diam.,



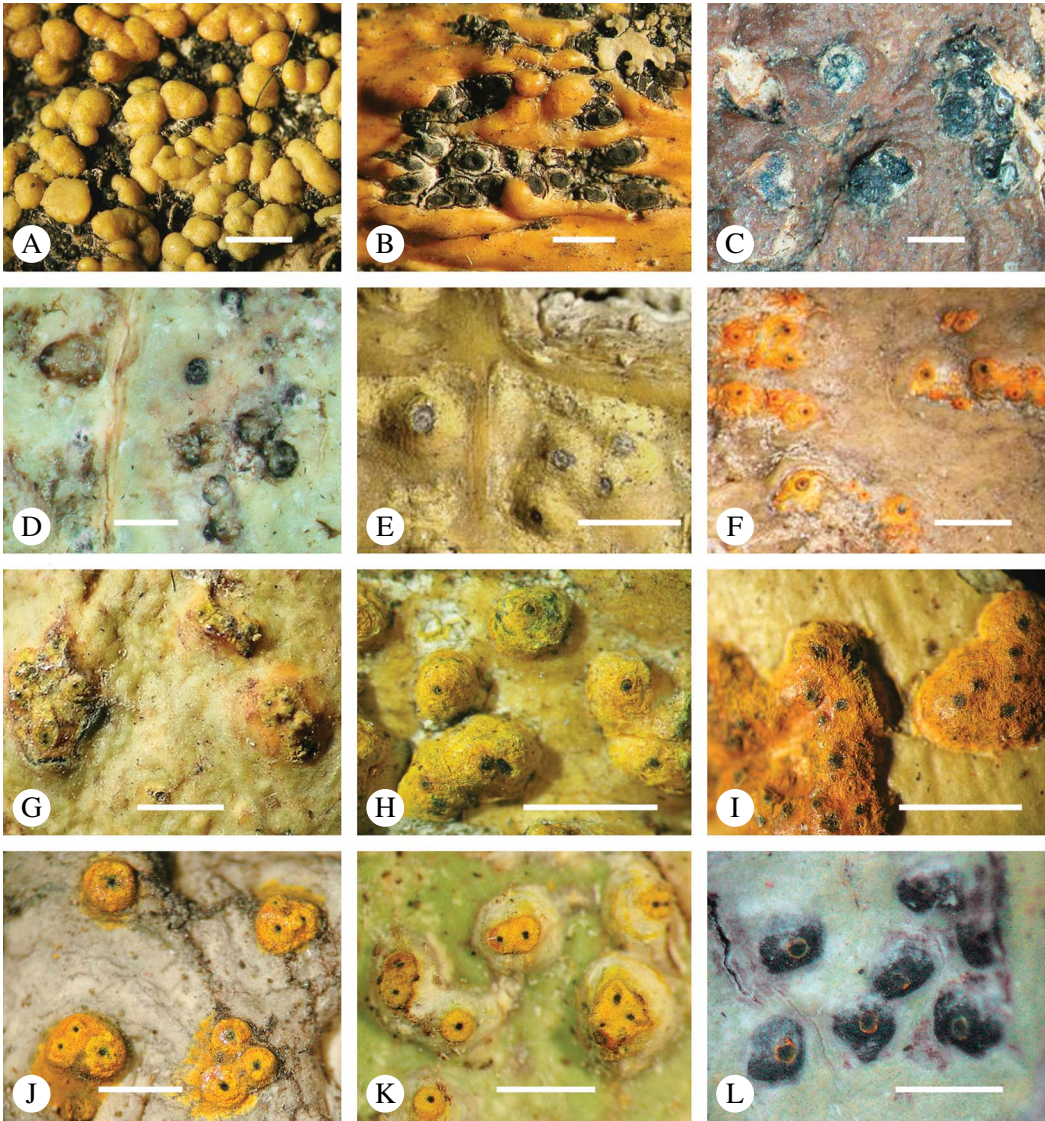


FIG. 22. Habitus of *Astrothelium* species. A & B, *A. megalophthalmum* (Brazil, lectotype); C & D, *A. olivaceofuscum* (C, 'South America', holotype; D, Costa Rica, *Aptroot* 60454); E, *A. dicoloratum* (Venezuela, holotype); F, *A. intersogalbineum* (Singapore, holotype); G–K, *A. macrocarpum* (G, Cuba, holotype of *Trypethelium ochrothelizum*; H, Brazil, lectotype of *Astrothelium ochrothelioides*; I, Brazil, lectotype of *Trypethelium discolor*; J, Panama, *Mori* 4897; K, Costa Rica, *Lücking* 16309c); L, *A. flavocoronatum* (Thailand, holotype). Scales = 1 mm.

erumpent to prominent, partially covered by thallus but becoming exposed and black. *Hamathecium* clear. *Ascospores* 2 per ascus, densely muriform, fusiform,  $80\text{--}130 \times 23\text{--}36\ \mu\text{m}$ , hyaline, IKI–, without distinctly thickened median septum.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from India).



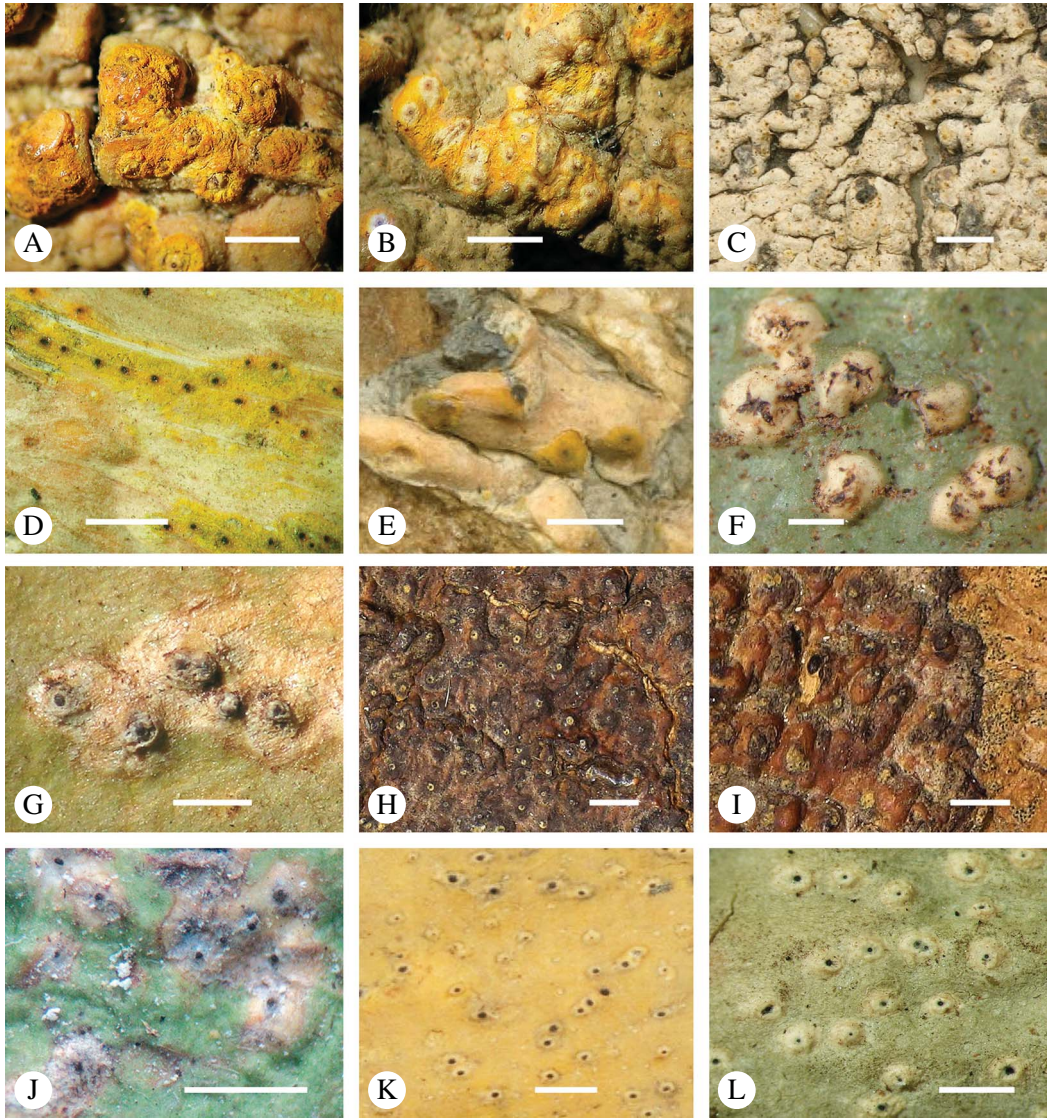


FIG. 23. Habitus of *Astrothelium* species. A & B, *A. ochrothelium* (Colombia, lectotype); C, *A. versicolor* (Puerto Rico, holotype); D, *A. aureomaculatum* (Brazil, holotype); E, *A. grossum* (New Caledonia, holotype); F, *A. sordithecium* (Brazil, holotype); G, *A. leucothelium* (Colombia, holotype); H & I, *A. chrysostomum* (H, Malaysia, Borneo, lectotype; I, Malaysia, Borneo, lectotype of *Trypethelium leucostomum*); J, *A. neovariolosum* (Thailand, holotype); K & L, *A. laevigatum* (K, Brazil, holotype; L, Brazil, holotype of *Astrothelium simplicatum*). Scales = 1 mm.

***Astrothelium annulare* (Fée) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816657

*Pyrenula annularis* Fée, *Essai Crypt. Écorc.*: 73 (1824).—*Verrucaria annularis* (Fée) Spreng., *Syst. Veget.*

4(1): 245 (1827).—*Trypethelium annulare* (Spreng.) Mont., *Ann. Sci. Nat., Bot., sér. 2*, 19: 71 (1843).—*Pseudopyrenula annularis* (Spreng.) Müll. Arg., *Flora* 68: 331 (1885); type: South America, “corticis annosae Cinchonea lancifoliae” (M!—isotype).

*Verrucaria exasperata* Zenker, in Goebel & Kunze, *Pharmazeut. Waarenkunde* 1(3): 183 (1827).—



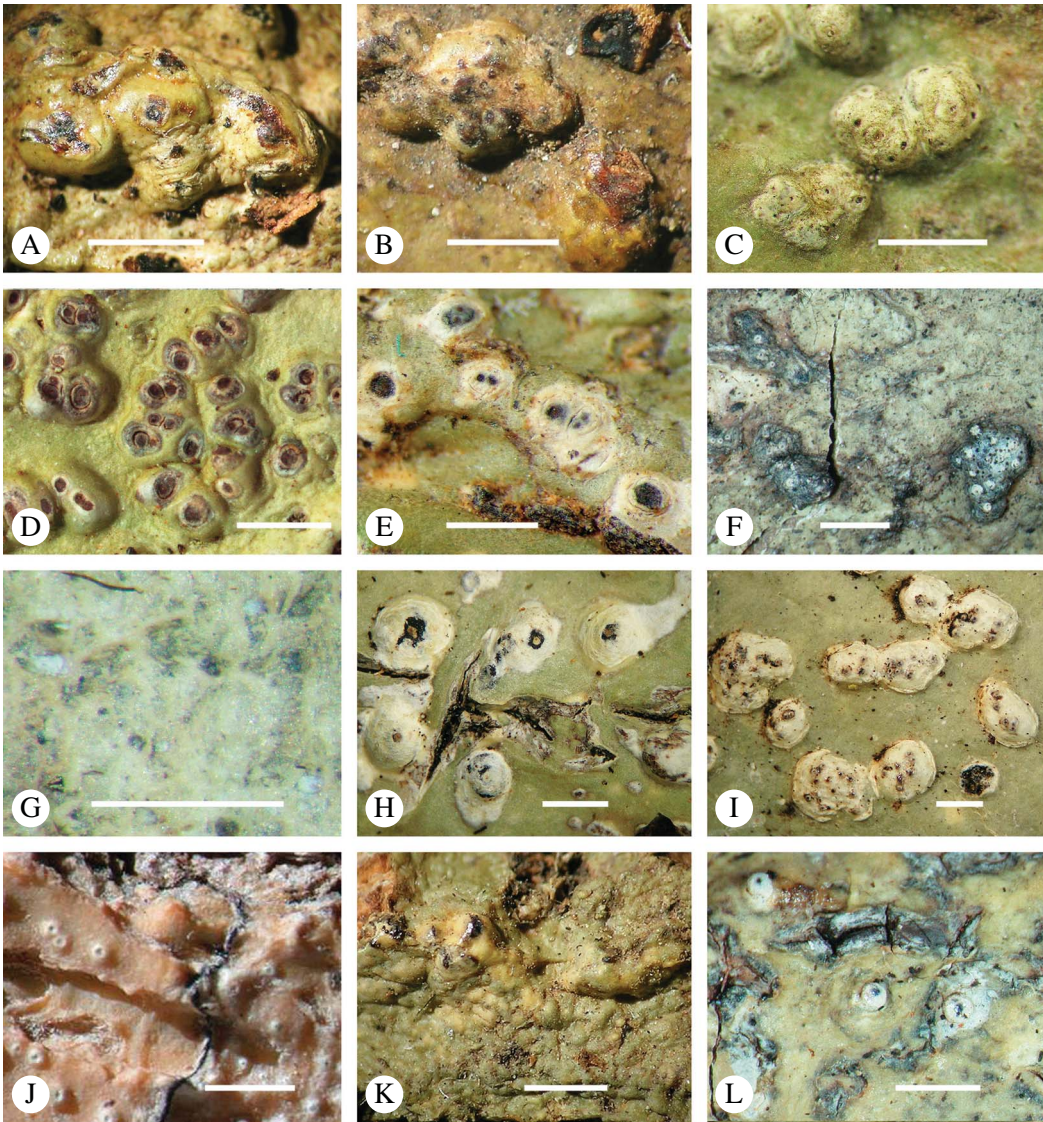


FIG. 24. Habitus of *Astrothelium* species. A–D, *A. variolosum* (A, unknown location, holotype; B, Guinea, holotype; C, Brazil, Cáceres 341; D, USA, Florida, Breuss 28962); E, *A. subinterjectum* (Brazil, holotype); F & G, *A. pseudocypheflatum* (Guyana, Sipman 40458); H & I, *A. interjectum* (H, Brazil, isotype; I, Brazil, Samuels 842); J, *A. ultralucens* (Venezuela, holotype); K & L, *A. leucoconicum* (K, Brazil, holotype; L, Venezuela, Sipman 27215). Scales = 1 mm.

*Trypethelium exasperatum* (Zenker) Zahlbr., *Catal. Lich. Univ.* 1: 492 (1922); type: South America, *s. col.* (lost).

*Trypethelium annulare* var. *detrusum* Mont., *Ann. Sci. Nat., Bot. sér.* 2, 19: 71 (1843); type: French Guiana, Leprieur *s. n.* (PC-Mont—syntypes, not seen).

*Verrucaria myriomma* Nyl., *Ann. Sci. Nat. Bot. sér.* 5, 7: 348 (1867).—*Pseudopyrenula myriomma* (Nyl.) Müll. Arg.,

*Flora* 66: 248 (1883); type: Colombia, Pie de Cuesta, Lindig 98 (H-Nyl 1117!—holotype; BR—istotype).

(Fig. 21A)

*Thallus* corticate, olive-green to brownish, smooth to uneven.



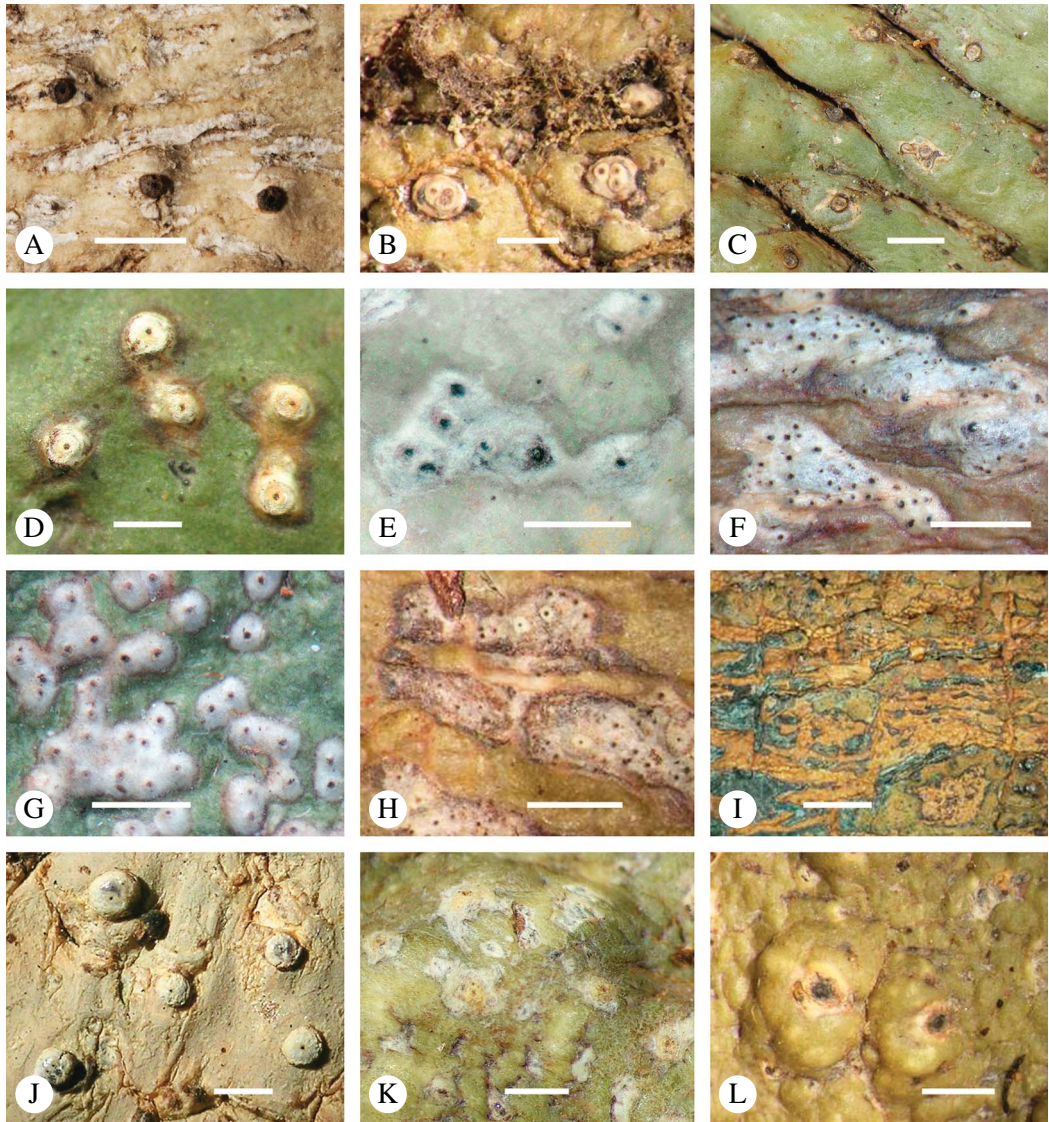


FIG. 25. Habitus of *Astrothelium* species. A, *A. nigrocacuminum* (Bolivia, holotype); B, *A. sinuosum* (Brazil, holotype); C, *A. obtectum* (Brazil, holotype); D, *A. eustomum* (Brazil, Cáceres 2076); E, *A. neglectum* (Thailand, holotype); F, *A. sexloculatum* (Guyana, holotype); G, *A. siamense* (Thailand, holotype); H, *A. octoseptatum* (Brazil, holotype); I, *A. septemseptatum* (Guyana, holotype); J, *A. diplocarpoides* (Cuba, holotype); K, *A. macrostomoides* (Brazil, holotype); L, *A. macrostomum* (Brazil, holotype). Scales = 1 mm.

*Ascomata* trypethelioid, with apical ostioles, solitary to confluent, not pseudo-stromatic, 0.6–0.8 mm diam., immersed-erumpent, covered by thallus except for the dark ostiole surrounded by a narrow, whitish rim. *Hamathecium* clear. *Ascospores* 8 per

ascus, 3-septate, fusiform,  $62\text{--}80 \times 20\text{--}25 \mu\text{m}$ , hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.



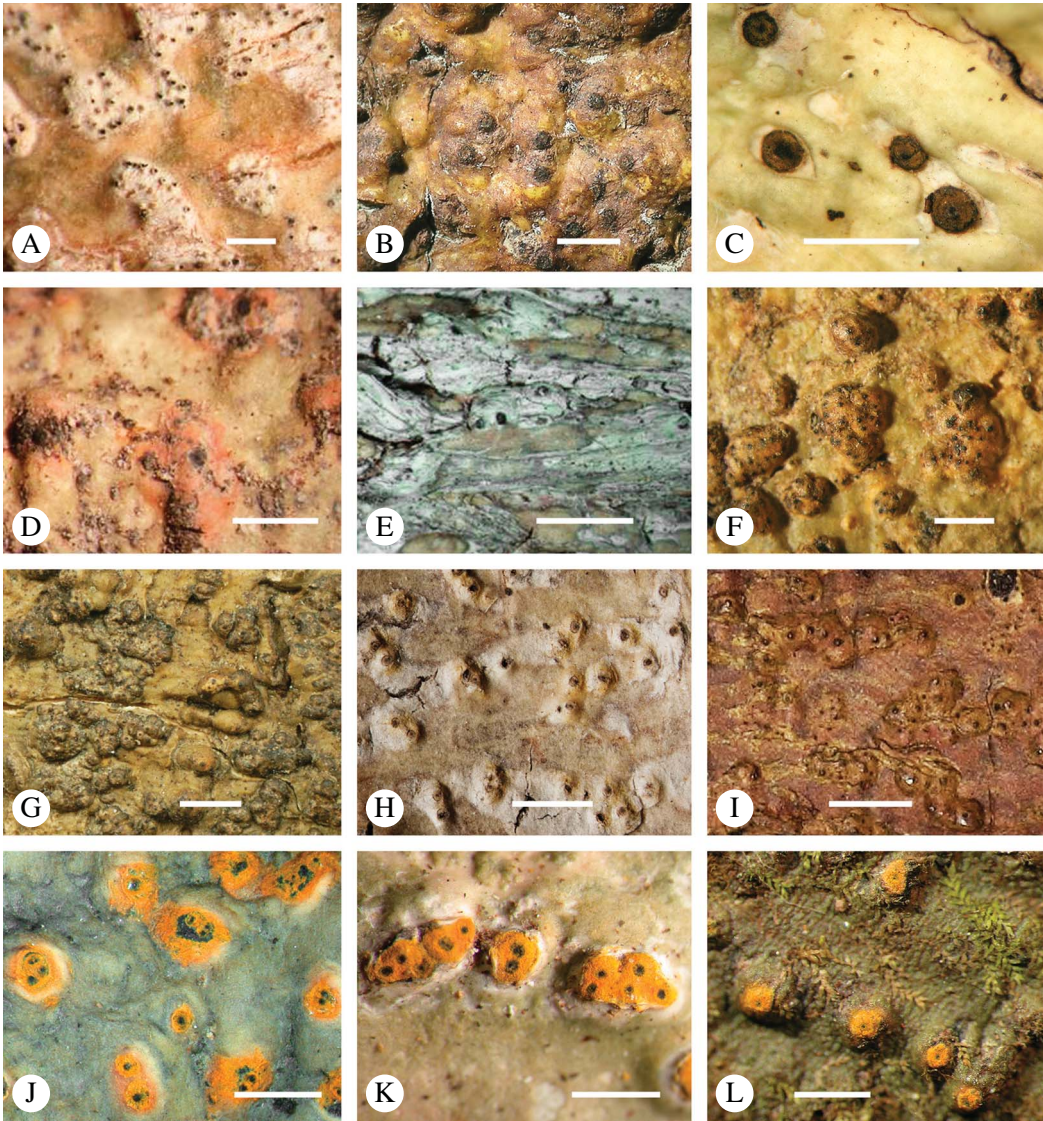


FIG. 26. Habitus of *Astrothelium* species. A, *A. eumultiseptatum* (Brazil, isotype); B & C, *A. diplocarpum* (B, Colombia, holotype; C, USA, Florida, Harris 29938); D, *A. bivelum* (Brazil, isotype); E, *A. pseudoferrugineum* (Indonesia, isotype); F & G, *A. ferrugineum* (F, isolectotype; G, lectotype of *Trypethelium ferrugineum* var. *inornatum*); H, *A. pallidoflavum* (Bolivia, holotype); I–L, *A. cinnamomeum* (I, Brazil, lectotype; J, Hong Kong, Aptroot 43277; K, Brazil, Cáceres & Aptroot 11061; L, Brazil, Cáceres 312). Scales = 1 mm.

**Distribution.** Neotropical (reported from Costa Rica, Colombia, French Guiana).

**Discussion.** According to Hekking & Sipman (1988), *Verrucaria exasperata* Zenker is conspecific with *Trypethelium annulare* var. *detrusum* Mont. and hence

both are included here in the synonymy of *Astrothelium annulare*.

***Astrothelium aurantiacum* (Makhija & Patw.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816658



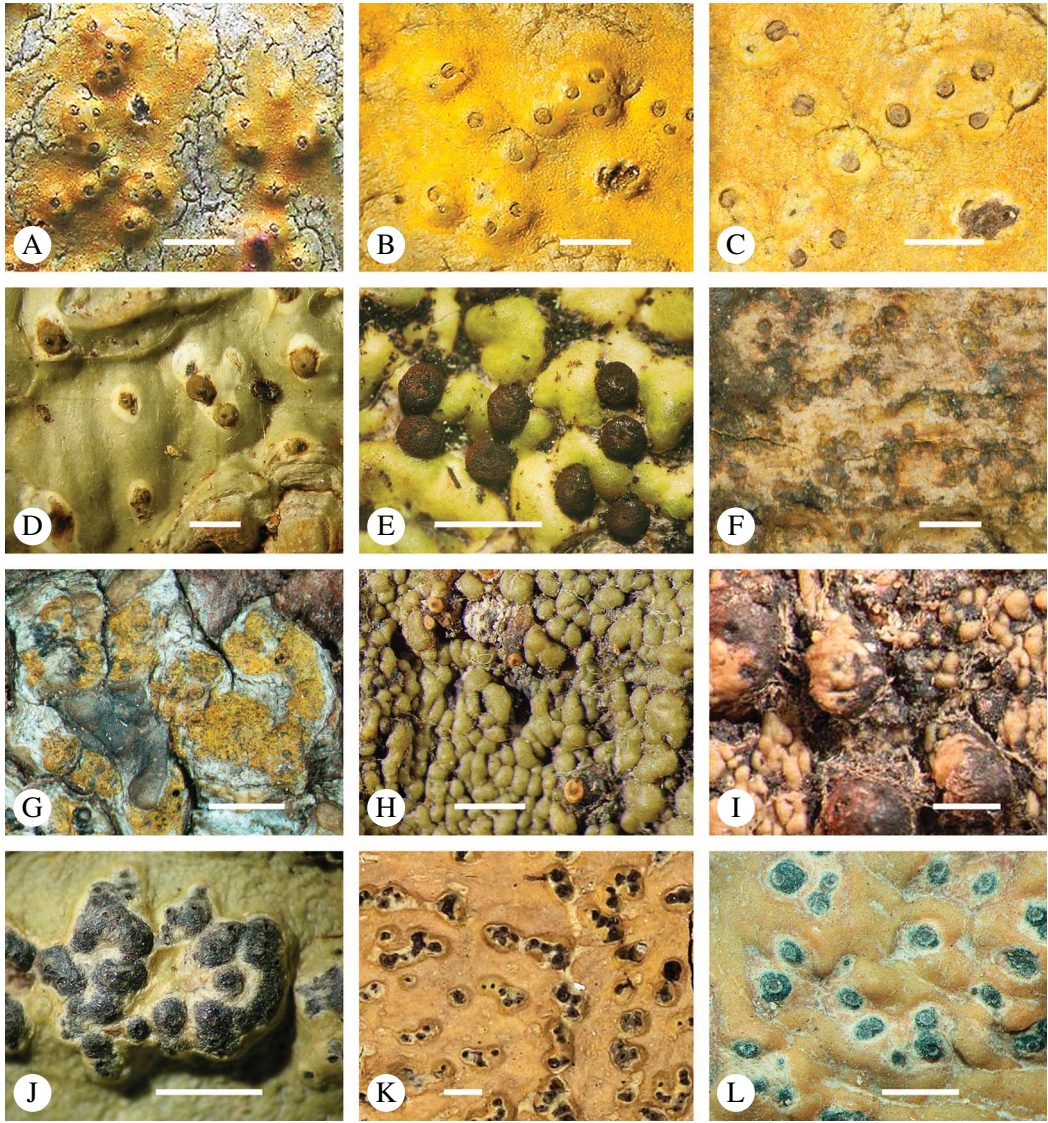


FIG. 27. Habitus of *Astrothelium* species. A–C, *A. croceum* (Brazil, holotype); D & E, *A. ocellatum* (D, Brazil, holotype; E, Costa Rica, *Sipman* 48120); F & G, *A. scorioides* (F, Colombia, holotype; G, French Guiana, *Aptroot* 15442); H, *A. simplex* (Brazil, isotype); I, *A. pseudannulare* (Ecuador, holotype); J–L, *A. stramineicolor* (J, Malaysia, Labuan, lectotype; K, Malaysia, Borneo, lectotype of *Trypethelium stramineum*; L, India, isotype of *Astrothelium subvariolosum*). Scales = 1 mm.

*Laurera aurantiaca* Makhija & Patw., *Mycotaxon* 31: 572 (1988); type: India, Karnataka, Agumbe-Shringera road, *Patwardhan & Nagarkar* s. n. (AMH—holotype, not seen).

(Fig. 33K)

*Thallus* corticate, olive-green to brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.8–1.3 mm diam., strongly prominent to sessile, hemispherical to barrel-shaped



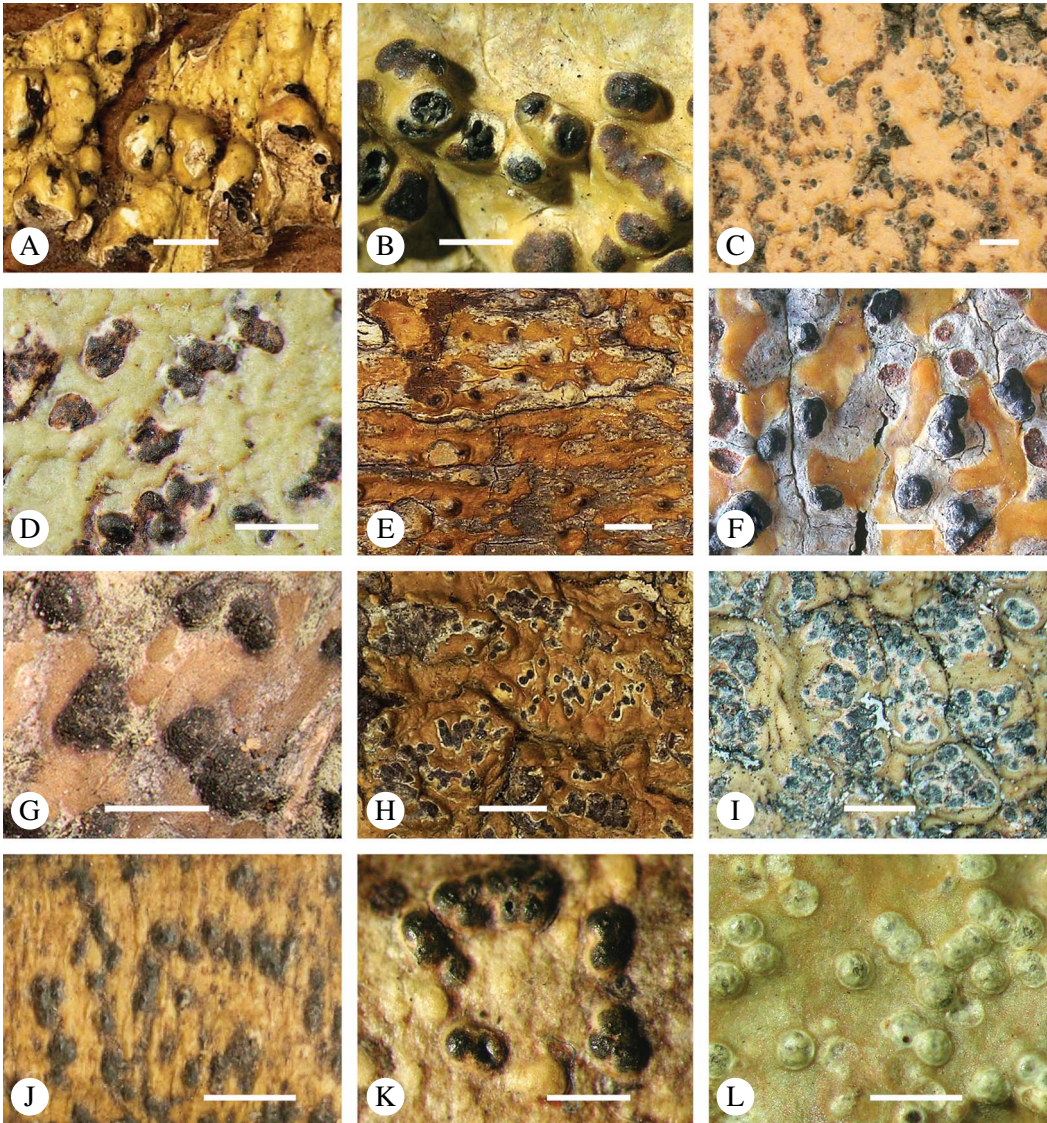


FIG. 28. Habitus of *Astrothelium* species. A, *A. pyrenastrosulphureum* (Brazil, holotype); B, *A. acrophaeum* (Cuba, lectotype); C & D, *A. scorizum* (C, Cuba, holotype; D, Brazil, *Lücking* 29814); E, *A. peranceps* (Malaysia, Borneo, lectotype); F, *A. nigricans* (Brazil, holotype); G, *A. nigrum* (Brazil, isotype); H & I, *A. subfuscum* (H, Singapore, holotype; I, Australia, *Aptroot* 22236c); J, *A. obscurum* (Brazil, holotype); K, *A. oligocarpum* (Australia, lectotype); L, *A. subdissocians* (Thailand, holotype). Scales = 1 mm.

with flattened top, covered by thallus but ostiolar area greyish. *Hamathecium* interspersed with red, K+ purple droplets. *Ascospores* 8 per ascus, densely muriform, ellipsoid,  $115\text{--}135 \times 26\text{--}33 \mu\text{m}$ , with distinctly thickened median septum, hyaline, IKI-.

*Chemistry.* Thallus and ascumata UV-, K-. TLC: no substances detected except for red anthraquinone in hamathecium.

*Distribution.* Eastern palaeotropical (previously reported from India and Papua New Guinea).



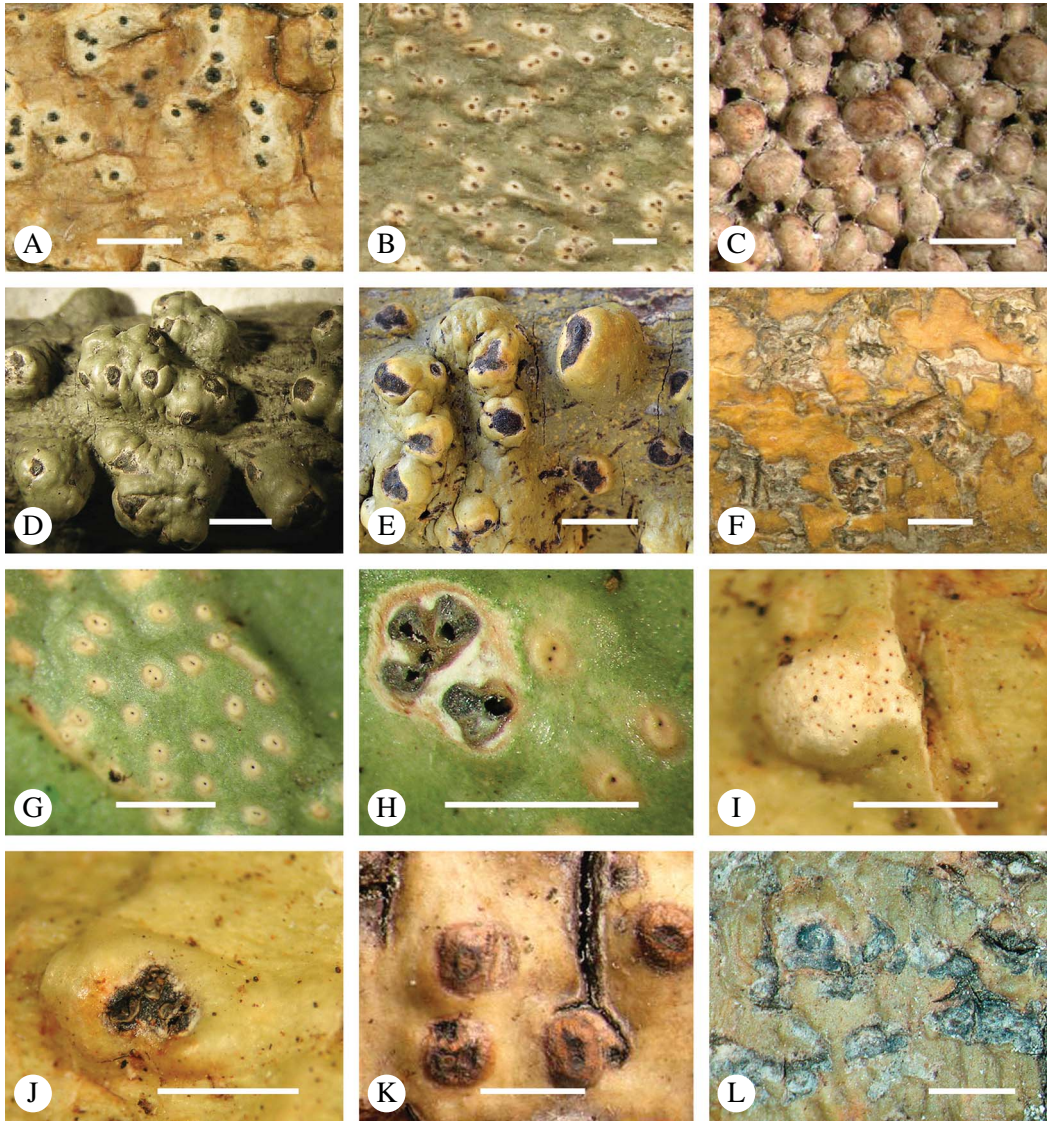


FIG. 29. Habitus of *Astrothelium* species. A & B, *A. crassum* (A, 'South America', lectotype; B, Colombia, holotype of *Astrothelium confusum*); C, *A. globosum* (Brazil, isotype); D & E, *A. fallax* (D, Sri Lanka, isolectotype; E, Sri Lanka, isotype); F, *A. marcidum* ('South America', holotype); G & H, *A. intermedium* (Costa Rica, holotype); I & J, *A. pleiostomum* (Brazil, holotype of *Trypethelium violascens*); K, *A. trypethelioides* (Venezuela, holotype); L, *A. subclandestinum* (Brazil, holotype). Scales = 1 mm.

*New country record. Malaysia: Sarawak: Gunong Mulu National Park, 1978, Coppins 5139 (ABL, E).*

***Astrothelium auratum* (R. C. Harris)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816659

*Laurera aurata* R. C. Harris, *Acta Amazon. (Suppl.)* 14: 67 ('1984') [1986]; type: Brazil, Acre, km 12 on road to Porto Velho, Lowy 961 (NY!—isotype).

(Fig. 32D)

*Thallus* corticate, olive-green to brownish, uneven to verrucose.



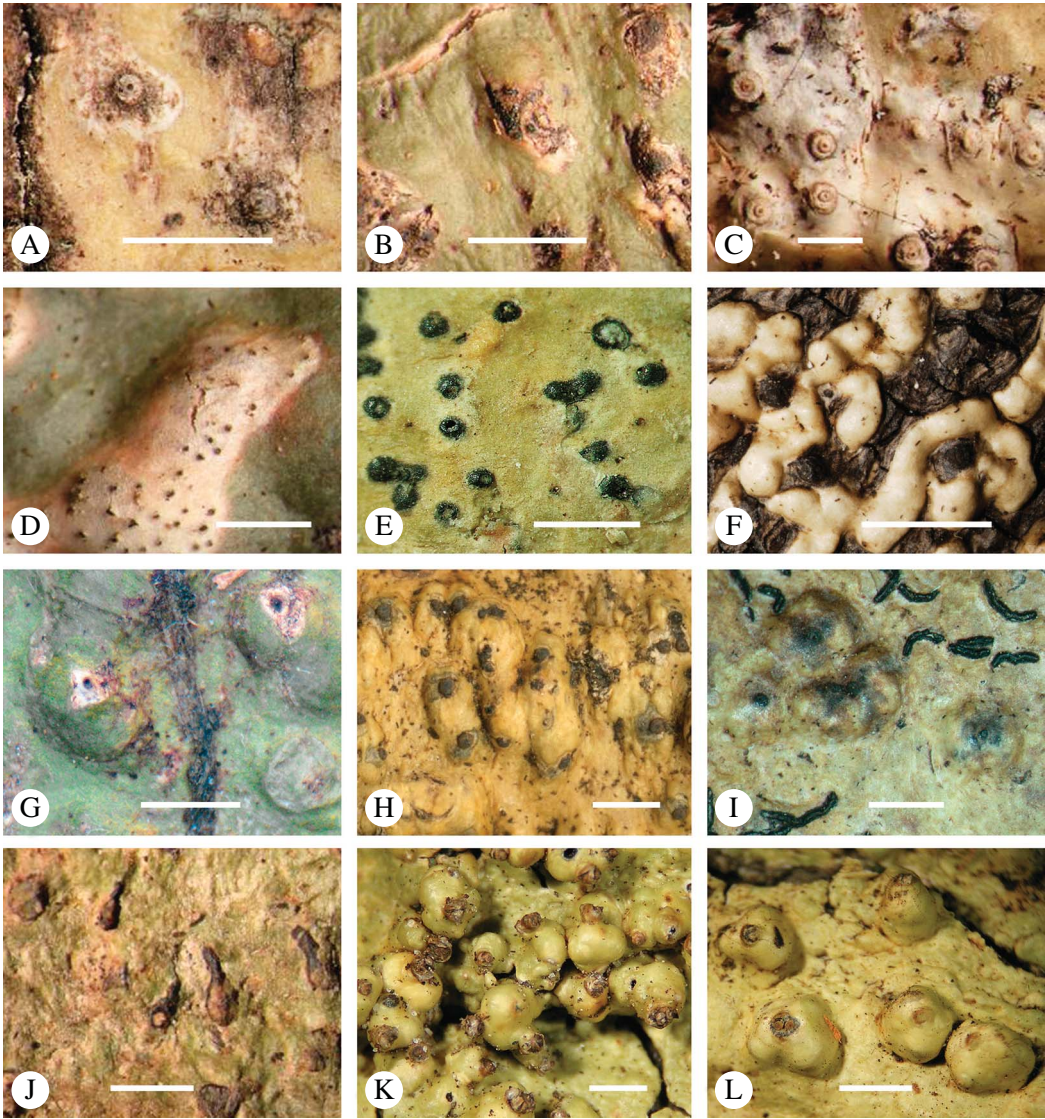


FIG. 30. Habitus of *Astrothelium* species. A, *A. quatuorseptatum* (Brazil, isotype); B, *A. supraclandestinum* (Brazil, isotype); C, *A. zebrinum* (Guyana, holotype); D, *A. novenseptatum* (Brazil, isotype); E, *A. heterophorum* (Philippines, holotype of *Pseudopyrenula elmeri*); F, *A. neodiplocarpum* (Bolivia, holotype); G, *A. macrostiolum* (Thailand, holotype); H & I, *A. robustum* (H, Costa Rica, holotype; I, Colombia, Sipman & Velosa 33504); J, *A. robustosporum* (Brazil, isotype); K & L, *A. gigasporum* (Brazil, isotype). Scales = 1 mm.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata 1–2 mm diam., prominent to sessile, each with 5–15 ascomata, with yellow-orange pigment. *Hamathecium* inspersed, IKI–. *Ascospores* 8 per ascus, muriform, ellipsoid, 60–75 × 20–30 μm,

without distinctly thickened median septum, hyaline, IKI+ violet.

*Chemistry.* Thallus UV–, K–; pseudostromata with yellow-orange, K+ purple, UV+ red anthraquinone.



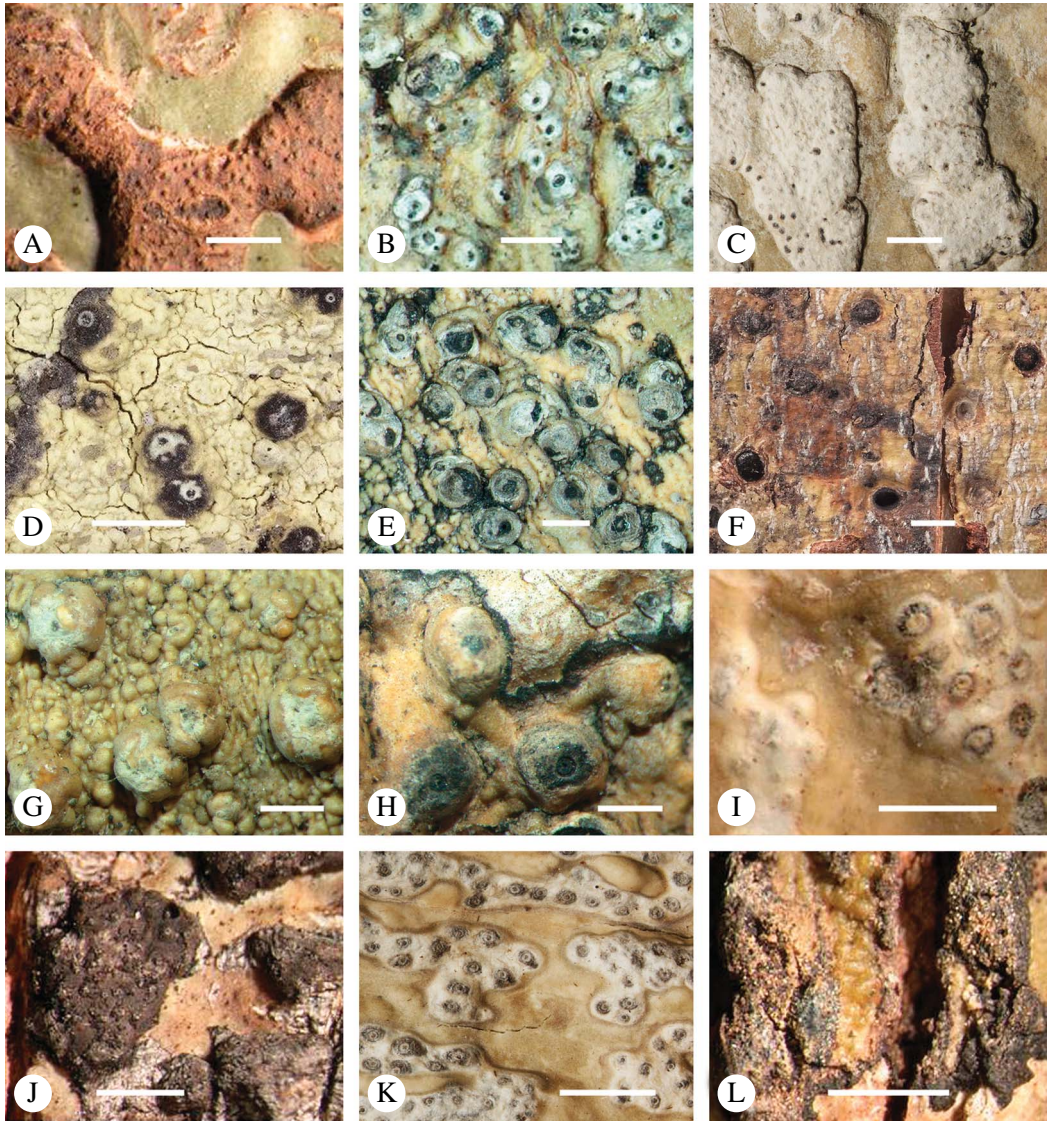


FIG. 31. Habitus of *Astrothelium* species. A, *A. flavoduplex* (Brazil, isotype); B, *A. sanguineoxanthum* (Brazil, holotype); C, *A. elixii* (Bolivia, holotype); D, *A. stramineum* (Brazil, holotype); E, *A. meristosporoides* (Papua New Guinea, Aptroot 19135); F–H, *A. meristosporum* (F, India, holotype of *Verrucaria anoptella*; G, India, isotype of *Laurera columellata*; H, India, isotype of *L. indica*); I, *A. lucidothvallinum* (Guyana, holotype); J, *A. ochroleucoides* (Brazil, isotype); K, *A. variabile* (Bolivia, holotype); L, *A. xanthosuperbum* (Brazil, isotype). Scales = 1 mm.

**Distribution.** Neotropical; reported from Brazil.

**New country records.** **Venezuela:** Amazonas: Alto Orinoco, 15 km W of Esmeralda, 110 m, 1997, Hafellner & Komposch 178-5-43 (GZU).—**Guyana:** Potaro-Siparuni:

surroundings of Paramakatoi Village, 800 m, 1996, Sipman 41197 p.p. (B).

***Astrothelium aureomaculatum* (Vain.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816660



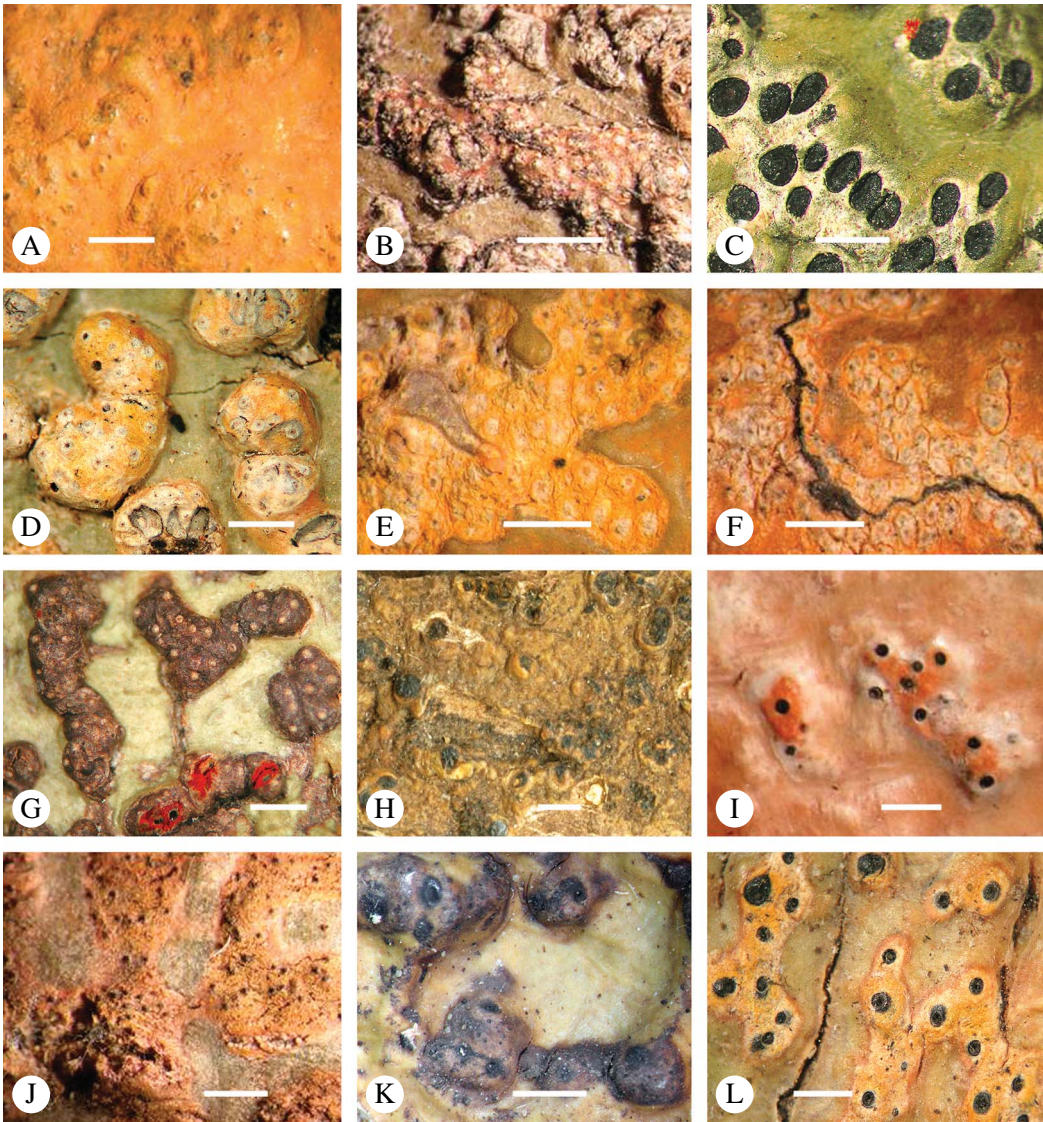


FIG. 32. Habitus of *Astrothelium* species. A, *A. condoricum* (Ecuador, holotype); B, *A. duplicatum* (Brazil, isotype); C, *A. sierraleonense* (Sierra Leone, holotype); D, *A. auratum* (Brazil, isotype); E, *A. graphicum* (Brazil, isotype); F, *A. flavomaculatum* (Ecuador, holotype); G, *A. sanguinarium* (Brazil, Brako 7136); H, *A. deforme* (Malaysia, Borneo, lectotype); I, *A. laurerosphaerioides* (Guyana, holotype); J, *A. mesoduplex* (Brazil, isotype); K, *A. vezdae* (India, holotype); L, *A. chrysoglyphum* (Dominica, Imshaug 33509A). Scales = 1 mm.

*Pseudopyrenula aureomaculata* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 207 (1890).—*Trypethelium aureomaculatum* (Vain.) Zahlbr., *Catal. Lich. Univ.* 1: 488 (1922); type: Brazil, Minas Gerais, Caraça, Vainio s.n. (TUR-Vain 30749!—holotype; BM!—isotype; Vainio, *Lich. Bras.* 1473).

(Fig. 23D)

*Thallus* ecorticate, light brownish to greenish grey, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic; pseudostromata 0.5–1.0 mm broad, immersed to erumpent,



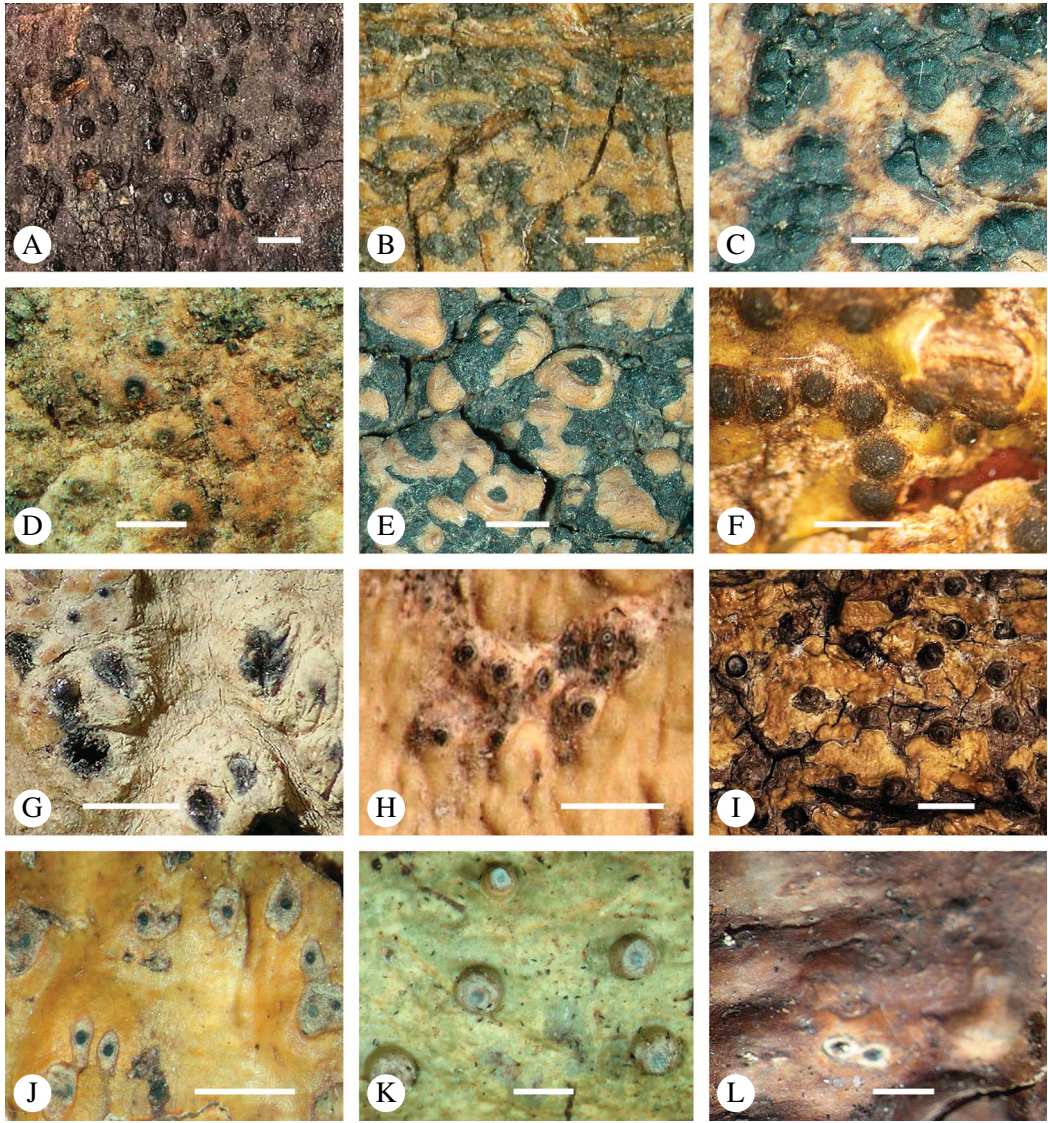


FIG. 33. Habitus of *Astrothelium* species. A–E, *A. subdiscretum* (A, India, isotype; B, Cuba, holotype of *Bathelium phaeomelodes*; C, India, isotype of *Laurera verrucoaggregata*; D, India, isotype of *L. subspaerioides*; E, Netherlands Antilles, van Slageren 8406b); F, *A. ambiguum* (Brazil, lectotype); G, *A. indicum* (India, isotype); H, *A. colombiense* (Colombia, holotype); I, *A. megaleium* (Malaysia, Sarawak, holotype); J, *A. macrosporum* (India, isotype); K, *A. aurantiacum* (Papua New Guinea, Aptroot 18148); L, *A. sikkimense* (India, isotype). Scales = 1 mm.

with several joined ascomata, forming irregular groups or lines, with yellow pigment cover except for blackish ostiolar areas. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform,  $28\text{--}35 \times 10\text{--}15\ \mu\text{m}$ , hyaline, IKI–.

*Chemistry.* Thallus UV+ yellow, K–, with lichexanthone; pseudostromata with yellow, K+ purple, UV+ red anthraquinone.

*Discussion.* This species is removed here from synonymy with *Astrothelium versicolor*,



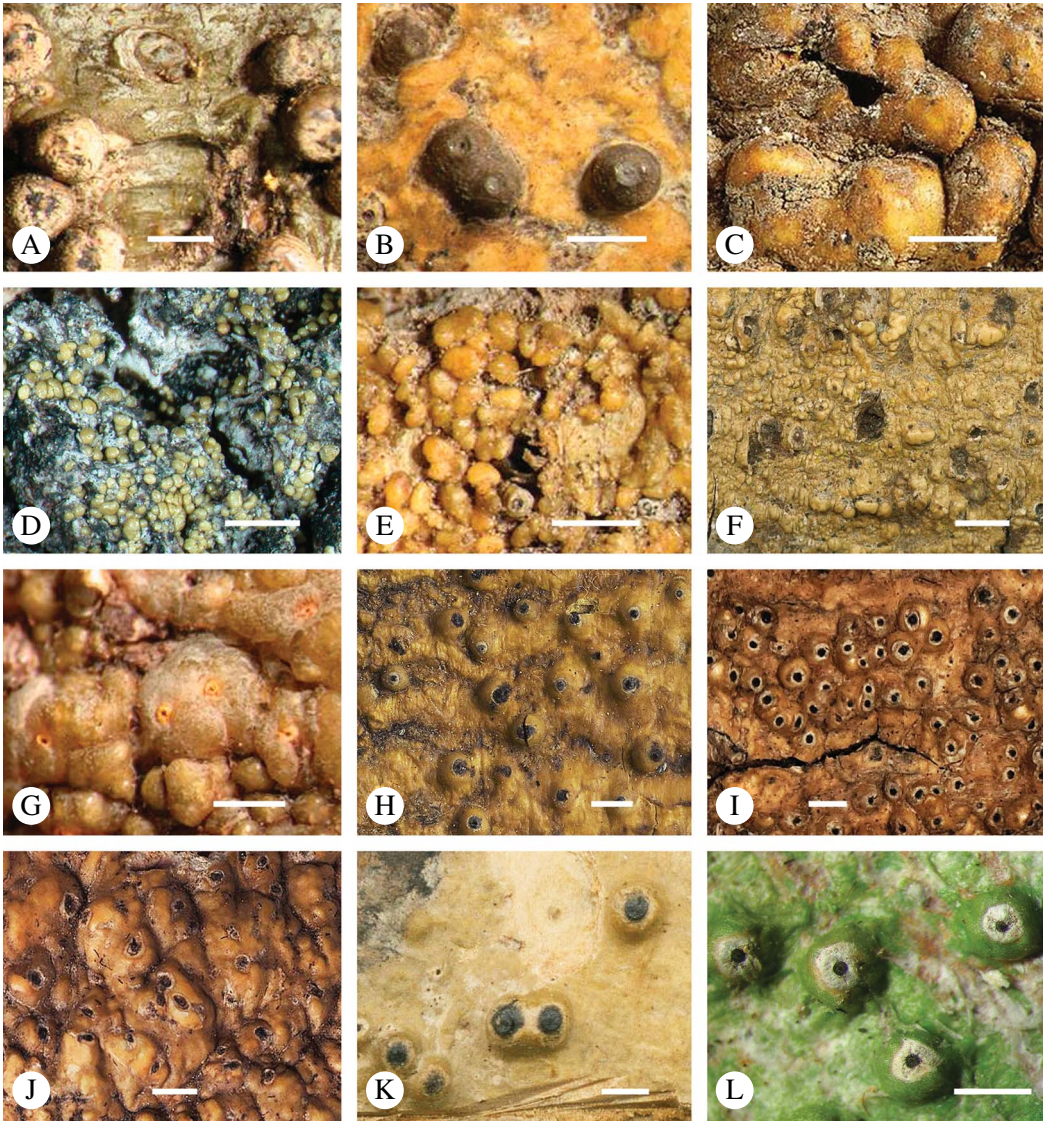


FIG. 34. Habitus of *Astrothelium* species. A, *A. alboverrucoides* (Indonesia, Sumatra, holotype); B, *A. flavomeristosporum* (Philippines, holotype); C, *A. philippinense* (Philippines, holotype); D, *A. papillosum* (Papua New Guinea, Aptroot 37607); E, *A. komposchii* (Venezuela, holotype); F, *A. irregulare* (Brazil, holotype); G, *A. flavostiolatum* (Ecuador, holotype); H–L, *A. megaspernum* (H, Angola, isotype of *Thelenella fulva*; I, Brazil, holotype of *Trypethelium ostendatum*; J, Sri Lanka, isotype of *Laurera megasperma* f. *immersa*; K, São Tomé and Príncipe, holotype of *Verrucaria euthelia*; L, Costa Rica, *Lücking* s. n.). Scales = 1 mm.

from which it differs substantially in thallus and ascoma morphology, the latter having a thick, bullate, whitish thallus with the joined ascomata dispersed.

*Distribution.* Neotropical (reported from Brazil).

***Astrothelium basilicum* (Kremp.)  
Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816661

*Verrucaria basilica* Kremp., *Bol. Acad. Nac. Ci. Republ. Argentina* 3: 126 (1879).—*Pseudopyrenula basilica*



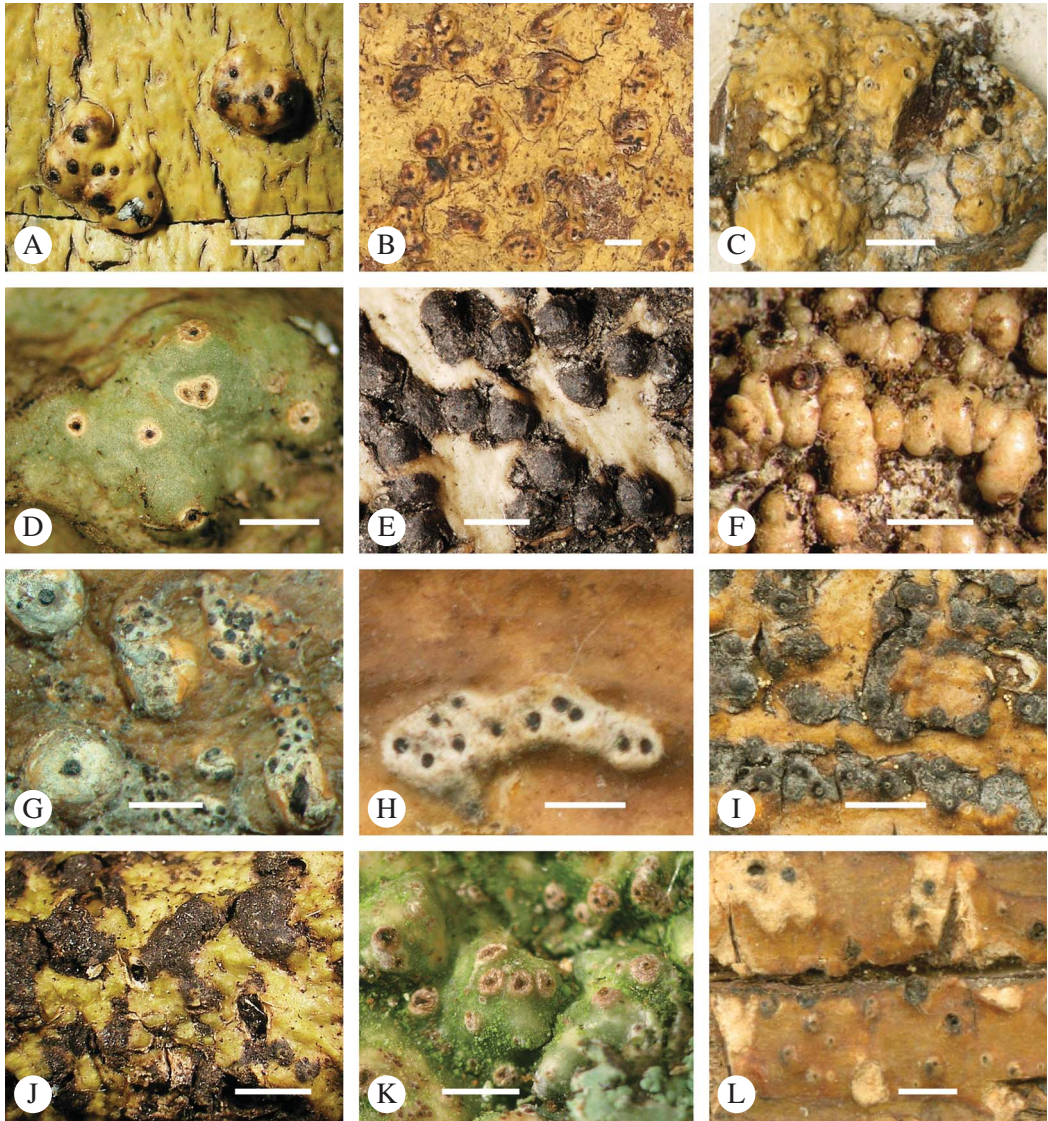


FIG. 35. Habitus of *Astrothelium* species. A & B, *A. variatum* (A, Colombia, holotype; B, Cuba, holotype of *Heufleria subvariata*); C & D, *A. gigantosporum* (C, Cuba, holotype; D, Puerto Rico, *Harris* 27863B); E, *A. amylosporum* (Bolivia, holotype); F, *A. tetrasporum* (Brazil, isotype); G, *A. alboverrucum* (India, isotype); H, *A. sphaerioides* (French Guiana, lectotype); I & J, *A. subdisjunctum* (I, Cuba, holotype; J, Costa Rica, holotype of *Laurera dodgei*); K, *A. nicaraguense* (Nicaragua, *Lücking* 28546); L, *A. exostemmatis* (Jamaica, holotype). Scales = 1 mm.

(Kremp.) Müll. Arg., *Flora* 72: 68 (1889).—*Porina basilica* (Kremp.) Zahlbr., *Catal. Lich. Univ.* 1: 367 (1922).—*Trypethelium basilicum* (Kremp.) R. C. Harris, *Lichenogr. Thomsoniana*: 141 (1998); type: Uruguay, *Lorentz & Hieronymus* s. n. (M!—lectotype; Harris, *Lichenogr. Thomsoniana*: 141, 1998; BM!—isolectotype).

(Fig. 21K)

*Thallus* corticate, olive-green, verrucose-bullate.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent,



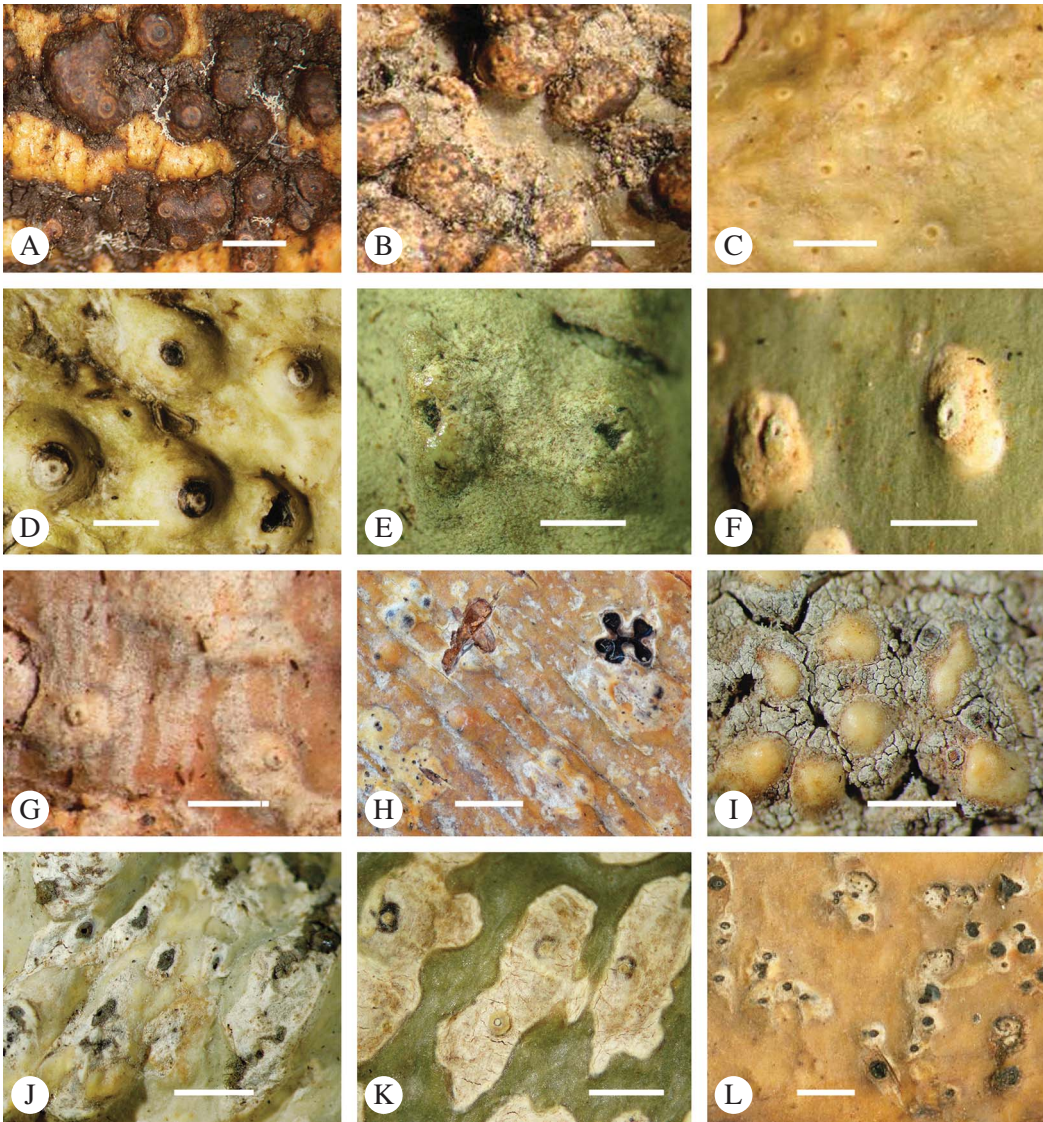


FIG. 36. Habitus of *Astrothelium* species. A, *A. chapadense* (Brazil, holotype); B, *A. corallinum* (Guyana, holotype); C, *A. lucidomedullatum* (Ecuador, holotype); D, *A. carrascoense* (Bolivia, holotype); E, *A. megalostomum* (Brazil, holotype); F, *A. eustomurale* (Brazil, isotype); G, *A. lucidostromum* (Guyana, holotype); H, *A. sepultum* (Peru, isotype of *Trypethelium connivens*); I, *A. cryptolucens* (Panama, holotype); J & K, *A. norisianum* (J, Panama, holotype; K, Venezuela, Guariglia 1485); L, *A. consimile* (Cuba, holotype). Scales = 1 mm.

0.8–1.5 mm diam., erumpent to prominent, covered by thallus except for blackish ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, 11–19-septate, fusiform, 140–190 × 20–25 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Uruguay).



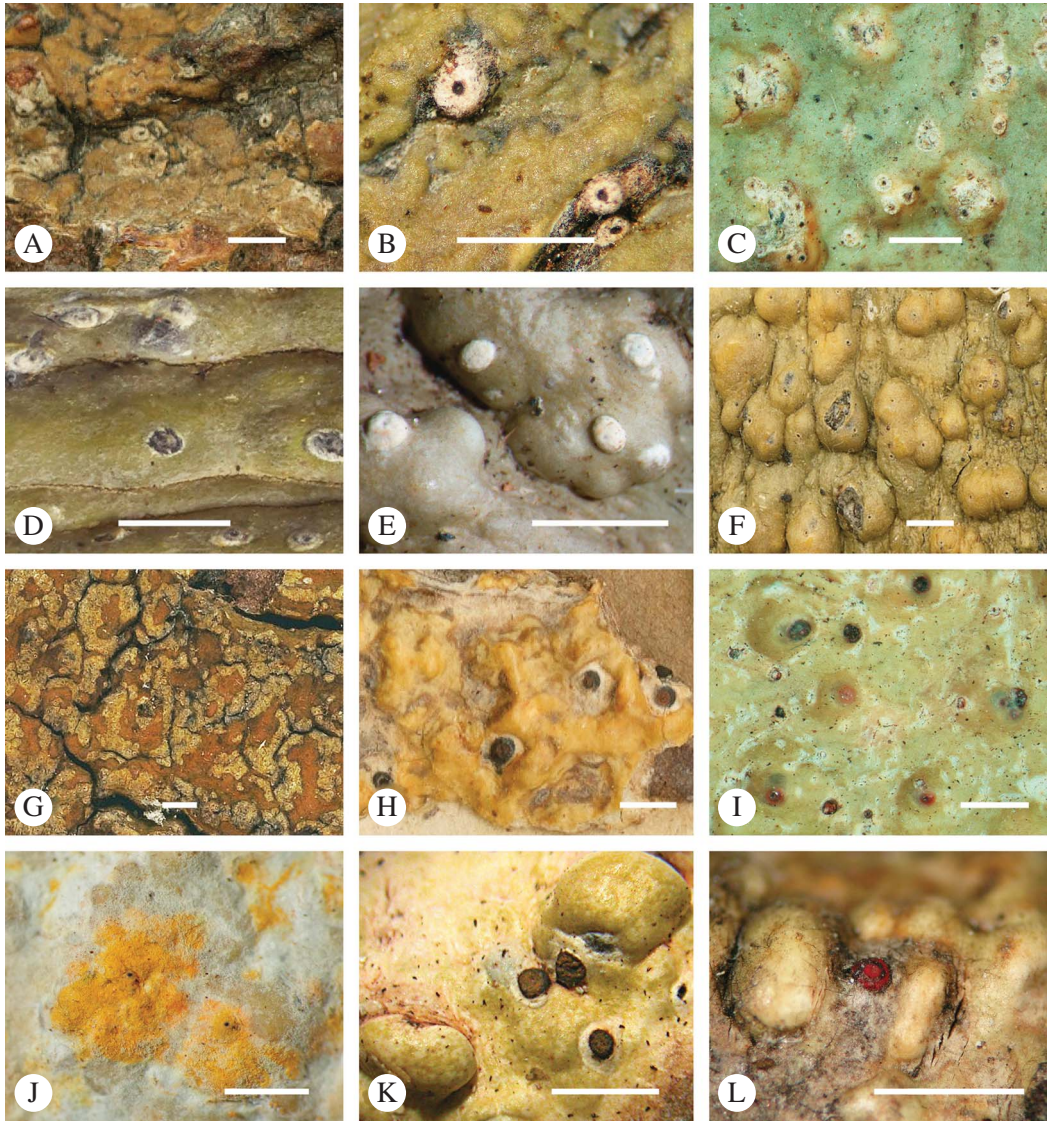


FIG. 37. Habitus of *Astrothelium* species. A–C, *A. defossum* (A, French Guiana, holotype; B, French Guiana, Tucker 16330; C, Guyana, Sipman 39596); D, *A. octosporum* (Brazil, holotype); E, *A. megeustomum* (Brazil, isotype); F, *A. confluens* (Brazil, lectotype); G, *A. praetervisum* (French Guiana, holotype); H, *A. subaequans* (Cuba, holotype); I, *A. amazonum* (Brazil, isotype); J, *A. carassense* (Brazil, holotype); K, *A. diplocarpum* (Colombia, holotype); L, *A. purpurascens* (Brazil, isotype of *Cryptothelium rhodotithon*). Scales = 1 mm.

***Astrothelium bicolor* (Taylor) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816662

*Trypethelium bicolor* Taylor, in Hooker, *London J. Bot.* 6: 157 (1847).—*Bathelium bicolor* (Taylor) C.W. Dodge,

*Nova Hedwigia, Beih.* 12: 20 (1964); type: Africa (BM!—isotype).

?*Trypethelium scorja* var. *convexum* Nyl., *Mém. Soc. Acad. Maine-et-Loire* 4: 74 (1858).—*Trypethelium mastoideum* var. *convexum* (Nyl.) Müll. Arg., *Mém. Soc. Phys. Hist. Nat. Genève* 30(3): 12 (1888): type: “*Crotone cascarillae*” (PC—not seen).



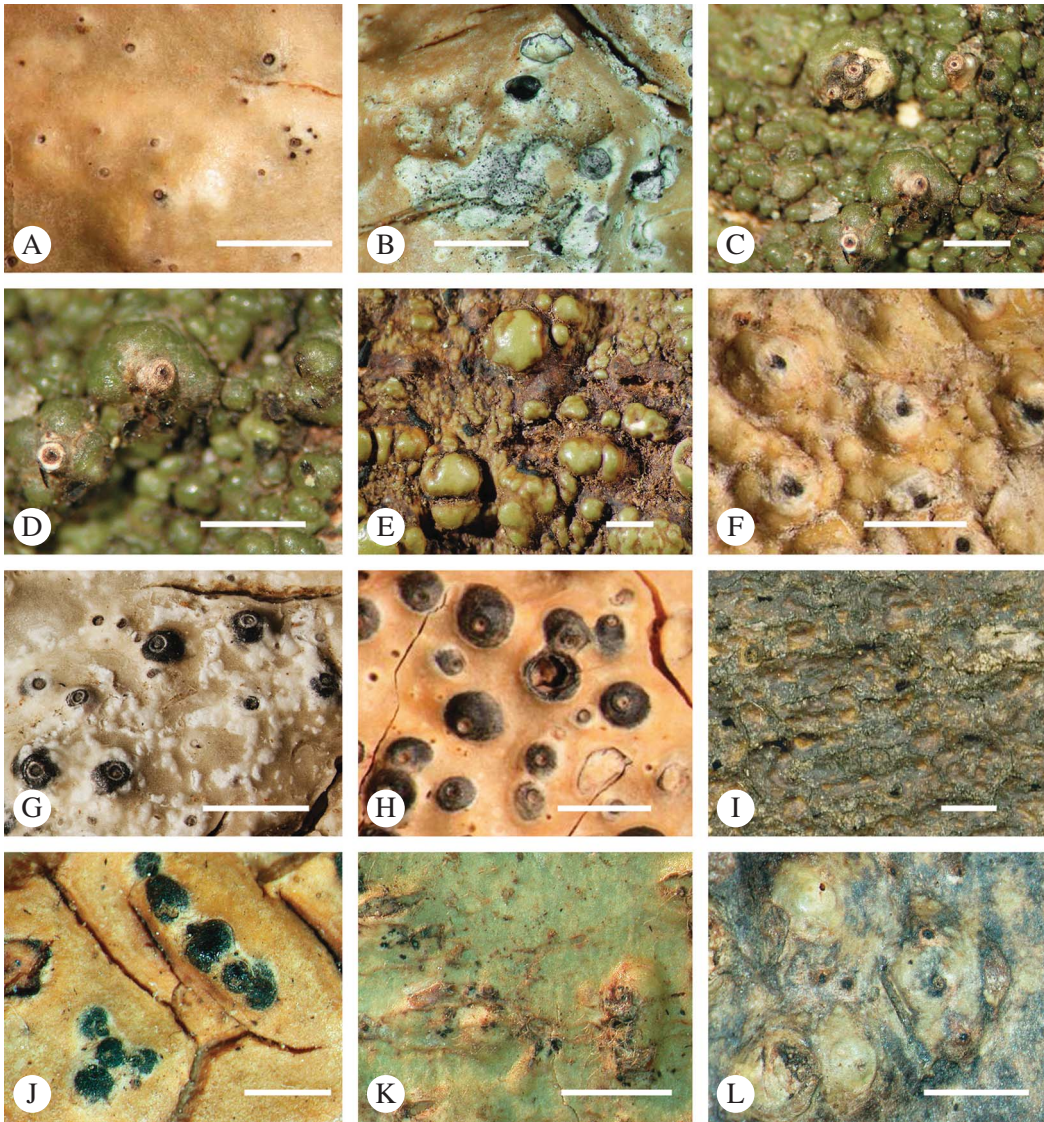


FIG. 38. Habitus of *Astrothelium* species. A, *A. curvatum* (Brazil, isotype); B, *A. santessonii* (Guyana, Sipman 58142); C & D, *A. puiggarii* (Brazil, Osorio SM25); E, *A. megacrypticum* (Panama, holotype); F, *A. longisporum* (Brazil, isotype); G, *A. pyrenuliforme* (Bolivia, holotype); H, *A. ecuadoriense* (Ecuador, holotype); I, *A. lugescens* (São Tomé and Príncipe, holotype); J, *A. andamanicum* (India, isotype); K & L, *A. tenue* (K, Guyana, Bleij s. n.; L, Singapore, Sipman et al. 46164). Scales = 1 mm.

*Trypethelium polychroum* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 391 (1885); type: Cuba, Wright s. n. (G!—lectotype, designated here; BM!—isolectotype; Müller, *Verr. Cub.* 178).

?*Trypethelium scoria* var. *janeirense* Zahlbr., *Sitzungsber. K. Akad. Wiss., math.-naturv. Classe* **111**(1): 369 (1902); type: Brazil, Rio de Janeiro, von Höhnelt 145 (W—holotype, not seen).

?*Trypethelium formosanum* Zahlbr., *Feddes Repert.* **31**: 204 (1933); type: Taiwan, Taihoku, Soozan, *Asahina* 311 (W—holotype, not seen).

?*Trypethelium boninense* Kurok., *Bull. Nat. Sci. Mus. Tokyo* **12**: 691 (1969); type: Japan, Ogasawarashoto (Bonin Islands), Inoue 18960 (TNS—not seen).



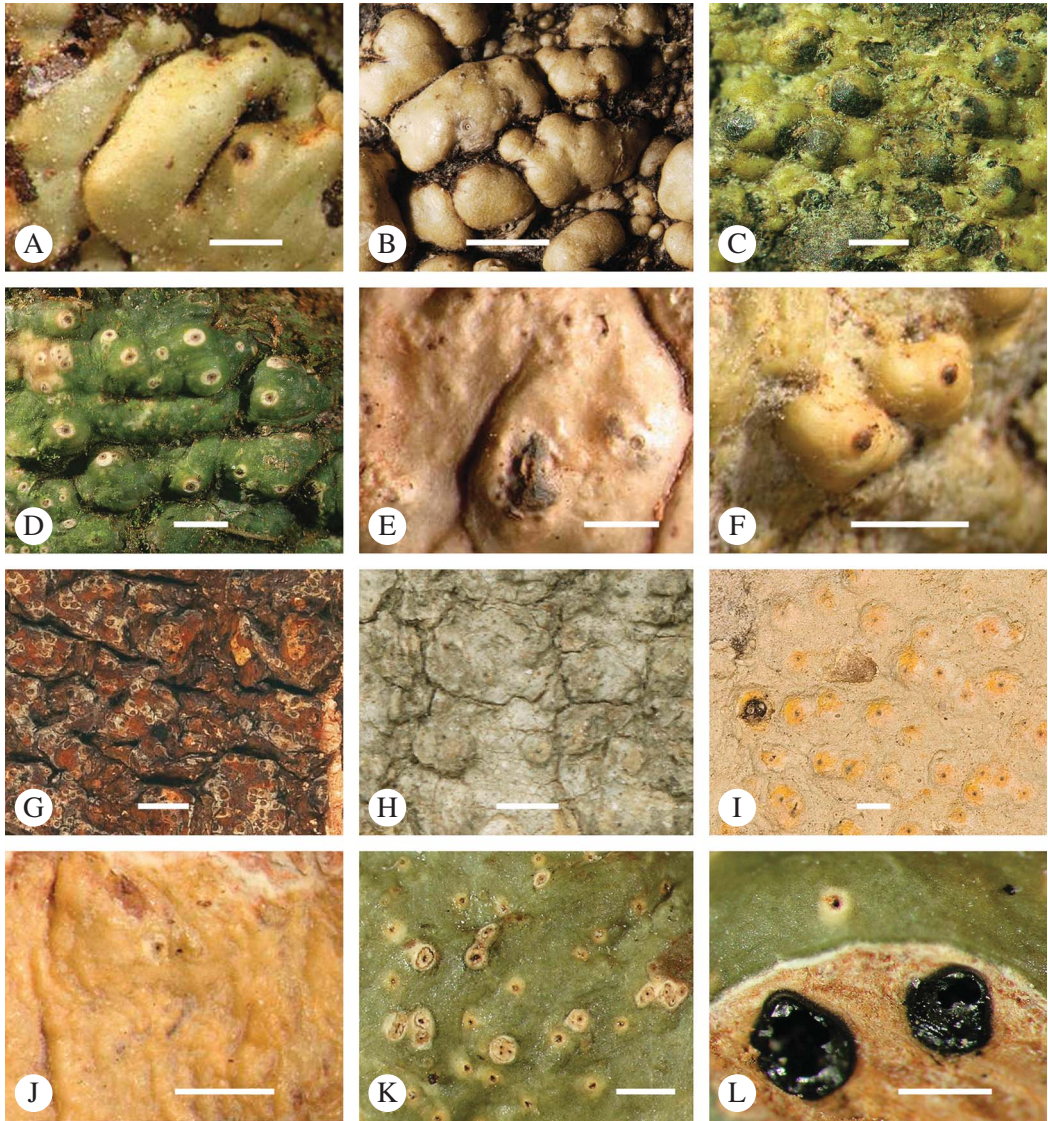


FIG. 39. Habitus of *Astrothelium* species. A, *A. guianense* (French Guiana, holotype); B, *A. bullatum* (Bolivia, holotype); C, *A. campylocartilagineum* (Brazil, holotype); D, *A. nicaraguense* (Nicaragua, isotype); E, *A. testudineum* (Brazil, isotype); F, *A. mediocrassum* (Guyana, holotype); G, *A. cinereum* (French Guiana, lectotype); H, *A. leioplacum* (Paraguay, holotype); I, *A. saxicola* (Brazil, holotype); J, *A. flavomurisporum* (Brazil, isotype); K & L, *A. cecidiogenum* (Costa Rica, holotype). Scales = 1 mm.

(Fig. 18J)

*Thallus* corticate, green to yellowish or brown, smooth to somewhat bullate.

*Ascogonia* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata

0.7–1.5 mm broad, erumpent to prominent, rounded to irregular but not becoming confluent or reticulate, covered by thallus but often slightly paler than the surrounding thallus or sometimes whitish. *Hamathecium* clear. *Ascospores* 8 per ascus,



3-septate, fusiform, 15–27 × 7–10 µm, hyaline, IKI–.

**Chemistry.** Thallus and pseudostromata UV–, K–. TLC: no substances detected.

**Distribution.** Pantropical (previously reported from, e.g. Mexico, Guadeloupe, Puerto Rico, Cuba, Dominican Republic, Netherlands Antilles, Costa Rica, Nicaragua, El Salvador, Ecuador, Bolivia, Guyana, Brazil, Argentina, Seychelles, India, China, Hong Kong, Taiwan, Japan, Malaysia, Philippines, Indonesia, Papua New Guinea, Solomon Islands, Australia, New Caledonia, Fiji and Hawai'i).

**Discussion.** This reinstated taxon belongs in the *Astrothelium nitidiusculum* complex, in which the epithet *bicolor* is the oldest for specimens with a clear hamathecium and ascomata arranged in pseudostromata; previously, this and other names were included in a wide species concept of *Trypethelium nitidiusculum*. *Astrothelium bicolor* appears to be the most common species in the complex. Due to the fact that the types of some presumed synonyms could not be tested for hymenium inspersion, some of these may eventually turn out to be conspecific with other species in this complex, such as *A. nitidiusculum* s. str. or the inspersed *A. scoria*.

**New or confirmed country records.** **Mexico:** Chiapas: Ocozocoautla, 1994, Wolf & Sipman 2205 (B).—**Guadeloupe:** Marie Galante, 1992, Vivant (ABL).—**Puerto Rico:** Mayagüez: Reserva Forestal Maricao, 1989, Sipman 25757 (B).—**Dominican Republic:** Distrito Nacional: Sierra Prieta, 1987, Harris 20151 (ABL, NY).—**Netherlands Antilles:** St. Eustatius: Quill, 2008, Sipman 56749 (B). Saba: The Bottom, 2007, Sipman 54960 (B).—**Costa Rica:** Puntarenas: Parque Nacional Carara, 2002, Sipman 483821 (ABL, B).—**Nicaragua:** Rio San Juan: El Castillo, 2001, Breuss 18994 (LI).—**El Salvador:** Ahuachapán: Parque Nacional El Imposible, 1998, Sipman et al. 44882 (B).—**Ecuador:** Esmeraldas: San Lorenzo, 1982, Aptroot & Hensen 11022 (ABL). Pichincha: 19 km S of Santo Domingo, 1982, Aptroot & Hensen 11251 (ABL).—**Guyana:** Upper Takutu: Kusad Mountain, 1992, Sipman 57532 (B).—**Brazil:** Minas Gerais: Caraçá, 1997, Sipman 40779 (B).—**Argentina:** Misiones: Iguazú, Ferraro et al. 10669 (ABL, CTES).—**Seychelles:** Mahé: Old Mission, 1973,

Norkett 16442 (ABL, B).—**India:** West Bengal: Sundarbans, Chamta, 2003, Jagadeesh Ram 13547 (ABL).—**China:** Yunnan: Xishuangbanna, Menglun, 2002, Aptroot 57141 (ABL).—**Hong Kong:** New Territories: Tai Po Kau, 2000, Aptroot 48748 (ABL).—**Malaysia:** Pahang: Fraser's Hill, 1964, Degelius s. n. (UPS).—**Philippines:** Luzon: Sorsogon, Irosin, 1915, Elmer 14659 (B).—**Indonesia:** Java: Bogor, Gunung Salak, 1991, Sipman & Tan 30065 (B).—**Papua New Guinea:** Madang: 10 km W of Brahman Mission, 1995, Sipman 38792 (B).—**Solomon Islands:** Guadalcanal Island: 1965, Hill 9215 (BM).—**Australia:** Queensland: 8 km W of Ravenshoe, 1984, Streimann 30176 (B).—**New Caledonia:** Ouenarou, 1970, Degelius P127 (UPS).—**Fiji:** Viti Levu: Nadarivatu, 1968, Degener & Degener 31814a (B).—**Hawai'i:** Hawai'i: Pahoehoe, 1969, Degener & Degener 32285b (B).

***Astrothelium buckii* (R. C. Harris)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816663

*Trypethelium buckii* R. C. Harris, *Acta Amazon. (Suppl.)* 14: 72 ('1984') [1986]; type: Brazil, Amazonas, along Rio Negro, 100 km NW of Manaus, Paraná Concelção, Buck 2157 (NY!—isotype).

(Fig. 14J)

**Thallus** corticate, olive-green to brownish, smooth to uneven.

**Ascomata** trypethelioid, with apical ostioles, solitary to irregularly confluent but not pseudostromatic, 0.6–0.9 mm diam., erumpent, covered with thallus but upper part reddish brown and ostiolar area blackish, internally with hyaline or red, K+ red crystals. **Hamathecium** inspersed. **Ascospores** 8 per ascus, 3-septate, fusiform, (32–)37–47 × 14–16 µm, hyaline, IKI–.

**Chemistry.** Thallus and ascomata UV–, K–; ascomata internally K+ red, with anthraquinone.

**Distribution.** Neotropical (reported from Costa Rica, Venezuela, Brazil).

**Discussion.** This species is taken out of the synonymy with *Astrothelium cartilagineum* as suggested by Aptroot et al. (2008), differing from the latter by the inspersed hamathecium.

***Astrothelium calosporum* (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816664

*Pseudopyrenula calospora* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 409 (1885).—*Trypethelium calosporum* (Müll. Arg.) R. C. Harris, *Lichenogr. Thomsoniana*: 141 (1998); type: Cuba, Wright s. n. (G!—holotype; BM!—isotype; Müller, *Verr. Cub.* 234).

*Pseudopyrenula calospora* var. *rhodocheila* Vain., *Proc. Amer. Acad. Arts Sci.* **58**: 145 (1923); type: Trinidad, La Selva Valley, Thaxter 63 (S!—isotype).

(Fig. 17I)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.7–0.9 mm diam., immersed-erumpent, completely covered by thallus except for ostiole furnished with pink pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 14–18-septate, fusiform, 110–150 × 17–22 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–; ostiole K+ red, with anthraquinone.

*Distribution.* Neotropical (reported from Cuba and Trinidad).

***Astrothelium campylocartilagineum*  
Aptroot & Lücking nom. nov.**

Mycobank No.: MB 816665

*Campylothelium cartilagineum* Vain., *Acta Soc. Fauna Fl. Fem.* **7**(2): 195 (1890) non *Astrothelium cartilagineum* (Fée) Aptroot (see below); type: Brazil, Minas Gerais, Sitio, Vainio s. n. (TUR-Vain 30835!—holotype; BM!—isotype; Vainio, *Lich. Bras. Exs.* 1145).

(Fig. 39C)

*Thallus* corticate, olive-green, verrucose-bullate.

*Ascomata* pleurothelioid, with eccentric, separate ostioles, solitary, 0.7–1.0 mm diam., erumpent to prominent, covered by thallus but upper part often irregularly exposed and blackish. *Hamathecium* clear. *Ascospores* 2–4 per ascus, densely muriform, fusiform, 120–175 × 38–50 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Costa Rica and Brazil).

*Discussion.* This species is not synonymous with *Heufleria chlorogastrica*, as suggested by Harris (1986), since the type of the latter appears to belong in the genus *Phyllobathelium*.

***Astrothelium cartilagineum* (Fée)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816668

*Pyrenula cartilaginea* Fée, *Essai Crypt. Écorc.*: 76 (1824).—*Trypethelium cartilagineum* (Fée) Aptroot, in Aptroot *et al.*, *Biblioth. Lichenol.* **98**: 134 (2008) non *Campylothelium cartilagineum* Vain. (1890; see above); type: South America, “in America ad corticem Cinchonae lancifoliae et Portlandiae hexonae (quina nova)” (L!—isotype).

*Thallus* corticate, brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.4–0.5 mm diam., immersed to erumpent, covered by thallus except for dark ostiole surrounded by pale rim, internally with hyaline or red, K+ red crystals. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, (32–)37–47 × 14–16 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–; ascomata internally K+ red, with anthraquinone.

*Distribution.* Neotropical; previously reported from Trinidad, Costa Rica, French Guiana, Venezuela, and Brazil.

*Discussion.* This species is most similar to *Astrothelium buckii*, but differs by the clear hymenium.

*New country record. Guyana:* Upper Takutu. Kuyuwini Landing, 1992, Sipman 57073 (B); Karanambo ranch, 1992, Sipman 57280 (B).

***Astrothelium cecidiogenum* (Aptroot & Lücking)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816669



*Cryptothelium cecidiogenum* Aptroot & Lücking in Aptroot *et al.*, *Biblioth. Lichenol.* **98**: 57 (2008); type: Costa Rica, Alajuela, Volcán Tenorio National Park, Pilon Biological Station, Sipman 51911 (B!—holotype; INB-4055132!—isotype).

(Fig. 39K & L)

*Thallus* corticate, olive-green, smooth to uneven, pseudogall-inducing.

*Ascomata* mostly astrothelioid, several chambers joined with eccentric, fused ostioles, rarely pleurothelioid and with separate ostioles; joined ascomata diffusely pseudostromatic; pseudostromata 1–2 mm broad, prominent, confluent and forming reticulate or brain-like lines, covered with thallus except for the dark ostioles with irregular, whitish rim; pseudostromata 10–30 mm long and 5–10 mm wide, individual ascomata 0.7–1.2 mm diam. *Hamathecium* clear. *Ascospores* 8 per ascus, densely muriform, ellipsoid, 125–175 × 30–40 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution:* Neotropical (previously reported only from Costa Rica).

*New country record.* **Brazil:** Rio Grande do Sul: Maquiné, 2006, Koch s. n. (ABL, HAS).

***Astrothelium ceratinum* (Fée) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816670

*Pyrenula ceratina* Fée, *Essai Crypt. Écorc. Suppl.*: 77 (1837).—*Verrucaria ceratina* (Fée) Nyl., *Acta Soc. Sci. Fem.* **7**(2): 491 (1863).—*Pseudopyrenula ceratina* (Fée) Müll. Arg., *Mém. Soc. Phys. Hist. Nat. Genève* **30**: 29 (1888).—*Trypethelium ceratinum* (Fée) R. C. Harris, *Lichenogr. Thomsoniana*: 141 (1998); type: Peru, “ad corticem cinchonarum” (G!—lectotype; Harris, *Lichenogr. Thomsoniana*: 141 (1998)).

(Fig. 19E)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.3–0.4 mm diam., erumpent, covered

by thallus but upper portion darker or greyish. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 21–28 × 9–12 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Peru).

*New country records.* **Guyana:** Upper Mazaruni: N-slope of Mount Roraima, 1985, Sipman & Aptroot 18767 (*Lichenotheca Latinoamericana* 100, ABL).—**Ecuador:** Zamora-Chinchipec: Estacion San Francisco, 2004, Sipman 52735 (B).

***Astrothelium chapadense* (Malme) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816671

*Laurera chapadensis* Malme, *Ark. Bot.* **19**(1): 23 (1924).—*Meristosporium chapadense* Malme (1924), nom. inval; type: Brazil, Matto Grosso, Santa Anna da Chapada, Malme 2513 (S!—holotype; S!—isotype).

(Fig. 36A)

*Thallus* corticate, olive-green to brownish yellow, uneven to verrucose or almost squamulose.

*Ascomata* trypethelioid, with apical ostioles, irregularly confluent to pseudostromatic; pseudostromata 0.8–2.0 mm broad, prominent to sessile, dark brown, forming irregular groups or lines. *Hamathecium* clear. *Ascospores* 8 per ascus, densely muriform, ellipsoid, (60–)70–100(–130) × 20–30 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Costa Rica and Brazil).

*Discussion.* *Astrothelium chapadense* strongly resembles a species of *Bathelium*, but is included here in *Astrothelium* due to the lack of an internal anthraquinone pigment.

***Astrothelium chrysoglyphum* (Vain.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816672

*Thelenella chrysoglypha* Vain., *Hedwigia* 38: 258 (1899).—*Laurea chrysoglypha* (Vain.) Zahlbr., *Catal. Lich. Univ.* 1: 503 (1922); type: Guadeloupe, Parnasso, Duss 564 (TUR-Vain 31044!—holotype).

(Fig. 32L)

*Thallus* corticate, olive to yellowish but covered by orange pigment, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, aggregate to diffusely pseudostromatic, pseudostromata 1–2 mm broad, erumpent, covered by thallus and orange pigment except for blackish ostiolar area. *Hamathecium* clear. *Ascospores* 2 per ascus, densely muriform, fusiform, 80–150 × 25–40 μm, without distinctly thickened median septum, hyaline, IKI– or IKI+ brownish.

*Chemistry.* Thallus and ascomata UV+ red, K+ purple, with anthraquinone.

*Distribution.* Neotropical (reported from Guadeloupe).

***Astrothelium chrysostomum* (Kremp.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816673

*Trypethelium chrysostomum* Kremp., *Nouvo Giorn. Bot. Ital.* 7: 57 (1875); type: Malaysia, Sarawak, Beccari 50 (M!—lectotype, designated here following annotation by R. C. Harris).

*Trypethelium leucostomum* Kremp., *Nouvo Giorn. Bot. Ital.* 7: 57 (1875) non (Nyl.) C. W. Dodge (1953); type: Malaysia, Sarawak, Beccari 188 (M!—lectotype, designated here; M!—isolectotype).

(Fig. 23H & I)

*Thallus* corticate, olive-brown, uneven-rugose.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata solitary to confluent, 0.7–1.0 mm diam., immersed in thick thallus folds, covered except pale ostiolar area. *Hamathecium*

clear. *Ascospores* 8 per ascus, 3(–5)-septate, fusiform, 32–52 × 10–17 μm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Eastern palaeotropical (Malaysia: Sarawak).

*Discussion.* This taxon was first believed to be conspecific with *Astrothelium leucothelium* but differs substantially in thallus morphology and also in its distribution.

***Astrothelium cinereorosellum*  
(Kremp.) Aptroot & Lücking  
comb. nov.**

Mycobank No.: MB 816674

*Trypethelium cinereorosellum* Kremp., *Nouvo Giorn. Bot. Ital.* 7: 35 (1875); type: Sarawak, Beccari 48 (M!—lectotype; Makhija & Patw., *J. Hattori Bot. Lab.* 73: 194, 1993).

*Verrucaria antoniae* Kremp., *Nouvo Giorn. Bot. Ital.* 7: 51 (1875).—*Pyrenula antoniae* (Kremp.) van Overeem-de Haas, *Bull. Jard. Bot. Buitenzorg, Ser. 3*, 4: 113 (1922).—*Pseudopyrenula antoniae* (Kremp.) Zahlbr., *Catal. Lich. Univ.* 1: 354 (1922); type: Sarawak, Beccari (M!—lectotype; Harris, *Lichenogr. Thomsoniana*: 140, 1998).

*Trypethelium microstomum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 201 (1993); type: India, Andaman Islands, South Andaman, Baratang, Bishmu Nala, 22 ii 1985, Patwardhan & Nagarkar AMH 85.663 (ABL!—isotype).

*Trypethelium flavocinereum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 198 (1993); type: India, Kerala, Cardamom Hills, Munnar-Devicolam road, 25 January 1976, Patwardhan & Prabhu AMH 76.672 (ABL!—isotype).

(Fig. 12D & E)

*Thallus* corticate, light greenish grey to yellowish or whitish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary or forming irregular groups or lines but not distinctly pseudostromatic, 0.3–0.5 mm diam., erumpent to prominent, covered by thallus except dark ostiole. *Hamathecium* interspersed. *Ascospores* 8 per ascus, (5–)7–9-septate, fusiform, (33–)40–50 (–73) × 8–14 μm, hyaline, IKI–.



**Chemistry.** Thallus UV+ yellow, K–, with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone).

**Distribution.** Palaeotropical; previously reported from India, Thailand, Borneo, Papua New Guinea, and Australia.

**New country record. Indonesia:** Java: Cibodas, 1450 m, 1939, Groenhart 1942 (ABL, L).

***Astrothelium cinereum* (Müll. Arg.)  
Aptroot & Lücking comb. et stat. nov.**

MycoBank No.: MB 816675

*Heufleria praetervisiva* var. *cinerea* Müll. Arg., *Flora* 68: 251 (1885).—*Cryptothelium praetervisum* var. *cinereum* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* 1: 522 (1922); type: French Guiana, Leprieur 41 (G!—lectotype, designated here).

(Fig. 39G)

**Thallus** corticate, olive-brown, uneven to coarsely bullate-folded.

**Ascomata** mostly astrothelioid, several chambers joined with eccentric, fused ostioles, rarely pleurothelioid and with separate ostioles; joined ascomata pseudostromatic, pseudostromata 0.7–1.5 mm diam., erumpent to prominent, forming irregular lines, covered by thallus except for dark ostiole surrounded by whitish rim. *Hamathecium* clear. *Ascospores* 8 per ascus, densely muriform, fusiform, 33–52 × 16–22 µm, without thickened median septum, hyaline, IKI–.

**Chemistry.** Thallus and pseudostromata UV–, K–. TLC: no substances detected.

**Distribution.** Neotropical (previously reported from French Guiana).

**Notes.** This taxon is very similar to *Astrothelium praetervisum* but appears to lack the thin orange pigment characteristic of the latter.

**New country record. Guyana:** Upper Mazaruni: Paruima Mission, 1997, Sipman 39819 (B). Upper Takutu: Kuyuwini Landing, 1992, Sipman 57079 (B).

***Astrothelium cinnamomeum* (Eschw.)  
Müll. Arg.**

*Flora* 68: 270 (1884).—*Pyrenastrum cinnamomeum* Eschw., in Martius, *Icon. Sel. Pl. Crypt.* 2: 18, t. 9, fig. 1 (1828); type: Brazil, Bahia, Caetitê, Martius s. n. (M!—holotype).

*Astrothelium conicum* Eschw., in Martius, *Syst. Lich.*: 18 (1833); Eschweiler, *Syst. Lich.*: 26 (1824), nom. nud.—*Heufleria conica* (Eschw.) Trevis., *Spighe e Paglie*: 19 (1853); type: Brazil, Martius s. n. (M!—holotype).

*Astrothelium minus* Müll. Arg., *Bot. Jahrb. Syst.* 6: 382 (1885); type: Cuba, Wright s. n. (G!—holotype; NY!—isotype; Müller, *Verr. Cub.* 235).

(Fig. 26I–L)

**Thallus** corticate, light olive-green to yellowish, smooth to uneven.

**Ascomata** astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic, pseudostromata 0.4–0.7 mm diam., erumpent to prominent, conical with flattened top, covered by thallus and upper portion with yellow-orange, K+ purple, UV+ red pigment, area beneath the upper portion often whitish. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 23–30 × 6–10 µm, hyaline, IKI–.

**Chemistry.** Thallus UV–, K–; pseudostromata with yellow to orange, K+ purple, UV+ red anthraquinone.

**Distribution.** Pantropical (previously reported from the USA, Mexico, Cuba, Trinidad, Tobago, Costa Rica, Guyana, French Guiana, Venezuela, Brazil, Seychelles, Hong Kong, Borneo and Australia).

**Discussion.** The synonymy of *Astrothelium conicum* (the type species of the genus) with *A. cinnamomeum* is confirmed by combining the observations of Müller (1884: 270), who observed the ascospores, and Harris (1986: 59), who observed no ascospores but saw the negative reaction with UV.

**New country record. China:** Yunnan: Xishuangbanna, Menglun, 2002, Aptroot 57255, 57026, 57267 (all ABL).

***Astrothelium coccineum*  
Córdova-Chávez et al.**

In Córdova-Chávez et al., *Cryptog., Mycol.* 35: 159 (2014); type: Mexico, Veracruz, La Cortadura,

Coatepec, 2062 m, 2013, *Córdova-Chávez* 464 (XAL!—holotype; ABL!—isotype).

(Fig. 14K)

*Thallus* corticate, olive-brown, verrucose-bullate.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata 0.7–1.5 mm broad, erumpent to prominent, rounded to irregular, covered by dark red pigment except for the blackish ostioles, internally with yellow pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, oblong-ellipsoid, 25–30 × 10–13 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV–, outside K+ purple, inside K+ crimson red. TLC: a red anthraquinone at Rf 7 and a yellow anthraquinone at Rf 2.

*Distribution.* Neotropical (reported from Mexico).

***Astrothelium confluens* (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816676

*Heufleria confluens* Müll. Arg., *Flora* **66**: 243 (1883).—*Cryptothelium confluens* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* **1**: 521 (1922); type: Brazil, Rio de Janeiro, Apiahy, *Puiggari* 143 (G!—lectotype, designated here).

(Fig. 37F)

*Thallus* corticate, greyish green to pale yellowish, uneven to bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles, rarely pleurotremoid with separate ostioles; joined ascomata 1–3 mm diam., prominent, completely covered by thallus. *Hamathecium* clear. *Ascospores* 8 per ascus, densely muriform, fusiform, *c.* 130 × 20 µm, with distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; ascomata UV+ yellow, K–. TLC: lichexanthone on the ascomata.

*Distribution.* Neotropical (previously reported only from Brazil).

*New country record.* **Guyana:** Potaro-Siparuni: Kaieteur Falls National Park, 1996, *Sipman* 40482 (B).

***Astrothelium consimile* (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816677

*Heufleria consimilis* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 385 (1885).—*Cryptothelium consimile* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* **1**: 521 (1922); type: Cuba, *Wright* s. n. (G!—holotype).

(Fig. 36L)

*Thallus* corticate, olive-green yellowish, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles, rarely pleurotremoid with separate ostioles; joined ascomata dispersed to confluent or diffusely pseudostromatic, 0.8–1.2 mm diam., immersed-erumpent, covered by thallus but upper portion whitish with blackish ostiole area. *Hamathecium* clear. *Ascospores* 2 per ascus, densely muriform, fusiform, 85–130 × 23–36 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* No reactions or substances in the type material; however, the specimen from Brazil has the medulla UV+ yellow.

*Distribution.* Neotropical (previously reported from Cuba).

*New country record.* **Brazil:** Rondônia: Porto Velho, Parque Natural Municipal, 2012, *Cáceres & Aptroot* 15568 (ABL, ISE).

***Astrothelium crassum* (Fée) Aptroot**

In Aptroot *et al.*, *Biblioth. Lichenol.* **98**: 44 (2008).—*Trypethelium crassum* Fée, *Essai Crypt. Écorc.*: 66 (1824).—*Pyrenodium crassum* (Fée) Fée, *Essai Crypt. Écorc. Suppl.*: 69 (1837); type: South America, “ad ramae *Crotonis cascarillae*” (G!—lectotype; L!—isolecotype).

*Trypethelium clandestinum* Fée, *Essai Crypt. Écorc.*: 68 (1824).—*Polyblastia clandestina* (Fée) Trevis., *Spighe e Pagie*: 15 (1853), non Jatta (1900).—*Astrothelium clandestinum* (Fée) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* **5**: 141 (1857).—*Pyrenastrum clandestinum* (Fée) Müll. Arg., *Bot. Jahrb. Syst.*

6: 386 (1885); type: South America, "Cinch. jaune" (G—holotype, not seen; L—isotype).

*Astrothelium confusum* Müll. Arg., *Flora* 68: 247 (1885); type: Colombia, Rio Magdalena, Lindig 141 (G!—holotype; BM!, BR—isotypes).

(Fig. 29A & B)

*Thallus* corticate, olive-green to yellowish brown, rather thick, uneven to bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to confluent, 0.3–0.4 mm diam., erumpent, covered by thallus but upper portion whitish and ostiolar area blackish. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 21–27 × 8–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical; previously reported from Costa Rica, Guyana, Venezuela, Brazil, India, New Caledonia and Papua New Guinea.

*New country records.* **Puerto Rico:** Ponce: Caribbean National Forest, 1989, Aptroot & Aptroot 25523 (ABL).—**Colombia:** Amazonas: Araracuara, opposite Isla Morrocoy, 240 m, 1988, Sipman & Duivenvoorden 28502 (B).—**Ecuador:** Los Ríos: 45 km S of Quevedo, 1982, Aptroot & Hensen 10422 (ABL).—**Madagascar:** Tamatave: Andasibe (Périnet), 1984, Aptroot & Hensen 13396 (ABL).—**Indonesia:** Java: South Semeru Lands, Tempur Sewa, 1939, Groenhart 1679, 2595 (ABL, L).

### **Astrothelium croceum Malme**

*Ark. Bot.* 19(1): 12 (1924); type: Brazil, Matto Grosso, Serra da Chapada, Malme, 26 vii 1984 (S!—holotype).

(Fig. 27A–C)

*Thallus* corticate, light olive-green to yellowish, yellowish grey, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to confluent, 0.4–0.7 mm diam., erumpent, covered by thallus and yellow-orange, K+ purple, UV+ red pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 30–35 × 10–12 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–, without lichexanthone or pigment; ascomata with yellow-orange, K+ purple, UV+ red anthraquinone.

*Distribution.* Neotropical (reported from Brazil).

### **Astrothelium deforme (Fée) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816678

*Trypethelium deforme* Fée, *Ann. Sci. Nat.* 23: 454 (1831).—*Meissneria varia* Fée, *Essai Crypt. Écorc. Suppl.*: 66 (1837).—*Bathelium deforme* (Fée) Trevis., *Spighe e Paglie*: 20 (1853).—*Trypethelium varium* (Fée) Nyl., *Mém. Soc. Acad. Maine-et-Loire* 4: 78 (1858).—*Bathelium varium* (Fée) Trevis., *Flora* 44: 21 (1861).—*Laurera varia* (Nyl.) Zahlbr., in Engler & Prantl, *Natürl. Pflanzenfamil.* 1(1\*): 71 (1903); type: Malaysia, Sarawak, Beccari (G-G00128943!—lectotype, designated here).

(Fig. 32H)

*Thallus* corticate, olive-green, uneven- verrucose.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.5–1.0 mm diam., erumpent, covered by thallus but upper portion blackish, internally with orange, K+ purple pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, fusiform, 90–105 × 26–36 µm, without thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; ascomata UV–, externally K–, internally K+ purple.

*Distribution.* Eastern palaeotropical (reported from Malaysia: Sarawak).

*Discussion.* Fée later replaced his earlier epithet *deforme* by *varia* because he found the species to be variable rather than deformed; however, according to the retroactive nomenclatural rules, his earlier epithet has to be taken up.

### **Astrothelium defossum (Müll. Arg.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816679



*Heufleria defossa* Müll. Arg., *Flora* **68**: 250 (1885).—*Cryptothelium defossum* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* **1**: 521 (1922) non *Campylotheleium defossum* Müll. Arg. (1891); type: French Guiana, Leprieur 168 (G!—holotype).

(Fig. 37A–C)

*Thallus* corticate, olive-green to light greyish green, uneven to bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles, rarely pleurotremoid with separate ostioles; joined ascomata dispersed to confluent or diffusely pseudostromatic, 0.8–1.3 mm diam., erumpent, covered by thallus but upper, often papilliform portion whitish with blackish ostiole. *Hamathecium* clear. *Ascospores* 8 per ascus, densely muriform, fusiform, 100–150 × 30–45 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry*. Thallus UV–, K–; ascomata UV+ yellow, K–. TLC: lichexanthone on the ascomata.

*Distribution*. Neotropical (previously reported from Venezuela and French Guiana).

*New country record*. **Guyana**: Upper Mazaruni: Paruima Mission, 1997, Sipman 39596 (B).

***Astrothelium degenerans* (Vain.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816680

*Pseudopyrenula degenerans* Vain., *J. Bot.* **34**: 292 (1896).—*Trypethelium degenerans* (Vain.) Zahlbr., *Catal. Lich. Univ.* **1**: 490 (1922).—*Bathelium degenerans* (Vain.) R. C. Harris, *More Florida Lichens*: 117 (1995); type: Dominica, Laudat, Elliott s. n. (TUR-Vainio 30782! —holotype; BM!—isotype).

(Fig. 16J–L)

*Thallus* corticate, olive-green to yellowish or brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata 1–2 mm diam., erumpent, forming irregular groups including numerous

ascomata, dark brown, internally with yellow-orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 15–25 × 6–9 µm, hyaline, IKI–.

*Chemistry*. Thallus UV–, K–; pseudostromata UV–, externally K–, internally K+ red, with anthraquinone.

*Distribution*. Pantropical (previously reported from Mexico, Dominica, Jamaica, Puerto Rico, Costa Rica, El Salvador, Venezuela, Galapagos and Thailand).

*New country records*. **Netherlands Antilles**: Saba: Maskehorn, 2007, Sipman 54934 (B).—**Ecuador**: Manabí: Puerto Lopez, 1982, Aptroot & Hensen 10573, 10594 (ABL).

***Astrothelium diplocarpoides* Müll. Arg.**

*Bot. Jahrb. Syst.* **6**: 384 (1885).—*Astrothelium diplocarpoides* Nyl. (1876) nom. nud; type: Cuba, Wright s. n. (H-Nyl 191!—holotype; BM!—isotype; Müller, *Verr. Cub.* 143).

(Fig. 25J)

*Thallus* corticate, light olive-green but with distinct, whitish to pale yellowish pruina (lichexanthone), smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, 0.8–1.5 mm diam., prominent to almost sessile, covered by thallus and whitish pruina. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 5–7-septate, fusiform, 80–85 × 20 µm, hyaline, IKI–.

*Chemistry*. Thallus and ascomata UV+ yellow, K–. TLC: lichexanthone.

*Distribution*. Neotropical (reported from Cuba).

***Astrothelium diplocarpum* Nyl.**

*Flora* **47**: 618 (1864).—*Heufleria diplocarpa* (Nyl.) Müll. Arg., *Bot. Jahrb. Syst.* **6**: 385 (1885).—*Cryptothelium diplocarpum* (Nyl.) Zahlbr., *Catal. Lich. Univ.* **1**: 521 (1922); type: Colombia, Pie de Cuesta, Lindig s. n. (H-Nyl 109!—holotype).

(Figs 26C & D, 37K)

*Thallus* corticate, olive-green to yellowish brown, uneven-bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, 0.7–1.0 mm diam., immersed-erumpent, covered by thallus except for the papilliform, orange to brown, K+ red ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, 9-septate to submuriform, fusiform, 90–110 × 22–28 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; ascomata with brown, K+ red anthraquinone.

*Distribution.* Neotropical (previously reported from the USA, Costa Rica, Colombia and Ecuador).

*New country record. Venezuela: Bolivar:* Cerro Guaiquinima, 1000 m, 1990, *Sipman* 26568 (B).

***Astrothelium dissimilum* (Makhija & Patw.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816681

*Trypethelium dissimilum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 195 (1993); type: India, Meghalaya, Mawsyram, 30 October 1977, *Patwardhan & Nagarkar* AMH 77.1169 (ABL!—isotype).

(Fig. 17C & D)

*Thallus* corticate, olive-green, uneven- verrucose.

*Ascomata* trypethelioid, with apical ostioles, confluent to pseudostromatic; pseudostromata 0.8–2.0 mm diam., prominent, dark brown, internally with yellow, K+ purple crystals. *Hamathecium* clear. *Ascospores* 8 per ascus, (3–)5(–9)-septate, fusiform, 25–40 × 6–9 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, externally K–; pseudostromata internally K+ red, with anthraquinone.

*Distribution.* Eastern palaeotropical (India and South Korea).

*Discussion.* The material from South Korea is tentatively assigned to this species, although the ascomata are smaller and less emergent (Fig. 17D).

***Astrothelium effusum* (Aptroot & Sipman) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816682

*Laurera effusa* Aptroot & Sipman in Aptroot *et al.*, *Biblioth. Lichenol.* 98: 61 (2008); type: Costa Rica, Puntarenas, La Amistad International Park, Altamira Station, 1500–1600 m, *Sipman* 48034e (B!—holotype; INB-3944626!—isotype).

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.6–1.0 mm diam., immersed-erumpent, covered by thallus except dark ostiole surrounded by pale ring. *Hamathecium* inspersed. *Ascospores* 8 per ascus, muriform, ellipsoid, 80–100(–125) × 28–48 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Costa Rica).

***Astrothelium endochryseum* (Vain.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816683

*Pseudopyrenula endochrysea* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 206 (1890).—*Trypethelium endochryseum* (Vain.) Zahlbr., in Engler & Prantl, *Natürl. Pflanzenfamil.* 1(1\*): 70 (1903).—*Bathelium endochryseum* (Vain.) R. C. Harris, *More Florida Lichens*: 117 (1995); type: Brazil, Minas Gerais, Caraça, *Vainio* s. n. (TUR-Vain 30793!—holotype; BM!—isotype; Vainio, *Lich. Bras.* 1157).

(Fig. 16B & C)

*Thallus* corticate, green to yellowish or brown, verrucose.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 1–2 mm diam., erumpent to prominent, dark brown, internally with yellow to orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 35–50 × 12–15 µm, hyaline, IKI–.

**Chemistry.** Thallus UV–, K–; pseudostromata UV–, externally K–, internally K+ red, with anthraquinone.

**Distribution.** Neotropical (Brazil).

### ***Astrothelium eustomum* (Mont.)**

**Müll. Arg.**

*Flora* 68: 247 (1885).—*Pyrenastrum eustomum* Mont., *Ann. Sci. Nat. Bot., sér. 2* 19: 63 (1843); type: French Guiana, Leprieur 179 (PC!—holotype; G!—isotype).

*Trypethelium celatum* Stirt., *Proc. Roy. Philos. Soc. Glasgow* 13: 193 (1881); type: India, Assam, Lezhore, Watt (BM!—isotype).

*Astrothelium acroleucum* Malme, *Ark. Bot.* 19(1): 15 (1924); type: Brazil, Matto Grosso, Santa Anna da Chapada, Malme 2358 (S!—lectotype, designated here).

(Fig. 25D)

**Thallus** corticate, olive-green to greyish green, smooth to uneven.

**Ascomata** astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to pseudostromatic, 0.4–0.8 mm diam., erumpent with flattened tops, with whitish to pale yellowish cover contrasting with the thallus. *Hamathecium* clear. *Ascospores* 8 per ascus, 3–5-septate, fusiform, 22–30 × 6–8 µm, hyaline, IKI–.

**Chemistry.** Thallus UV–, K–; pseudostromata UV+ yellow, K–, with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone).

**Distribution.** Pantropical; previously reported from Costa Rica, Cuba, Guyana, French Guiana, Colombia, Venezuela, Brazil, Bolivia, India, Sri Lanka, Thailand and Australia.

**Discussion.** The three types cited above show the two extremes in terms of ascoma emergence and pseudostroma development, with *Pyrenastrum eustomum* and *Trypethelium celatum* showing the ascomata almost fully immersed in the thallus and mostly dispersed, and *Astrothelium acroleucum* showing erumpent pseudostromata.

**New country records.** **Madagascar:** Tamatave: Andasibe (Périnet), 1984, Aptroot & Hensen 13384 (ABL).—**Papua New Guinea:** Central: Varirata National Park, 1995,

Sipman 38662 (B).—**Solomon Islands:** Guadalcanal Island: 1965, Hill 9119 (BM).

### ***Astrothelium exostemmatis* (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB816684

*Bathelium exostemmatis* Müll. Arg. *Mém. Soc. Phys. Hist. Nat. Genève* 30(3): 17 (1888); *Laurera exostemmatis* (Müll. Arg.) Zahlbr. in Engler & Prantl, *Natürl. Pflanzenfamil.* 1(1\*): 71 (1903); type: Jamaica, “cort. Exostemmatis” (G!—holotype; M— isotype, not seen).

(Fig. 35L)

**Thallus** corticate, olive-brown to pale brownish, smooth to uneven.

**Ascomata** trypethelioid, with apical ostioles, solitary to irregularly clustered to diffusely pseudostromatic, 0.8–1.2 mm diam., when confluent pseudostromata up to 5 mm diam., immersed–erumpent, covered by thallus except dark ostiole surrounded by irregular whitish rim. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, ellipsoid, distinctly curved, 70–80 × 20–25 µm, without distinctly thickened median septum, hyaline, IKI–.

**Chemistry.** Thallus and ascomata UV–, K–. TLC: no substances.

**Distribution.** Neotropical (previously reported from Jamaica).

**New country record.** **Ecuador:** Pastaza: Puyo, 1100 m, 1982, Aptroot & Hensen 10406 (ABL).

### ***Astrothelium fallax* Müll. Arg.**

*Bot. Jahrb. Syst.* 6: 383 (1885).—*Trypethelium pallescens* Leight., *Trans. Linn. Soc. London* 27: 185 (1869) non Fée (1831); type: Sri Lanka, Thwaites 195 (BM!—lectotype, designated here; PC!, S!—isolectotypes).

(Fig. 29D & E)

**Thallus** corticate, olive-green to yellowish, uneven to strongly bullate, inducing pseudogall formation.

**Ascomata** astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic, 0.8–1.5(–2.0) mm diam., prominent to sessile, covered by thallus



except for the blackish ostiole area surrounded by a whitish ring, forming large warts with uneven to bumpy surface. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 30–39 × 10–13 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical; previously reported from Cuba, India and Sri Lanka.

*New country record.* **Guyana:** *Upper Mazaruni:* Mount Latipu, 1985, *Sipman & Aptroot* 19120 (ABL, B).

***Astrothelium feei* (C. F. W. Meissn.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816685

*Trypethelium feei* C. F. W. Meissn., in Fée, *Ann. Sci. Nat., Bot. sér. 1* 23: 442 (1831).—*Trypethelium scoria* var. *feei* (C. F. W. Meissn.) Trevis., *Flora* 44: 10 (1861).—*Bathelium feei* (C. F. W. Meissn.) Aptroot, in Aptroot *et al.*, *Biblioth. Lichenol.* 98: 51 (2008); type: South America, “Cascarill.” (G!—holotype; L!—isotype).

*Trypethelium mastoideum* var. *macerum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 390 (1885); type: Cuba, *Müller, Verr. Cub.* 153 (G!—lectotype, designated here; BM!—isolectotype).

(Fig. 16F–I)

*Thallus* corticate, olive-brown to olive-green or yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata 1–2 mm diam., erumpent, dark brown, internally with yellow-orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 18–25 × 5–9 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV–, externally K–, internally K+ yellow, with anthraquinone.

*Distribution.* Neotropical; previously reported from the USA, Costa Rica, Colombia, French Guiana and Galapagos.

*Discussion.* The difference in pseudostroma chemistry from the similar *Astrothelium degenerans* seems to warrant the distinction of

the two species, but it is not correlated with distribution or any other character.

*New country records.* **El Salvador:** *Ahuachapán:* Parque Nacional El Imposible, 1999, *Sipman & Bohnke* 44912 (B).—**Venezuela:** Acosta, Aqua Salada, 1989, *Kalb & Kalb* s. n. (hb. Kalb).—**Guyana:** Marudi Mts, Aishalton, 1982, *Stoffers et al.* 251e (ABL).

***Astrothelium ferrugineum* (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816686

*Trypethelium ferrugineum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 392 (1885); type: Cuba, *Wright* s. n. (G!—lectotype, designated here; Müller, *Lich. Cub.* 593).

*Trypethelium ferrugineum* var. *inornatum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 392 (1885); type: Cuba, *Wright* s. n. (G!—lectotype, designated here; Müller, *Verr. Cub.* 157).

(Fig. 26F & G)

*Thallus* corticate, olive-green but sparsely covered by orange pigment, uneven to shallowly verrucose.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic; pseudostromata 0.8–1.5 mm diam., prominent, covered by thallus and sparse orange pigment except for the blackish ostioles. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, 20–27 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV+ red, K+ purple, with anthraquinone.

*Distribution.* Neotropical (Cuba).

*Distribution.* This species has recently been synonymized with *Trypethelium aeneum* (Harris 1995), but it is kept separate here as no morphological intermediates occur and the world distribution and ecology seems to differ; this appears to be a very rare species.

***Astrothelium floridanum* Zahlbr.  
ex M. Choisy**

In Choisy, *Icon. Lich. Univ.*: pl. 5 (1928).—*Trypethelium floridanum* (Zahlbr. ex M. Choisy) R. C. Harris, *Acta*

*Amazon. (Suppl.)* 14: 73 ('1984') [1986]; type: USA, Florida, *Rapp* (W—holotype, not seen).

(Fig. 20A & B)

*Thallus* corticate, olive-green to brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent but not distinctly pseudostromatic, 0.3–0.6 mm diam., erumpent, covered by thallus except for the blackish ostiolar area surrounded by a whitish rim. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, 35–45 × 14–16 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical, extending into temperate regions; previously reported from the USA, Costa Rica and Japan.

*Discussion.* The synonymization with *Astrothelium marcidum* by Aptroot *et al.* (2008) was based on a specimen in L that was apparently incorrectly thought to be an isotype of that taxon. The correct type has astrothelioid ascomata (see below).

*New country records.* **Puerto Rico:** *Ponce:* Caribbean National Forest, 1150 m, 1989, *Aptroot & Aptroot* 25608 (ABL).—**Venezuela:** *Bolivar:* Cerro Guaiquinima, 1000 m, 1990, *Sipman* 26683 (B).—**Colombia:** *Amazonas:* Araracuara, opposite Isla Mariñame, 240 m, 1988, *Sipman & Duivenvoorden* 28337 (B).

***Astrothelium galligenum* (Aptroot)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816687

*Trypethelium galligenum* Aptroot, *Tropical Bryology* 14: 29 (1998); type: Papua New Guinea, Central Province, Owen Stanley Range, Kagi Village, along Kokoda Trail towards Gap, *Aptroot* 39461 (B!—holotype; ABL!—isotype).

(Fig. 21B)

*Thallus* corticate, pale greenish, uneven to bullate, causing pseudogall formation.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata

0.8–1.5 mm diam., erumpent, apically whitish and blackish ostioles surrounded by a brown rim. *Hamathecium* interspersed with yellow, K+ purple oil. *Ascospores* 8 per ascus, 7-septate, 50–60 × 12–17 µm, central septum euseptate and wider, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–; hamathecium internally K+ purple, with anthraquinone.

*Distribution.* Eastern palaeotropical (Papua New Guinea).

***Astrothelium gigantosporum* (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816688

*Bathelium gigantosporum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 394 (1885).—*Laurea gigantospora* (Müll. Arg.) Zahlbr., in Engler & Prantl, *Natürl. Pflanzenfamil.* 1(1\*): 71 (1903); type: Cuba, *Wright* s. n. (G!—holotype).

(Fig. 35C & D)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic, pseudostromata 1–3(–5) mm diam., erumpent to prominent, covered by thallus except for dark ostioles surrounded by whitish rim. *Hamathecium* clear. *Ascospores* 2 per ascus, densely muriform, fusiform, 200–280 × 50–65 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Cuba and Costa Rica).

*New country record.* **Ecuador:** *Zamora-Chinchipec:* Cordillera Numbala, Reserva Biológica San Francisco, 2004, *Sipman* 52875, 52646 (B).

***Astrothelium gigasporum* R. C. Harris**

*Acta Amazon. (Suppl.)* 14: 61 ('1984') [1986]; type: Brazil, Amazonas, along Rio Curicuriari, Cachoeira Piraiwara, *Buck* 2532 (ABL, NY!—isotypes).

(Fig. 30K & L)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata diffusely pseudostromatic, pseudostromata 0.8–1.5 mm diam., prominent to sessile, covered by thallus but with strongly protruding, papilliform, brown ostioles. *Hamathecium* clear. *Ascospores* 8 per ascus, 19–22-septate, fusiform, 105–115 × 18–20 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical; previously reported from Guyana, Venezuela and Brazil.

*New country records.* **Colombia:** Amazonas: Araracuara, Villazul, 300 m, 1988, *Sipman & Duijvenvoorden* 28498 (B).—**French Guiana:** Saül, 1988, *Sipman* 31687 (B).

***Astrothelium grossoides* Aptroot & Lücking nom. nov.**

Mycobank No.: MB 816689

*Trypethelium grossum* Müll. Arg., *Bot. Jahrb. Syst.* 5: 139 (1884), non *Astrothelium grossum* Müll. Arg. (1888); type: Papua New Guinea, *Naumann* 409 (BM!—isotype).

(Fig. 12I)

*Thallus* corticate, olive-green to brownish, uneven-bullate, pseudogall-inducing.

*Ascomata* trypethelioid, with apical ostioles, dense to diffusely pseudostromatic, 0.4–0.5 mm diam., immersed, covered by thallus. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 3-septate, 15–32 × 9–12 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Eastern palaeotropical; reported from Papua New Guinea, where it is locally abundant, and New Caledonia.

***Astrothelium grossum* Müll. Arg.**

*Flora* 71: 141 (1888); type: New Caledonia, *Pancher*, 1870 (G!—holotype).

(Fig. 23E)

*Thallus* corticate, greenish to yellowish, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to confluent but usually not pseudostromatic, 0.4–0.6 mm diam., erumpent to prominent, wart-shaped, covered by thallus and yellow-orange, K+ purple, UV+ red pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, 30–35 × 10–15 µm, hyaline, IKI–.

*Chemistry.* Thallus UV+ yellow, K–, with lichexanthone; ascomata with yellow to orange, K+ purple, UV+ red anthraquinone.

*Distribution.* Reported only from New Caledonia, from where we also observed additional specimens.

*Discussion.* This taxon corresponds to what has traditionally been named *Astrothelium versicolor*. The type of the latter has a very peculiar thallus morphology and hence we suspect that many collections identified with the name *A. versicolor* might represent *A. grossum*.

***Astrothelium heterophorum* Nyl.**

*Bull. Soc. Linn. Normand., sér. 2* 2: 133 (1868); type: New Caledonia, Lifu, *Thiébaud* (H-NYL—holotype, not seen).

*Trypethelium elmeri* (Vain.) R. C. Harris, *Lichenogr. Thomomiana*: 143 (1998).—*Pseudopyrenula elmeri* Vain., *Ann. Acad. Sci. Fenn., ser. A* 6: 354 (1921); type: Philippines, Luzon, Irosin, Sorsogon, *Elmer* 14655 (TUR-Vain 30812!—holotype; ABL!, G!—isotypes).

(Fig. 30E)

*Thallus* corticate, olive-green to yellowish, smooth to uneven.

*Ascomata* pleurothelioid and with separate ostioles or in part astrothelioid, several chambers joined with eccentric, fused ostioles; single or joined ascomata dispersed,



0.5–1.0 mm diam., immersed-erumpent, covered by thallus except for blackish ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, 9–19-septate, fusiform, 60–80 × 12–17 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (Philippines and New Caledonia).

***Astrothelium indicum* (Upreti & Ajay Singh) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816690

*Laurera indica* Upreti & Ajay Singh, *Bull. Jard. Bot. Nat. Belg.* 57: 372 (1987) non Makhija & Patw. (1988); type: India, Bengal, *Kurz* 202 (H-Nyl 122!—holotype; BM!—isotype).

(Fig. 33G)

*Thallus* corticate, olive-green to brownish but whitish pruinose, uneven-rugose.

*Ascomata* trypethelioid with apical ostioles, more or less grouped but not distinctly pseudostromatic, groups of ascomata 0.8–1.2 mm diam., erumpent, covered by thallus and whitish pruina except for the blackish ostiolar area. *Hamathecium* interspersed. *Ascospores* (4–)8 per ascus, muriform, ellipsoid, (33–)50–70 × 13–17 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (India and Thailand).

***Astrothelium infossum* (Nyl.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816691

*Verrucaria infossa* Nyl., *Flora* 69: 178 (1886).—*Pseudopyrenula infossa* (Nyl.) Zahlbr., *Catal. Lich. Univ.* 1: 357 (1922).—*Trypethelium infossum* (Nyl.) R. C. Harris, *Lichenogr. Thomsoniana*: 144 (1998); type:

São Tomé, Bom Successo, *Moller* s. n. (H-Nyl 1034!—holotype; BM!—isotype).

(Fig. 18G)

*Thallus* corticate, olive-brown to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.3–0.4 mm diam., immersed, covered by thallus except for blackish ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 22–27 × 7–9 µm, hyaline, IKI+ violet.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Africa (São Tomé).

*Discussion.* A very inconspicuous species except for the amyloid ascospores, a rare feature in the family. Otherwise, the species falls within the *Astrothelium nitidiusculum* complex.

***Astrothelium infuscatulum* (Müll. Arg.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816692

*Trypethelium infuscatulum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 389 (1885).—*Pseudopyrenula infuscatula* (Müll. Arg.) Vain., *Ann. Acad. Sci. Fenn., ser. A* 6(7): 197 (1915); type: Cuba, *Wright* s. n. (G!—holotype; L!—isotype; Müller, *Verr. Cub.* 175).

(Fig. 18H & I)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata 1–2 mm broad, erumpent, irregular to linear, with flattened surface, blackish brown except for a pale brown rim around the ostioles. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 25–30 × 7–10 µm, hyaline, IKI+ violet.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical; previously reported from Cuba, Colombia, Venezuela and Guyana.

*Discussion.* The conspicuous pseudostromata resemble those of *Astrothelium degenerans* and *A. feei*, but lack the internal yellow-orange pigment and are conspicuously flattened above. The amyloid ascospores also set *A. infuscatulum* apart.

*New country record. Surinam: Brokopondo:* Brownsberg, 1985, *Aptroot* 14865 (ABL).

***Astrothelium inspersaeneum***  
**E. L. Lima *et al.***

In Lima *et al.* *Bryologist* **116**: 327 (2013); type: Brazil, Pernambuco, Buíque, Catimbau National Park, on bark of tree, 900 m, 3 February 2012, *Lima* 394 (ISE!—holotype).

(Fig. 14G)

*Thallus* corticate, light olive-brown to yellowish, covered by orange pigment.

*Ascomata* trypethelioid, with apical ostioles, usually aggregated in groups or lines but not distinctly pseudostromatic, 0.2–0.4 mm diam., erumpent, covered by thallus and orange pigment except black ostiolar area. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 3-septate, oblong-ellipsoid, 20–25 × 8–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K+ purple. TLC: an anthraquinone, probably parietin.

*Distribution.* Neotropical (previously reported only from Brazil).

*Discussion.* This species is most similar in aspect and internal structures to *Astrothelium neogalbineum*, but differs markedly by the inspersed hamathecium and the absence of lichexanthone.

*New country record. Peru: San Martin:* Tarapoto, Santesson & Thor P71:32 (S).

***Astrothelium interjectum*** R. C. Harris

*Acta Amazon. (Suppl.)* **14**: 61 ('1984') [1986]; type: Brazil, Amazonas, Serra Aracá, *Samuels* 838 (NY!—isotype).

(Fig. 24H & I)

*Thallus* light olive-green to greyish green, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic; pseudostromata 1–2(–3) mm diam., erumpent to prominent, whitish and darker ostiolar areas. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 25–30 × 6–11 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV+ yellow, K–, with lichexanthone.

*Distribution.* Pantropical; previously reported from Costa Rica and Brazil.

*New country records. Colombia: Nariño:* Tumaco, Estacion Forestal La Espriella, 1986, *Sipman & Velosa* 33041 (B).—*Guyana: Upper Takutu:* Kuyuwini Landing, 1992, *Sipman* 57017 (B).—*Papua New Guinea: Madang:* Gogol Valley, Tgubi logging site, 1992, *Sipman* 35965 (ABL, B); 11 km W of Brahman Mission, 1995, *Aptroot* 38706 (ABL).

***Astrothelium intermedium*** Aptroot & Lücking

In Aptroot *et al.*, *Biblioth. Lichenol.* **98**: 46 (2008); type: Costa Rica, Puntarenas, Las Cruces Biological Station, *Lücking* s. n. (F!—holotype).

(Fig. 29G & H)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata diffusely pseudostromatic; pseudostromata 1–2 cm diam. (individual ascomata 0.3–0.5 mm diam.), erumpent, irregular to linear and in part confluent and anastomosing, covered by thallus except dark ostioles surrounded by a pale rim. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, 29–33 × 12–15 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Costa Rica).

***Astrothelium irregulare* (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816693

*Bathelium irregulare* Müll. Arg., *Hedwigia* **30**: 234 (1891).—*Laurea irregularis* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* **1**: 504 (1922); type: Brazil, Theresopolis, *Schenck* 4643 (G!—holotype).

(Fig. 34F)

*Thallus* corticate, olive-green to brownish, uneven- verrucose.

*Ascomata* trypethelioid, with apical ostioles, solitary or rarely irregularly confluent, 0.6–1.0 mm diam., erumpent to prominent, covered by thallus. *Hamathecium* interspersed. *Ascospores* 8 per ascus, densely muriform, fusiform, 135–165 × 36–52 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Brazil).

***Astrothelium isabellinum* Eschw.**

In Martius, *Icon. Plant. Cryptog.* **2**: 20 (1828).—*Astrothelium isabellinum* Eschw. (1824), nom. nud.—*Heufertia isabellina* (Eschw.) Trevis., *Flora* **44**: 23 (1861).—*Cryptothelium isabellinum* (Eschw.) Zahlbr., *Catal. Lich. Univ.* **1**: 522 (1922); type: Brazil, s. col. (M—holotype, not seen).

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata diffusely pseudostromatic; pseudostromata 1–2 mm diam., erumpent, covered by thallus, internally with red pigment. *Hamathecium* clear. *Ascospores* 2 per ascus, densely muriform, fusiform, 150–200 × 40–50 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV–, externally K–, internally with K+ purple anthraquinone.

*Distribution.* Neotropical (Brazil).

***Astrothelium keralense* (Upreti & Ajay Singh) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816694

*Laurea keralensis* Upreti & Ajay Singh, *Bull. Jard. Bot. Nat. Belg.* **57**: 374 (1987); type: India, Kerala, Quilon, Kundara, *Singh & Ranjan* 102951 (LWG—holotype, not seen).

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.6–1.0 mm diam., erumpent to prominent, hemispherical, covered by thallus. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, fusiform, 50–60 × 15–20 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (India and Thailand).

***Astrothelium kunzei* (Fée) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816695

*Trypethelium kunzei* Fée, *Ann. Sci. Nat.* **23**: 445 (1831); type: Surinam, *Kunze* s. n. (G!—holotype).

(Fig. 15H & I)

*Thallus* corticate, olive-brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 0.5–1.0 mm broad, immersed, forming irregular, partly reticulate lines, covered by thallus and orange pigment except dark ostioles. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 20–27 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV+ red, K+ purple, with anthraquinone.

*Distribution.* Neotropical (Panama and Surinam).



*Discussion.* The epithet *kunzei* is taken up here for material in the *Astrothelium aeneum* aggregate that produce distinct, immersed, linear-reticulate pseudostromata. This distinction is supported by molecular data (Lücking *et al.* 2016a).

***Astrothelium laevigatum* Müll. Arg.**

*Flora* 66: 245 (1883); type: Brazil, Apiahy, *Puiggari* 1689 (G!—holotype).

*Astrothelium simplicatum* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 194 (1890); type: Brazil, Minas Gerais, Sitio, *Vainio* 1006 (TUR-Vain 30870!—holotype; BM!—isotype).

(Fig. 23K & L)

*Thallus* corticate, greenish grey (lichenanthone colour), smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, not pseudostromatic, 0.3–0.5 mm diam., erumpent, covered by thallus but upper part whitish contrasting with the dark ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 20–26 × 7–9 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV+ yellow, K–, with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone).

*Distribution.* Neotropical (Brazil).

***Astrothelium leioplacum* (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816696

*Clathroporina leioplaca* Müll. Arg., *Revue Mycol.* 10: 182 (1888); type: Paraguay, *Balansa* s. n. (G!—holotype).

*Clathroporina irregularis* Müll. Arg., *Revue Mycol.* 10: 182 (1888); type: Paraguay, *Balansa* 231 (G!—lectotype, designated here).

(Fig. 39H)

*Thallus* corticate, olive-grey, smooth to uneven.

*Ascomata* pleurothelioid, with separate ostioles, 0.4–0.6 mm diam., erumpent, completely covered by thallus. *Hamathecium*

clear. *Ascospores* 8 per ascus, densely muriform, fusiform, 33–52 × 16–22 µm, without thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Paraguay).

***Astrothelium leucoconicum* Nyl.**

*Flora* 52: 126 (1869); type: Brazil, Rio de Janeiro, *Glaziou* s. n. (H-Nyl 118!—holotype).

(Fig. 24K & L)

*Thallus* corticate, light olive-green to yellowish, uneven to shallowly bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, not pseudostromatic, 0.4–0.7 mm diam., erumpent, covered by thallus but upper part whitish contrasting with the dark ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 50–72 × 20–26 µm, hyaline, IKI–.

*Chemistry.* Thallus UV+ yellow, K–, with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone); ascomata UV–, K–.

*Distribution.* Neotropical (previously reported from Brazil).

*New country record.* **Venezuela:** *Bolivar:* Cerro Guaiquinima, 1500 m, 1990, *Sipman* 27215 (B).

***Astrothelium leucothelium* Nyl.**

*Ann. Sci. Nat., Bot., sér.* 5 7: 348 (1867); type: Colombia, Rio Negro, *Lindig* s. n. (H-Nyl 117!—holotype; S!—isotype).

(Fig. 23G)

*Thallus* corticate, greenish grey (lichenanthone colour), becoming brownish yellow, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata solitary to confluent or diffusely pseudostromatic, 0.4–0.6 mm diam.,

erumpent, covered by thallus but upper part whitish, with dark ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, 3(–5)-septate, fusiform, 32–52 × 10–17 µm, hyaline, IKI–.

**Chemistry.** Thallus and ascomata UV+ yellow, K–. TLC: lichexanthone.

**Distribution.** Neotropical (previously reported from Costa Rica, Colombia and Brazil).

**New country records.** **Venezuela:** *Merida:* Moro Negro, 1980, López Figueras & Rodríguez 22888 (ABL, MERF).—**French Guiana:** Saül, 1988, Sipman 31769, 31757 (ABL, B).

***Astrothelium lugescens* (Nyl.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816697

*Verrucaria lugescens* Nyl., *Flora* **69**: 177 (1886).—*Anthracothecium lugescens* (Nyl.) Zahlbr., *Catal. Lich. Univ.* **1**: 463 (1922).—*Campylothehium lugescens* (Nyl.) Upreti & Ajay Singh, *Bull. Soc. Bot. Fr., Let. Bot.* **134**: 293 (1987); type: São Tomé and Príncipe, *Henriques* s. n. (H-Nyl 1067!—holotype).

(Fig. 38I)

**Thallus** corticate, olive-green, smooth to uneven.

**Ascomata** pleurothelioid, with separate ostioles, 0.6–1.0 mm diam., erumpent, covered by thallus. *Hamathecium* clear. *Ascospores* 1 per ascus, densely muriform, fusiform, 210–230 × 45–70 µm, without distinctly thickened median septum, hyaline, IKI–.

**Chemistry.** Thallus and ascomata UV–, K–. TLC: no substances detected.

**Distribution.** African palaeotropical (São Tomé and Príncipe).

***Astrothelium luridum* (Zahlbr.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816698

*Trypethelium luridum* Zahlbr., *Ann. Mycol.* **14**: 47 (1916); type: Japan, Thushima, *Faurie* 3744 (W—holotype, not seen).

*Trypethelium scoria* f. *endochraceum* Nyl., *Lich. Jap.*: 115 (1890); type: Malaysia, Labuan, *Almquist*, 1897 (S!—isotype).

*Trypethelium endosulphureum* Makhija & Patw., *J. Hattori Bot. Lab.* **73**: 197 (1993); type: India, Meghalaya, Mohmtheid-Cherapunji road, 20 October 1977, *Patwardhan & Nagarkar* AMH 77.905 (ABL!—isotype).

(Fig. 17F–H)

**Thallus** corticate, olive-brown to yellowish, smooth to uneven.

**Ascomata** trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 0.8–1.5 mm broad, erumpent to prominent, covered by thallus except for dark ostiolar area, internally with yellow pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 7–11-septate, fusiform, 55–88 × 13–28 µm, hyaline, IKI–.

**Chemistry.** Thallus and pseudostromata U–, internally K+ red, with anthraquinone.

**Distribution.** Asia, extending into temperate regions (India and Japan).

***Astrothelium macrocarpum* (Fée) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816699

*Porina macrocarpa* Fée, *Essai Crypt. Écorc.*: 81 (1824); non Riddle 1920.—*Porophora macrocarpa* (Fée) Spreng., *Syst. Veget.* **4**(1): 241 (1827).—*Pyrenodium macrocarpum* (Fée) Fée, *Essai Crypt. Écorc. Suppl.*: 69 (1837).—*Pyrenula macrocarpa* (Fée) Massal., *Ricerch. Auton. Lich.*: 164 (1852).—*Astrothelium hypoxylon* var. *varmacrocarpum* (Fée) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* **5**: 141 (1857).—*Astrothelium sulphureum* var. *macrocarpum* (Fée) Nyl., in Hue, *Nouv. Archiv. du Muséum, sér. 3* **4**: 132 (1892); type: South America, “Cort. cinchonae” (M!—isotype).

*Astrothelium galbineum* Kremp., *Nuovo Giorn. Bot. Ital.* **7**: 58 (1875); type: Sarawak, *Beccari* 23 (M!—lectotype; Harris, *Acta Amazon. (Suppl.)* **14**: 60 (‘1984’) [1986]).

*Astrothelium ochrothelizum* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 382 (1885).—*Trypethelium ochrothelizum* Nyl., *Flora* **59**: 365 (1876), nom. nud.—*Trypethelium ochrothelizum* (Müll. Arg.) Nyl., *Sert. Lich. Trop. Labuan et Singap.*: 26 (1891); type: Cuba, *Wright* s. n. (G!—holotype; BM!—isotype; Müller, *Verr. Cub.* 144).

*Astrothelium conicum* var. *pallidum* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 382 (1885); type: Cuba, *Wright* s. n. (G!—lectotype, designated here; BM!—isolectotype; Müller, *Verr. Cub.* 605).

*Astrothelium ochrotheloides* Vain., *Acta Soc. Fauna Fl. Fem.* **7**(2): 194 (1890); type: Brazil, Minar Gerais,

Lafayette, *Vainio* s. n. (TUR-Vain 30868!—lectotype, designated here; Vainio, *Lich. Bras. Exs.* 310).

*Trypethelium discolor* Müll. Arg., *Hedwigia* 34: 35 (1895); type: Brazil, Minas Gerais, Serra do Ouro Preto, Ule 298 (G!—holotype).

(Fig. 22G–K)

*Thallus* corticate, olive-green to yellowish, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic; pseudostromata 0.5–1.0 mm diam., erumpent to prominent, conical with flattened top, covered by thallus with lateral part whitish and upper part with yellow-orange pigment and dark ostiole. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 21–28 × 7–11 µm, hyaline, IKI–.

*Chemistry.* Thallus UV+ yellow, K–, with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone); pseudostromata with yellow-orange K+ purple, UV+ red anthraquinone, probably parietin.

*Discussion.* The rather well-known name *Astrothelium galbineum* has to be replaced by the older epithet *macrocarpum*, which was in use for a century but then surprisingly went out of use. The synonymy of *A. ochrothelioides* is based on the original description of the ascospores; Harris (1986: 59) reported that no spores remain. Typical *A. macrocarpum* has conical pseudostromata in which only the upper part is covered by pigment, whereas the types of *A. ochrothelioides* and *Trypethelium discolor* have wart-shaped pseudostromata completely covered by pigment; thus, more than one species might be contained here.

*Distribution.* Pantropical; previously reported from the USA, Cuba, Costa Rica, Panama, Venezuela, Guyana, French Guiana, South Africa, India, Sri Lanka, Singapore, Thailand, Borneo, Papua New Guinea and Australia.

*New country records.* **Colombia:** Amazonas: Araracuara, opposite airstrip, 350 m, 1988, Sipman & Duivenvoorden 27863 (B).—**Gabon:** Nzé, 2006, Ertz 9719 (BR).

***Astrothelium macrosporum* (Makhija & Patw.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816700

*Trypethelium macrosporum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 200 (1993); type: India, Meghalaya, Cherapunji Road, 27 October 1977, Patwardhan & Nagarkar AMH 77.826 (ABL!—isotype).

(Figs 21F & 33J)

*Thallus* corticate, olive-green to yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.7–1.0 mm diam., erumpent, covered by thallus except dark ostiolar area surrounded by irregular whitish rim. *Hamathecium* finely inspersed. *Ascospores* 8 per ascus, 9–13-septate, occasionally with a longitudinal septum, fusiform, 120–195 × 17–22 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (India).

***Astrothelium marcidum* (Fée) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816701

*Pyrenula marcida* Fée, *Essai Crypt. Écorc.*: 77 (1824).—*Verrucaria marcida* Spreng. (1827) nom. nud.—*Trypethelium marcidum* (Fée) Müll. Arg., *Mém. Soc. Phys. Hist. Nat. Genève* 30(3): 11 (1888); type: South America “ad corticem Cinchonarum”, “b” (G!—holotype).

(Fig. 29F)

*Thallus* corticate, olive-brown, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic, pseudostromata 0.7–1.0 mm diam., immersed-erumpent, covered by thallus or yellowish white layer. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 35–45 × 14–16 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.



*Distribution.* Neotropical.

*Discussion.* The epithet *marcidum* was suggested to replace the epithet *floridanum* by Aptroot *et al.* (2008), as both agree in thallus morphology, ascospore type, and lack of secondary substances. The type material of *Pyrenula marcida* is in very bad shape, with almost all ascomata abraded; however, re-examination revealed that the ascoma organization is astrothelioid, not trypethelioid as in *Astrothelium floridanum*, since several remaining ascoma bases show a pyriform shape with the tip pointing centrally.

***Astrothelium megaleium* (Kremp.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 8166702

*Trypethelium megaleium* Kremp., *Nuovo Giorn. Botan. Ital.* 21(3): 13 (1875).—*Bathelium megaleium* (Kremp.) Müll. Arg., *Linnaea* 63: 45 (1880).—*Laurera megaleia* (Kremp.) Zahlbr., *Catal. Lich. Univ.* 1: 505 (1922); type: Malaysia, Sarawak, *Beccari* s. n. (M!—holotype).

?*Trypethelium oligosporum* Mont. & Bosch, in Mont., *Sylloge Gener. Spec. Cryptog.*: 374 (1865).—*Bathelium oligosporum* (Mont. & Bosch) Trevis., *Flora* 44: 21 (1861).—*Laurera oligospora* (Mont. & Bosch) Zahlbr., *Catal. Lich. Univ.* 1: 505 (1922); type: Indonesia, Java, *Junguhm* s. n. (L—holotype lost).

(Fig. 33I)

*Thallus* corticate, olive-brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.8–1.5 mm diam., erumpent, mostly exposed, dark brown. *Hamathecium* interspersed. *Ascospores* 2 per ascus, densely muriform, fusiform, 210–225 × 32–35 µm, with distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (Malaysia: Sarawak, and Indonesia).

*Discussion.* The synonymy of *Trypethelium oligosporum* is uncertain, as the type is lost, and therefore this older epithet is not taken up.

***Astrothelium megalophthalmum* (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816703

*Trypethelium megalophthalmum* Müll. Arg., *Hedwigia* 34: 35 (1895); type: Brazil, Santa Catarina, Serra Geral, *Ule* 291 (G!—holotype; NY—isotype).

(Fig. 22A & B)

*Thallus* corticate, olive-green, verrucose-bullate.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic; pseudostromata 1–3(–5) mm diam., immersed-erumpent, with upper portion of ascomata exposed, blackish brown. *Hamathecium* clear. *Ascospores* 8 per ascus, 3–7-septate, fusiform, 85–120 × 20–32 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Brazil).

***Astrothelium megalostomum* (Vain.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816704

*Heufleria megalostoma* Vain., *Acta Soc. Fauna Fl. Fern.* 7(2): 193 (1890).—*Cryptothelium megalostomum* (Vain.) Zahlbr., *Catal. Lich. Univ.* 1: 522 (1922).—*Campylothelium megalostomum* (Vain.) Aptroot, *Fungal Diversity* 9: 29 (2002); type: Brazil, Minas Gerais, Serra do Caraça, *Vainio* s. n. (TUR-Vain 303838!—holotype; Vainio, *Lich. Bras. Exs.* 1587).

(Fig. 36E)

*Thallus* corticate, light olive-green, smooth to rough.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, 0.8–1.3 mm diam., erumpent, covered by thallus except dark ostiolar area. *Hamathecium* interspersed. *Ascospores* 2 per ascus, densely muriform, fusiform, 170–220 × 50–64 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; ascomata UV+ yellow, with lichexanthone, K–.

*Distribution.* Neotropical (Brazil).

***Astrothelium megaspermum* (Mont.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816705

*Trypethelium megaspermum* Mont., *Ann. Sci. Nat., Bot.*, sér. 2 19: 68 (1843).—*Bathelium megaspermum* (Mont.) Trevis., *Spighe e Paglie*: 20 (1861).—*Laurera megasperma* (Mont.) Riddle, *Bull. Torrey Bot. Club* 44: 323 (1917); type: French Guiana, Leprieur 603 (FH-TAYL 11!—isotype).

*Trypethelium ostendatum* Kremp., *Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn* 5: 398 (1874).—*Bathelium ostendatum* (Kremp.) Müll. Arg., *Linnaea* 63: 45 (1880).—*Laurera ostendata* (Kremp.) Zahlbr., *Catal. Lich. Univ.* 1: 506 (1922); type: Brazil, Minas Gerais, Serra d'Estrella, Warming 79 (M!—holotype).

*Verrucaria euthelia* Nyl., *Flora* 69: 177 (1886); type: São Tomé and Príncipe, Moller s. n. (H-Nyl 1064!—holotype).

*Thelenella fulva* Vain., *Catal. Welwitsch Afric. Plants* 2: 451 (1901).—*Clathroporina fulva* (Vain.) Zahlbr., *Catal. Lich. Univ.* 1: 418 (1922).—*Polyblastiopsis fulva* (Vain.) C. W. Dodge, *Ann. Missouri Bot. Gard.* 40: 275 (1953); type: Angola, Golungo Alto, Mata Quisuculo, Welwitsch 230 (TUR-Vain 31066!—holotype; BM!—isotype).

*Julella zenkeriana* P. Henn., *Bot. Jahrb. Syst.* 38: 127 (1905); type: Cameroon, Bipinde, Zenker 1980 (B!—holotype).

*Polyblastiopsis pertusarina* Zahlbr., *Feddes Repert.* 31: 199 (1933); type: Taiwan, Mount Arisan, Toroyen, Asahina 299 (W—holotype, not seen).

*Campylothelium nitidum* Zahlbr., *Ann. Mycol.* 33: 39 (1935) non Müll. Arg. (1891).—*Campylothelium zahlbruckneri* R. G. Werner, *Bull. Soc. Sci. Nat. Maroc.* 24: 130 (1944); type: USA, Florida, Sanford, Rapp 84 (W—holotype, not seen).

*Clathroporina diplolea* Zahlbr., *Ann. Mycol.* 33: 37 (1935); type: USA, Florida, Rapp (W—holotype, not seen).

*Laurera megasperma* f. *immersa* Letr.-Gal., *Rev. Bryol. Lichénol.* 26: 234 (1957); type: Sri Lanka, Petsch (BM!—holotype).

*Laurera megasperma* f. *conica* Letr.-Gal., *Rev. Bryol. Lichénol.* 27: 67 (1958); type: Ivory Coast, Mont Orombe Boka, Dimbokro, 20 August 1954, Santesson 107240 (UPS—holotype, not seen).

(Fig. 34H–L)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.8–1.5 mm diam., prominent, hemispherical with flattened top, covered by thallus except for dark ostiolar area surrounded by whitish rim. *Hamathecium* interspersed. *Ascospores* generally 4 per ascus, densely muriform, oblong-fusiform,

140–220 × 30–75 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical; previously reported from the USA, Costa Rica, Cuba, Jamaica, Puerto Rico, French Guiana, Brazil, Argentina, Ivory Coast, Angola, Cameroon, India, Sri Lanka, Thailand, Vietnam, Taiwan, New Caledonia and Papua New Guinea.

*New country records.* **Colombia:** Nariño: Tumaco, Estacion Forestal La Espriella, 1986, Sipman & Velosa 33054 (B).—**Guyana:** Upper Takutu: Kuyuwini Landing, 1992, Sipman 58222 (B).—**Ecuador:** Napo: 5 km N of Sta. Rosa, 400 m, 1982, Aptroot & Hensen 10611, 10612 (ABL).—**Peru:** Maynas: Iquitos, 1980, Schumm & Pudor 11952 (hb. Schumm).—**Gabon:** Nzé, 2006, Ertz 9725 (BR).—**DR Congo:** Mongala: Lisala, 2009, Ertz 14181 (BR).—**Malaysia:** Pahang: Fraser's Hill, 1989, Sipman et al. 45022 (B).—**China:** Yunnan: Xishuangbanna, Menglun, 2002, Aptroot 57355 (ABL).—**Indonesia:** Sulawesi: Tondano, 1000 m, 1988, Hensen s. n. (ABL).

***Astrothelium meiophorum* (Nyl.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816732

*Trypethelium annulare* var. *meiophorum* Nyl., *Bull. Soc. Linn. Normand.*, sér. 2 2: 132 (1868).—*Trypethelium meiophorum* (Nyl.) Müll. Arg., *Hedwigia* 31: 286 (1892); type: New Caledonia, Pancher s. n. (G!—lectotype, designated here; BM!—isolectotype).

*Trypethelium flavoalbum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 197 (1993); type: India, Meghalaya, near Sohararim, 20 October 1977, Patwardhan & Nagarkar AMH 86.697 (ABL!—isotype).

*Trypethelium parvicarpum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 205 (1993); type: India, Nicobar Islands, Kamorta, Daring, 18 January 1987, Nagarkar & Patwardhan AMH 87.389 (ABL!—isotype).

(Fig. 19C & D)

*Thallus* corticate, light olive-green to yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, irregularly grouped to diffusely pseudostromatic; pseudostromata 0.5–0.7 mm broad, erumpent, covered by thallus except for broad, dark ostiolar area. *Hamathecium* clear.

*Ascospores* (2–)8 per ascus, fusiform-ellipsoid, 3-septate, 20–25 × 7–8 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (previously reported from India and New Caledonia).

*Discussion.* Unfortunately the type material of *Trypethelium annulare* var. *meiophorum* is extremely small and hence the new synonyms listed here are somewhat tentative, although morphologically they seem to agree well, particularly the type of *T. parvicarpum*. We were unable to confirm the statement of 2-spored asci given in the protologue of *Astrothelium meiophorum*, since only two ascomata are left in the type, but we believe that this observation is based on an ascus with most ascospores already expelled. The two synonyms listed regularly have 8-spored asci. Additional material found under this name from New Caledonia is *A. scoria*. It should also be mentioned that the ascospores in the type specimen of *Trypethelium parvicarpum* are c. 23 × 7 µm, larger than given in the protologue of that taxon.

*New country record.* **China:** Yunnan: Xishuangbanna, 2002, Aptroot 57350 (ABL).

***Astrothelium meristosporoides*  
(P. M. McCarthy & Vongsheew.)  
Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816706

*Laurera meristosporoides* P. M. McCarthy & Vongsheew. in Vongsheewarat *et al.*, *Mycotaxon* **70**: 228 (1999); type: Thailand, Phisanulok Prov., Phu Hin Rong Kla National Park, Vongsheewarat 173 (CANB—holotype, not seen).

(Fig. 31E)

*Thallus* corticate, light greenish yellow, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, prominent, whitish and black ostiolar area, 0.7–1.5 mm diam. *Hamathecium* interspersed. *Ascospores* 8 per ascus, muriform, fusiform,

68–120 × 18–24 µm, with somewhat thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV+ yellow, K–, with lichexanthone or 1,8-dihydroxy-3,6-dimethoxyxanthone.

*Distribution.* Palaeotropical (previously reported only from Thailand).

*New country record.* **Papua New Guinea:** Central: Varirata National Park, 800 m, 1987, Aptroot 19135 (ABL).

***Astrothelium meristosporum* (Mont. & Bosch) Aptroot & Lücking  
comb. nov.**

MycoBank No.: MB 816707

*Trypethelium meristosporum* Mont. & Bosch, in Junghuhn, *Pl. Jungh.* **4**: 487 (1855).—*Meristosporum javanicum* A. Massal., *Atti I. R. Istitut. Veneto, Ser. 3* **5**: 328 (1860).—*Bathelium meristosporum* (Mont. & Bosch) Trevis., *Flora* **44**: 21 (1861).—*Melanothea javanica* (A. Massal.) Zahlbr., in Engler & Prantl, *Natürl. Pflanzenfamil.* **1**(1\*): 70 (1903).—*Laurera meristospora* (Mont. & Bosch) Zahlbr., *Catal. Lich. Univ.* **1**: 505 (1922); type: Indonesia, Java, Junghuhn (L!—isotype).

*Bathelium chrysocarpum* Müll. Arg., *Hedwigia* **30**: 54 (1891).—*Laurera chrysocarpa* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* **1**: 503 (1922); type: Australia, Queensland, Bellenden Ker, Bailey 540 (G!—holotype; BRI!—isotype).

*Verrucaria anoptella* Stirt., *Proceed. Philosoph. Soc. Glasgow* **13**: 190 (1881).—*Clathroporina anoptella* (Stirt.) Zahlbr., *Catal. Lich. Univ.* **1**: 415 (1922).—*Polyblastiopsis anoptella* (Stirt.) Ajay Singh, *Nova Hedwigia* **36**: 238 (1982); type: India, Assam, Watt s. n. (BM!—holotype).

*Thelenella interrupta* Vain., *Hedwigia* **46**: 180 (1907).—*Clathroporina interrupta* (Vain.) Zahlbr., *Catal. Lich. Univ.* **1**: 418 (1922); type: Thailand, Koh Chang Island, Lem Dam, Schmidt 17 (TUR-Vain 31065—holotype, not seen).

*Laurera columellata* Makhija & Patw., *Mycotaxon* **31**: 574 (1988); type: India, Karnataka, S. Kanara, Hiriadaka, Udipi-Hebri Road, 22 February 1978, Patwardhan AMH 78.59 (ABL!—isotype).

*Laurera andamanica* D. D. Awasthi, *Biblioth. Lichenol.* **40**: 3 (1991).—*Laurera indica* Makhija & Patw., *Mycotaxon* **31**: 578 (1988) non Upreti & Ajay Singh (1987); type: India, Andaman Islands, South Andaman, Baratang Islands, Bishnu Nala, 22 February 1985, Patwardhan & Sethy AMH 85.656 (ABL!—isotype).

(Fig. 31F–H)



*Thallus* corticate, light olive-green, uneven to verrucose.

*Ascomata* trypethelioid, with apical ostioles, 1.0–1.5 mm diam., prominent, hemispherical with flattened top, covered by thallus except whitish to greyish ostiolar area, 0.7–2.0 mm diam. *Hamathecium* hyaline or slightly yellowish, interspersed. *Ascospores* (4–)8 per ascus, muriform, oblong-fusiform, 120–220 × 25–40 µm, constricted at the markedly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV+ yellow, K–, with lichexanthone or 1,8-dihydroxy-3,6-dimethoxyxanthone.

*Distribution.* Palaeotropical (previously reported from India, Sri Lanka, Thailand, Indonesia, Papua New Guinea, Australia); the specimen reported here from French Guiana is atypical.

*Discussion.* As can be expected for a species with such large ascospores, there is considerable variation in size, even within a single ascoma.

*New country records.* **French Guiana:** Montsinery, 20 km W of Cayenne, along forest track called Risque tout, 50 m, 1985, *Aptroot* 15125 (ABL, B).—**Malaysia:** Belum, Halong Trail, 1994, *Nätebusch* s. n. (hb. Kalb).—**Solomon Islands:** Kolombangara, 1965, *Hill* 10377 (BM).

***Astrothelium neogalbineum***  
**(R. C. Harris) Aptroot & Lücking**  
**comb. nov.**

MycoBank No.: MB 816708

*Trypethelium neogalbineum* R. C. Harris, *Acta Amazon. (Suppl.)* 14: 74 ('1984') [1986]; type: Brazil, Pará, Santarém, *Spruce* 259 (BM!—isotype).

(Fig. 12A & B)

*Thallus* corticate, olive-green to greyish green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 0.5–1.0 mm broad, immersed-erumpent, irregular to elongate or becoming reticulate, dark brown with orange pigment, especially

laterally. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 18–26 × 7–8 µm, hyaline, IKI–.

*Chemistry.* Thallus UV+ yellow, with lichexanthone; pseudostromata UV+ red, K+ purple, with anthraquinone.

*Distribution.* Neotropical (previously reported from Costa Rica and Brazil).

*New country record.* **Guyana:** East Demarara: along Linden Highway, Soesdyke, *Sipman* 40277 (B).

***Astrothelium nigratum* (Müll. Arg.)**  
**Aptroot & Lücking comb. et stat. nov.**

MycoBank No.: MB 816709

*Astrothelium minus* var. *nigratum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 382 (1885); type: Cuba, *Wright* s. n. (G!—holotype; FH-TUCK 3982—istotype, not seen; Müller, *Verr. Cub.* 638).

(Fig. 19B)

*Thallus* corticate, olive-brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic, 0.2–0.3 mm diam., immersed-erumpent, exposed and brown-black. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 20–27 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported only from Cuba).

*New country records.* **Puerto Rico:** *Mayagüez:* Reserva Forestal Maricao, 1989, *A. & M. Aptroot* 24961 (ABL).—**Guyana:** *Rupununi:* Kuyuwini Landing, 1991, *Jansen-Jacobs et al.* 2573 (ABL).

***Astrothelium nigricans* Malme**

*Astrothelium nigricans* Malme, *Ark. Bot.* 19(1): 13 (1924); type: Brazil, Matto Grosso, Cuyabá, *Malme* 2003 (S!—holotype).

(Fig. 28F)

*Thallus* corticate, olive-green to yellowish, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata diffusely pseudostromatic, formed on irregularly linear to reticulate, whitish thallus portions, 0.6–1.0 mm diam., prominent, wart-shaped, completely exposed and black, covered. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 21–27 × 8–10 μm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Brazil).

***Astrothelium nigrorufum* (Makhija & Patw.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816710

*Trypethelium nigrorufum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 203 (1993); type: India, Andaman Islands, Baratang, Baludera, 23 February 1985, *Patwardhan & Sethy* AMH 85.845 (ABL!—isotype).

(Fig. 17A)

*Thallus* corticate, olive-brown to yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 1–2 mm broad, immersed-erumpent, exposed and brown-black, internally with yellow-orange, K+ purple pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 9–13-septate, fusiform, 29–35(–46) × 7–9 μm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV–, internally K+ purple, with anthraquinone.

*Distribution.* Eastern palaeotropical (India).

***Astrothelium nitidiusculum* (Nyl.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816711

*Verrucaria nitidiuscula* Nyl., *Ann. Sci. Nat. Bot. sér. 4* 20: 252 (1863).—*Pseudopyrenula nitidiuscula* (Nyl.) Müll. Arg., *Flora* 66: 248 (1883).—*Trypethelium nitidiusculum*

(Nyl.) R. C. Harris, *Acta Amazon. (Suppl.)* 14: 75 ('1984') [1986]; type: Colombia, Villeta, *Lindig* 2829 (M!, BR—iso-types).

*Pseudopyrenula neglecta* Müll. Arg., *Flora* 68: 332 (1885); type: French Guiana, *Leprieur* 479 (G!—holotype).

*Trypethelium hebetum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 198 (1993); type: India, Andaman Islands, South Andaman, Near Wright Myo, Shol Bay, 20 December 1986, *Patwardhan & Nagarkar* AMH 77.866 (ABL!—isotype).

(Fig. 19F–L)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to confluent but not distinctly pseudostromatic, 0.2–0.3 mm diam., erumpent, covered by thallus but upper portion whitish (or a white rim only) with dark ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 15–27 × 7–10 μm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical, reported from, for example, Colombia, Ecuador, Bolivia, Guyana, French Guiana, Brazil, India, and Papua New Guinea. The species has also been reported from the USA, Mexico, Bermudas, Bahamas, Cuba, Jamaica, Dominican Republic, Trinidad, Costa Rica, El Salvador, Isla del Coco, Guyana, French Guiana, Colombia, Venezuela, Galapagos, Brazil, Bolivia, Argentina, South Africa, Seychelles, India, Sri Lanka, Vietnam, Thailand, Taiwan, Hong Kong, Japan, Papua New Guinea and Australia, but these reports correspond to a much broader species concept including, for example, the now separated, more common taxa *A. bicolor* and *A. scoria*. Therefore, below are some additional records from countries from which the species had been reported previously in a wider sense.

*Discussion.* *Astrothelium nitidiusculum* is restricted here to include specimens with solitary to confluent, but not pseudostromatic ascomata. Even when dense or

confluent, the ascomata can clearly be individually discerned.

*Confirmed additional country records. Ecuador:* Morona-Santiago: Gualaquiza, 1982, *Aptroot & Hensen* 10454 (ABL).—*Guyana:* Upper Takutu: Kuyuwini Landing, 1992, *Sipman* 58140 (B).—*Papua New Guinea:* Madang: Balek Wildlife Reserve, 1992, *Aptroot* 30891 (ABL).

### ***Astrothelium nitidulum* Weerakoon & Aptroot**

*Cryptog.*, *Mycol.* 35: 58 (2014); type: Sri Lanka, Central Province, Coolbone tea estate Matale, *Cloonan* 083/53, 1982 (F!—holotype).

(Fig. 21E)

*Thallus* corticate, olive-brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to confluent and becoming diffusely pseudostromatic; pseudostromata 0.9–1.9 mm diam. (individual ascomata 0.6–0.9 mm diam.), erumpent to prominent, covered by thallus except for black ostiole with whitish centre. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 7-septate, fusiform, 40–49 × 12–15 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution:* Eastern palaeotropical (Sri Lanka).

### ***Astrothelium obscurum* Müll. Arg.**

*Flora* 66: 244 (1883); type: Brazil, Apiahy, *Puiggari* 2255 (G!—holotype).

(Fig. 28J)

*Thallus* corticate, olive-brown, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata largely confluent but not distinctly pseudostromatic, 0.3–0.4 mm diam., erumpent, applanately conical, exposed and dark brown. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 20–25 × 7–9 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Brazil).

### ***Astrothelium ocellatum* Malme**

*Ark. Bot.* 19(1): 14 (1924); type: Brazil, Matto Grosso, Santa Anna da Chapada, *Malme* 2411 (S!—holotype).

(Fig. 27D & E)

*Thallus* corticate, olive-green, smooth to uneven or shallowly bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata solitary to confluent but not pseudostromatic, 1.0–1.8 mm diam., erumpent, covered by thallus but papilliform ostiolar area ochraceous brown, with yellow-orange pigment and surrounded by an irregular whitish rim. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 55–65 × 15–25 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–, without lichexanthone; pseudostromata with yellow-orange, K+ purple, UV+ red anthraquinone.

*Distribution.* Pantropical (previously reported from Guyana, Brazil and Papua New Guinea).

*New country records. Venezuela:* Amazonas: Alto Orinoco, Surumoni, 1998, *Hafellner & Komposch* 15-13 (GZU).—*French Guiana:* Saül, 1988, *Sipman* 31772 (B).

### ***Astrothelium ochrothelium* (Nyl.) Müll. Arg.**

*Flora* 68: 255 (1885).—*Trypethelium ochrothelium* Nyl., *Acta Soc. Sci. Fenn* 7: 494 (1863); type: Colombia, Villeta, *Lindig* 2823 (H-Nyl 7574!—lectotype; Harris, *Acta Amazon. (Suppl.)* 14: 62 ('1984') [1986]; S!, BR—isolectotypes).

(Fig. 23A & B)

*Thallus* corticate, olive-green to yellowish or brownish, uneven to shallowly verrucose.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined



ascomata pseudostromatic; pseudostromata 0.8–1.5 mm broad, erumpent, irregular, often confluent, covered by thallus and upper portion with yellow-orange pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, (37–)43–45 × 15–23 µm, hyaline, IKI–.

**Chemistry.** Thallus UV+ yellow, K–, with lichexanthone; pseudostromata UV–, K+ purple, with yellow-orange anthraquinone.

**Distribution.** Neotropical (previously reported from Cuba, Guyana, Venezuela, Colombia and Brazil).

**New country record.** **French Guiana:** Kourou, 1958, *Degelius* s. n. (ABL, UPS).

***Astrothelium octosporoides* Aptroot & Lücking nom. nov.**

Mycobank No.: MB 816712

*Bathelium octosporum* Zahlbr., *Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Klasse* 111(1): 372 (1902).—*Laurera octospora* (Zahlbr.) Zahlbr., *Catal. Lich. Univ.* 1: 505 (1922) non *Astrothelium octosporum* (Vain.) Aptroot & Lücking (see below); type: Brazil, Teresopolis, von Höhnelt 150 (W—holotype, not seen).

**Thallus** corticate, olive-green, smooth to uneven.

**Ascomata** trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.8–1.5 mm diam., erumpent to prominent, hemispherical, covered by thallus. *Hamathecium* clear. *Ascospores* 8 per ascus, densely muriform, fusiform, 150–190 × 40–45 µm, without distinctly thickened median septum, hyaline, IKI–.

**Chemistry.** Thallus and pseudostromata UV–, K–. TLC: no substances detected.

**Distribution.** Neotropical (Brazil).

***Astrothelium octosporum* (Vain.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816713

*Heufleria octospora* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 192 (1890).—*Cryptothelium octosporum* (Vain.)

Zahlbr., *Catal. Lich. Univ.* 1: 522 (1922); type: Brazil, Minas Gerais, Sitio, *Vainio* s. n. (TUR-Vain 30839!—holotype; BM—isotype; Vainio, *Lich. Bras. Exs.* 1031).

(Fig. 37D)

**Thallus** corticate, olive-green to brownish, uneven to shallowly bullate.

**Ascomata** astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, 0.8–1.7 mm diam., immersed to erumpent, covered by thallus except dark ostiolar area surrounded by thin whitish rim. *Hamathecium* clear. *Ascospores* 8 per ascus, densely muriform, narrowly fusiform, 110–135 × 19–23 µm, without distinctly thickened median septum, hyaline, IKI–.

**Chemistry.** Thallus and ascomata UV+ yellow, K–. TLC: lichexanthone.

**Distribution.** Neotropical (Brazil).

***Astrothelium oligocarpum* (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816714

*Trypethelium oligocarpum* Müll. Arg., *Nuovo Giorn. Bot. Ital.* 23: 402 (1891); type: Australia, Queensland, Brisbane, *Bailey* 465 p.p. (G!—lectotype, designated here).

(Fig. 28K)

**Thallus** corticate, olive-green to yellowish, shallowly bullate.

**Ascomata** astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata grouped but not distinctly pseudostromatic, 0.3–0.4 mm diam., prominent, basally covered by thallus but upper part blackish. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 20–27 × 8–10 µm, hyaline, IKI–.

**Chemistry.** Thallus and pseudostromata UV–, K–. TLC: no substances detected.

**Distribution.** Eastern palaeotropical (Australia).

***Astrothelium olivaceofuscum* (Zenker)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816715

*Trypethelium olivaceofuscum* Zenker, in Goebel & Kunze, *Pharmazeut. Waarenkunde* 1(3): 190 (1827); type: South America (L!—holotype).

(Fig. 22C & D)

*Thallus* corticate, brownish to light greyish green or yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to often irregularly confluent but not distinctly pseudostromatic, 0.6–1.2 mm diam., erumpent, covered by thallus but protruding ostiole dark. *Hamathecium* clear. *Ascospores* 8 per ascus, 9–17-septate, fusiform, 85–100 × 8–16 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Costa Rica).

*New country records.* **Guyana:** Potaro–Siparuni Region: surroundings of Paramakatoi Village, 800 m, 1996, *Sipman* 41275 p.p. (B).—**Brazil:** Alagoas: Pilar, 2001, *Cáceres & Lücking* s. n. (ABL, URM).

***Astrothelium papillosum*  
(P. M. McCarthy) Aptroot & Lücking  
comb. nov.**

Mycobank No.: MB 816716

*Laurera papillosa* P. M. McCarthy, *Lichenologist* 27: 311 (1995); type: Papua New Guinea, Central Prov., 40 km NE of Port Moresby, near Dabamura, on Owers Corner Rd, 580 m, 10 February 1981, *Streimann & Naomi* 14908 (B!—isotype).

(Fig. 34D)

*Thallus* corticate, green, distinctly verrucose-papillose.

*Ascomata* trypethelioid to pleurothelioid, with apical or eccentric but then separate ostioles, 0.6–1.0 mm diam., immersed and covered by thallus except for brownish black ostioles. *Hamathecium* orange, interspersed.

*Ascospores* 8 per ascus, muriform, fusiform-ellipsoid, 130–195 × 26–34 µm, constricted at the markedly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (Papua New Guinea).

***Astrothelium papulosum* (Nyl.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816717

*Verrucaria papulosa* Nyl., *Ann. Sci. Nat. Bot., sér. 5* 7: 345 (1867).—*Pseudopyrenula papulosa* (Nyl.) Müll. Arg., *Flora* 66: 248 (1883).—*Trypethelium papulosum* (Nyl.) Makhija & Patw., *Int. J. Mycol. Lichenol.* 5: 242 (1992); type: Colombia, Pie de Cuesta, *Lindig* 96 (H-Nyl 1227!—lectotype; BR—isolectotype; Makhija & Patwardhan, *Int. J. Mycol. Lichenol.* 5: 242, 1992).

(Fig. 20E)

*Thallus* corticate, yellowish brown, uneven to verrucose-papillose.

*Ascomata* trypethelioid, with apical ostioles, aggregate in diffuse pseudostromata; pseudostromata 1–3(–5) mm diam. (individual ascomata 0.2–0.4 mm diam.), immersed to erumpent, covered by thallus except for dark ostioles. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 26–38 × 7–9 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Costa Rica and Colombia).

*New country record.* **Brazil:** Amapá: Floresta Nacional do Amapá, 2015, *Cáceres & Aptroot* 27267 (ABL, ISE).

***Astrothelium peranceps* (Kremp.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816718

*Trypethelium peranceps* Kremp., *Nuovo Giorn. Bot. Ital.* 7: 55 (1875); type: Malaysia, Sarawak, *Beccari* 112 (M!—lectotype; Harris, *Acta Amazon. (Suppl.)* 14: 60 ('1984') [1986]).

(Fig. 28E)

*Thallus* corticate, brownish, thin, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, 0.3–0.4 mm diam., prominent, conical to wart-shaped, covered by thallus but upper portion often exposed and dark brown. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 21–27 × 8–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (Malaysia: Sarawak).

*Discussion.* This name has been reinstated as a separate species in the *Astrothelium crassum* complex. This complex is still poorly understood, but the considerable morphological differences between specimens that agree in ascoma organization, ascospore type, and lack of secondary substances suggests the existence of several taxa. Within this complex, *A. peranceps* is distinguished by its thin thallus and widely dispersed, prominent and conical to wart-shaped ascomata.

***Astrothelium phaeothelium* (Nyl.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816719

*Trypethelium phaeothelium* Nyl., *Ann. Sci. Nat., Bot., sér. 57*: 347 (1867); type: Colombia, Rio Magdalena, Lindig 31 (H-Nyl 271!—holotype; BM!, BR, S!—isotypes).

(Fig. 20J)

*Thallus* corticate, olive-green to brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, irregularly confluent to pseudostromatic; pseudostromata 1–2 mm broad (individual ascomata 0.8–1.2 mm broad), prominent to sessile, blackish brown, with slightly protruding, black ostioles. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 75–90 × 17–23 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Colombia).

*Discussion.* This is another species morphologically similar to *Bathelium* but it has been included in *Astrothelium* due to the lack of internal pigment in the pseudostromata and the astrothelioid ascospores.

***Astrothelium phlyctaena* (Fée) Aptroot & Lücking comb. nov.**

Mycobank No.: MB816720

*Trypethelium phlyctaena* Fée, *Essai Crypt. Écorc.*: 68 (1824).—*Trypethelium scoria* var. *phlyctaena* (Fée) Trevis., *Flora* 44: 19 (1861); type: Saint Lucia, s. col. (G!—lectotype, designated here; BM!—isolectotype).

*Verrucaria catervaria* Fée, *Essai Crypt. Écorc.*: 90 (1824).—*Pyrenula catervaria* (Fée) Massal., *Framment. Lich.*: 25 (1855).—*Spermatodium catervarium* (Fée) Trevis., *Conspect. Verruc.*: 10 (1860).—*Pseudopyrenula catervaria* (Fée) Müll. Arg., *Flora* 66: 248 (1883).—*Trypethelium catervarium* (Fée) Tuck., *Genera Lich.*: 260 (1872); type: South America, “corticem cinchonarum” (G!—lectotype; Harris, *Acta Amazon. (Suppl.)* 14: 64 (‘1984’) [1986]).

*Verrucaria decolorata* Fée, *Essai Crypt. Écorc.*: 91 (1824); type: South America (G!—holotype; L!—isotype).

*Verrucaria tessella* Pers., in Gaudichaud, *Voy. Uranie*: 183 (1827).—*Pseudopyrenula tessella* (Pers.) Graff, *Mycologia* 9: 16 (1917); type: (L—holotype, lost).

*Verrucaria ochroleuca* Eschw., in Martius, *Icon. Sel. Pl. Crypt.* 2: 16, t. 8, figs 3, 4 (1828).—*Pseudopyrenula ochroleuca* (Eschw.) Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 209 (1890).—*Spermatodium ochroleucum* (Eschw.) Trevis., *Conspect. Verruc.*: 11 (1860).—*Trypethelium ochroleucum* (Eschw.) Nyl., *Flora* 52: 126 (1869); type: Brazil, Bahia, Caetitê, Martius s. n. (M!—lectotype, Harris, *Acta Amazon. (Suppl.)* 14: 75 (‘1984’) [1986]).

*Trypethelium duplex* Fée, *Ann. Sci. Nat., Bot.* 23: 437 (1831).—*Chooicia feei* Trevis. (1861) nom. illeg.—*Trypethelium cascarillae* Müll. Arg., *Mém. Soc. Phys. Hist. Nat. Genève* 30(3): 14 (1888) nom. illeg.—*Pseudopyrenula duplex* (Fée) Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 208 (1890); *Bathelium duplex* (Fée) C. W. Dodge, *Ann. Missouri Bot. Gard.* 40: 290 (1953); type: South America, “corticem Croton cascarillae” (G!—lectotype; Harris, *Lichenogr. Thomsoniana*: 142, 1998; BM!—isolectotype).

*Trypethelium quassiicola* Fée, *Ann. Sci. Nat., Bot., sér. 1* 23: 448 (1831); type: Jamaica, “in cortice Quassiae excelsae” (G!—lectotype, designated here; L—2 isolectotypes).

*Trypethelium pallescens* Fée, *Ann. Sci. Nat., Bot., sér. 1* 23: 440 (1831).—*Trypethelium ochroleucum* var. *pallescens*



(Fée) Müll. Arg., *Bot. Jahrb. Syst.* **6**: 392 (1885).—*Pseudopyrenula ochroleuca* var. *palescens* (Fée) Vain., *Acta Soc. Fauna Fl. Fem.* **7**(2): 209 (1890); type: Surinam, Weigelt s. n. (G!—lectotype, Müll. Arg., *Bot. Jahrb. Syst.* **6**: 392, 1885; L!—isolectotype).

*Trypethelium lepreurii* Mont., *Ann. Sci. Nat., Bot.*, sér. **2** **19**: 70 (1843); type: French Guiana, *Leprieur* s. n. (L—istotype).

*Trypethelium triplex* Nyl., *Flora* **52**: 125 (1869); type: Brazil, Rio de Janeiro, *Glaziou* s. n. (H-Nyl—holotype, not seen).

*Trypethelium euporum* Kremp., *Flora* **59**: 527 (1876); type: Brazil, Rio de Janeiro, *Glaziou* 6304 (M!—holotype).

*Trypethelium bicolor* var. *pyrenuloides* C. Knight, *Trans. Proc. New Zealand Instit.* **16**: 405 (1884).—*Trypethelium phlyctaena* var. *pyrenuloides* (C. Knight) Zahlbr., *Catal. Lich. Univ.* **1**: 498 (1922); type: New Zealand, *Knight* (WELT—holotype, not seen).

*Trypethelium ochroleucum* var. *depauperatum* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 392 (1885); type: Cuba, *Müller, Verr. Cub.* 571 (G!—lectotype, designated here; US—isolectotype, not seen).

*Trypethelium leprosum* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 393 (1885); type: Cuba, *Wright* s. n. (G!—lectotype, designated here; Müller, *Verr. Cub.* 155 p.p.).

*Trypethelium subalbans* Nyl., *Flora* **69**: 178 (1886).—*Bathelium subalbans* (Nyl.) C. W. Dodge, *Ann. Missouri Bot. Gard.* **40**: 290 (1953); type: São Tomé, *Henriques* s. n. (G!—lectotype, designated here; BM—isolectotype).

(Fig. 13F–L)

*Thallus* corticate, light greenish to brownish grey or yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic; pseudostromata 0.8–1.5(–2.0) mm broad., erumpent to prominent, covered by thallus but usually paler and cream-coloured. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 15–27 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV+ yellow, K–, with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone).

*Distribution.* Pantropical; reported from, for example, USA, Mexico, Puerto Rico, Cuba, Netherlands Antilles, Dominican Republic, Jamaica, Costa Rica, Nicaragua, Guyana, Surinam, French Guiana, Brazil, Uruguay, Ascension, São Tomé, Australia and New Zealand.

*Discussion.* In the complex traditionally labelled *Trypethelium ochroleucum*, the epithet *phlyctaena* is the oldest for specimens without hamathecium inspersion and with raised pseudostromata. This complex was even considered to include taxa with eccentric ostioles and hence was temporarily included in the synonymy of *Astrothelium variolosum* by Harris (1995), which is considered here a separate complex. Specimens previously labelled *Trypethelium ochroleucum* but with separate ascomata (not pseudostromatic) are assigned here to *Astrothelium pulcherrimum*.

*New or confirmed country records.* **Nicaragua:** *Ometepe Island:* Madera Volcan, 2001, *Breuss* 19160 (L).—**Netherlands Antilles:** *St. Eustatius:* Quill, 1980, *Sipman* 15092 (B). *Saba:* Mt. Scenery, 1980, *Sipman* 15355 (B).—**Puerto Rico:** *Ponce:* Guanica, 1989, *A. & M. Aptroot* 25765 (ABL).—**Dominican Republic:** *Monte Cristi:* El Morro, 1987, *Harris* 19604 (ABL, NY).—**Guyana:** *Upper Takutu:* Dadanawa ranch, 1992, *Sipman* 57378 (B).—**Uruguay:** Rocha, Sierra de San Miguel, 1989, *Osorio* 9187 (hb. Kalb).—**Ascension:** Elliot's Park, 1976, *James* s. n. (BM, ABL).

### *Astrothelium pleiostomum* Redinger

*Hedwigia* **73**: 58 (1933); type: Brazil, Amazonas, Santarem, Taperinha, *Ginzberger* (W—holotype, not seen).

*Trypethelium violascens* R. C. Harris, *Acta Amazon. (Suppl.)* **14**: 78, fig. 11 ('1984') [1986]; type: Brazil, Amazonas, along Igarapé Caititu off Rio Uatumá, *Buck* 2937 (NY!—holotype; ABL!—istotype).

(Fig. 29I & J)

*Thallus* corticate, olive-green to yellowish, uneven somewhat bullate, often gall-like.

*Ascomata* pleurothelioid with eccentric, separate ostioles, diffusely pseudostromatic; pseudostromata 0.8–1.3 mm diam., erumpent, covered by thallus but with upper portion whitish, internally with yellowish pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 28–33 × 8–10 µm, rather thin-walled, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–; pseudostroma internally K+ yellow, with anthraquinone.

*Distribution.* Neotropical (Brazil).

*Discussion.* This taxon is tentatively retained in *Astrothelium*, since the overall morphology and the ascospore type would also suggest placement in *Viridothelium*. The new synonymy of *Trypethelium violascens* is based on study of isotypes in ABL, which show that some characters are different from the description. The K-reaction is positive and the IKI-reaction is (at least now) absent; it was probably an artifact of fresh material.

***Astrothelium porosum* (Ach.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816721

*Trypethelium porosum* Ach., *Synops. Lich.* 106 (1814).—*Verrucaria porosa* (Ach.) Eschw., in Martius, *Flora Brasil.* 1: 135 (1833).—*Leightonia porosa* (Ach.) Trevis., *Flora* 44: 19 (1861).—*Trypethelium sprengelii* var. *porosum* (Ach.) Nyl., in Hue, *Nouv. Archiv. du Muséum, sér. 3* 4: 129 (1892).—*Bathelium porosum* (Ach.) C. W. Dodge, *Ann. Missouri Bot. Gard.* 40: 290 (1953); type: West Indies, “corticem Crotonis Cascarillae” (H-ACH 883!—holotype; S—isotype).

*Trypethelium erubescens* Kunze in Fée, *Ann. Sci. Nat., Bot., sér. 1* 23: 441 (1831).—*Trypethelium ochroleucum* var. *erubescens* (Kunze) Müll. Arg., *Flora* 68: 254 (1885); type: Surinam, Weigelt s. n. (L!—holotype).

*Trypethelium brachysporum* Malme, *Ark. Bot.* 19(1): 30 (1924).—*Polymeridium brachysporum* (Malme) Aptroot, in Aptroot & Cáceres, *Nova Hedwigia* 98: 11 (2014); type: Brazil, Mato Grosso, Cuyabá, Malme 2055 (S!—holotype; BM!—isotype).

(Fig. 12K & L)

*Thallus* corticate, light greenish to brownish grey or yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic; pseudostromata 0.8–1.5 mm diam., erumpent to prominent, covered by thallus but usually paler and cream-coloured. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 17–27 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV+ yellow, K–, with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone).

*Distribution.* Pantropical (see below).

*Discussion.* This taxon was until recently not distinguished from *Astrothelium phlyctaena* and *A. pulcherrimum*, and therefore its distribution is not well known. Together, these species have for a long time been labelled *Trypethelium ochroleucum* and under that name have been reported from the USA, Mexico, Bahamas, Jamaica, Cuba, Puerto Rico, Trinidad, Tobago, Costa Rica, El Salvador, Guyana, French Guiana, Surinam, Colombia, Venezuela, Galapagos, Brazil, Paraguay, Cape Verdes, Ascension, South Africa, Mozambique, Seychelles, India, Sri Lanka, China, Singapore, Philippines, Vietnam, Indonesia, Guam, Hawai'i, Northern Mariana Islands, New Caledonia, Papua New Guinea, Australia and New Zealand. Not all specimens on which these reports are based have been studied recently. *Astrothelium porosum* is the most common species of the three.

*New country records.* **USA:** Florida: Sanford, 1939, Johnson 3310 (ABL).—**Mexico:** Chiapas: Ocozocoautla, 1996, Wolf & Sipman s. n. (B).—**Guyana:** Upper Takutu: Dadanawa ranch, 1992, Sipman 57358 (B).—**French Guiana:** Cayenne, 1993, Sipman 31532 (*Lichenotheca Latinoamericana* 149, ABL).—**India:** West Bengal: Sundarbans, Jhila, 2003, Jagadeesh Ram 13640 (ABL).—**Indonesia:** Irian Jaya: 11 km W of Bupul, 1988, Hensen s. n. (ABL).—**Papua New Guinea:** Madang: Karkar, 1987, Aptroot 17623 (ABL).—**Australia:** Queensland: Cape Tribulation, 1983, Hale 64181 (ABL, US).

***Astrothelium praetervisum* (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816722

*Heufleria praetervisiva* Müll. Arg., *Flora* 68: 250 (1885).—*Cryptothelium praetervisum* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* 1: 522 (1922); type: French Guiana, Leprieur 13 (G!—holotype).

(Fig. 37G)

*Thallus* corticate, brownish to often partly orange-brown and with orange pigment, mottled with whitish areas producing pycnidia, smooth to uneven.

*Ascomata* pleurothelioid, with eccentric, separate ostioles, pseudostromatic; pseudostromata 0.4–0.6 mm diam., immersed-erumpent, often forming lines, covered by

thallus and partly with orange pigment except for blackish ostioles surrounded by whitish rim. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, fusiform,  $33\text{--}68 \times 12\text{--}22 \mu\text{m}$ , hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K+ partly purple, with anthraquinones.

*Distribution.* Neotropical (French Guiana).

### ***Astrothelium pseudocypbellatum***

**R. C. Harris**

*Acta Amazon. (Suppl.)* 14: 62 ('1984') [1986]; type: Brazil, Amazonas, São Gabriel, *Spruce* 247 (BM!—isotype).

(Fig. 24F & G)

*Thallus* light greyish green, uneven to rugose, with superficial pockets of calcium oxalate crystals resembling pseudocypbellae.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic; pseudostromata 0.8–1.7 mm diam., prominent, covered by thallus usually paler or darker cream-coloured. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate,  $23\text{--}27 \times 7\text{--}8 \mu\text{m}$ , hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV+ yellow, K–, with lichexanthone.

*Distribution.* Neotropical (previously reported only from Brazil).

*New country record.* **Guyana:** *Potaro-Siparuni:* Kaie-teur Falls National Park, 1996, *Sipman* 40458 (B).

### ***Astrothelium pseudoplatystomum*** **(Makhija & Patw.) Aptroot & Lücking** **comb. nov.**

Mycobank No.: MB 816723

*Trypethelium pseudoplatystomum* Makhija & Patw., *Int. J. Mycol. Lichenol.* 5: 244 (1992); type: Brazil, *Heufler* 130 (M—holotype, not seen).

*Thallus* corticate, green to yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 1–2 mm diam., erumpent to prominent, with flattened top, covered by thallus except upper portion, with individual ascomata appearing dark and arranged in an astroid way. *Hamathecium* clear. *Ascospores* 8 per ascus, (5–)10–14-septate, fusiform,  $29\text{--}52 \times 8\text{--}12 \mu\text{m}$ , hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Brazil).

### ***Astrothelium pseudovariatum*** **(Upreti & Ajay Singh) Aptroot &** **Lücking comb. nov.**

Mycobank No.: MB 816724

*Laurera pseudovariata* Upreti & Ajay Singh, *Bull. Jard. Bot. Nat. Belg.* 57: 378 (1987); type: India, West Bengal, Howrah, Sibpur, *Roychaudhury* 675 (CAL—holotype, not seen).

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, diffusely pseudostromatic; pseudostromata 0.8–1.7 mm diam., prominent, hemispherical, covered by thallus. *Hamathecium* interspersed. *Ascospores* 8 per ascus, (sub-) muriform,  $7\text{--}9 \times 2\text{--}3$ -septate,  $32\text{--}45 \times 11\text{--}13 \mu\text{m}$ , fusiform, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (India).

### ***Astrothelium puiggarii*** (Müll. Arg.) **Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816725

*Campylothelium puiggarii* Müll. Arg., *Flora* 66: 245 (1883); type: Brazil, Rio de Janeiro, *Puiggari* 1460 (G!—holotype; NY!—isotype).

*Campylothelium puiggarii* var. *pallescens* Müll. Arg., *Flora* 66: 245 (1883); type: Brazil, Rio de Janeiro, *Puiggari* 1757 (G!—holotype).



(Fig. 38C & D)

*Thallus* corticate, olive-green, verrucose-bullate.

*Ascomata* pleurothelioid, with eccentric, separate ostioles, solitary, 0.8–1.3 mm diam., prominent to almost sessile, covered by thallus except for the protruding, papilliform, brownish grey ostiole, 1.0–1.5 mm diam. *Hamathecium* inspersed. *Ascospores* 2 per ascus, densely muriform, fusiform, 70–90 × 20–25 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Costa Rica and Brazil).

*New country record.* **French Guiana:** Saül, 1986, Montfoort & Ek 222 (B).

***Astrothelium pulcherrimum* (Fée)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816726

*Trypethelium pulcherrimum* Fée, *Ann. Sci. Nat., Bot., sér. 1* 23: 450 (1831).—*Pseudopyrenula pulcherrima* (Fée) Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 208 (1890); type: South America, “in America ad corticem *Crotonis cascarillae*” (G!—lectotype, designated here; L!—isolectotype).

*Verrucaria diffluens* Nyl., *Ann. Sci. Nat., Bot., sér. 4* 20: 252 (1863).—*Pseudopyrenula diffluens* (Nyl.) Müll. Arg., *Flora* 66: 248 (1883); type: Colombia, Bogotá, Lindig 2770 (H-Nyl 2211!—lectotype, designated here; BM!, BR—isolectotypes).

*Trypethelium ochroleucum* var. *effusum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 392 (1885).—*Pseudopyrenula ochroleuca* var. *effusa* (Müll. Arg.) Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 209 (1890); type: Cuba, Wright s. n. (G!—lectotype, designated here; Müller, *Lich. Cub.*, Ser. II: 566).

*Trypethelium tricolor* Müll. Arg., *Bull. Soc. Roy. Bot. Belg.* 32(1): 166 (1893); type: Costa Rica, Puntarenas, Boruca, Tonduz s. n. (G!—holotype; BR, US—isoatypes; Pittier, *Pl. Costaric. Exs.* 6282).

*Pseudopyrenula duplex* var. *simplicior* Vain., *Bol. Soc. Boteriana, Ser. 2* 6: 177 (1930).—*Trypethelium duplex* f. *simplicius* (Vain.) Zahlbr., *Catal. Lich. Univ.* 10: 101 (1938).—*Bathelium duplex* f. *simplicius* (Vain.) C. W. Dodge, *Ann. Missouri Bot. Gard.* 40: 290 (1953); type: Mozambique, Palma, Pres de Lima 265 (TUR-Vain 34609—holotype, not seen).

*Pseudopyrenula portoricensis* J. Hedrick, *Mycologia* 22: 248 (1930); type: Puerto Rico, Mayagüez, Fink 1025 (MICH—holotype, not seen).

(Fig. 13B–D)

*Thallus* corticate, light olive-brown to brownish greenish grey to yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary but usually dense, 0.2–0.3 mm diam., erumpent, covered by thallus except dark ostioles surrounded by whitish rim. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 15–27 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV+ yellow, K–, with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone).

*Distribution.* Pantropical, but distribution incompletely known because the species was not previously separated from *Astrothelium phlyctaena* and *A. porosum* (all taken together as *Trypethelium ochroleucum* s. lat.). Previously reported from Cuba, Puerto Rico, Colombia and Mozambique.

*New country records.* **Guyana:** Upper Takutu, Karanambo ranch, 1992, Sipman 57281 (B).—**Indonesia:** Java: Malang, 1939, Groenhart 5095 (ABL, L).

***Astrothelium punctulatum* Malme**

*Ark. Bot.* 19(1): 14 (1924); type: Brazil, Matto Grosso, Santa Ana da Chapada, Malme, *Lich. Regn.* 2457 (S!—holotype; S!—isotype).

(Fig. 12G & H)

*Thallus* corticate, olive-green to greyish, verrucose-bullate, somewhat pseudogall-inducing.

*Ascomata* trypethelioid, with apical ostioles, solitary to confluent but often dense, 0.8–1.5 mm diam., immersed-erumpent in elevated thallus portions, covered by thallus except for dark ostiole surrounded by white ring. *Hamathecium* heavily inspersed. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 23–27 × 8–9 µm, hyaline, IKI–.

**Chemistry.** Thallus UV–, K–; ostioles UV+ yellow, K–, with lichexanthone.

**Distribution.** Neotropical (previously reported from Cuba and Brazil).

*New country record.* **Guyana:** Demerara-Berbice: Mabura Hill, 1988, *Bleij & Biesmeijer* s. n. (ABL). *Upper Takutu:* Kuyuwini Landing, 1992, *Sipman* 57021 (B).

***Astrothelium pupula* (Ach.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816727

*Pyrenula pupula* Ach., *Synops. Meth. Lich.*: 123 (1814).—*Pseudopyrenula pupula* (Ach.) Müll. Arg., *Flora* **68**: 331 (1885).—*Trypethelium pupula* (Ach.) R. C. Harris, *Lichenogr. Thomsoniana*: 146 (1998); type: West Indies, s. col. (H-ACH 832!—holotype).

*Pseudopyrenula porinoides* Müll. Arg., *Flora* **69**: 331 (1885).—*Verrucaria porinoides* Mont., *Ann. Sci. Nat., Bot. sér. 2* **19**: 59 (1843) non Ach.—*Pseudopyrenula pupuloides* M. Choisy, *Mém. Soc. Bot. France* **1953–1954**: 58 (1954); type: French Guiana, *Leprieur* 731 (G!—lectotype, designated here; BM!—isolectotype).

(Fig. 14A & B)

**Thallus** corticate, greyish green to yellowish (lichexanthone colour), smooth to uneven.

**Ascomata** trypethelioid, with apical ostioles, solitary, 0.4–0.6 mm diam., erumpent, covered by thallus except for blackish ostiolar area. **Hamathecium** clear. **Ascospores** 8 per ascus, fusiform-ellipsoid, 3-septate, 33–40 × 10–13 µm, hyaline, IKI–.

**Chemistry.** Thallus and ascomata UV+ yellow, K–. TLC: lichexanthone.

**Distribution.** Pantropical (previously reported from the West Indies, Costa Rica, French Guiana, Colombia, India and Sri Lanka).

*New country records.* **Puerto Rico:** *Aguadilla:* Bosque Estatal de Guajataca, 1989, *Aptroot & Aptroot* 25744 (ABL).—**Guyana:** *East Demarara:* Linden Highway, E of Timehri, 1985, *Sipman & Aptroot* 19587, 19602, 19558 (all ABL, B).—**Venezuela:** *Bolívar:* Cerro Guaiquinima, along Rio Carapo, 800 m, 1990, *Sipman* 27030 (B).—**Ecuador:** *Morona-Santiago:* Cordillera del Condor, 12 km E of Los Encuentros, 1982, *Aptroot* 10442 (ABL).—**Brazil:** *Minas Gerais:* Serra do Caraça, Parque Natural do Caraça, 1250 m, 1997, *Aptroot* 40918

(ABL).—**Malaysia:** *Sarawak:* 1866, *Beccari* 188 p.p. (M, originally filed as syntype of *Trypethelium leucostomum* Kremp.).—**Papua New Guinea:** *Central:* Varirata National Park, 1987, *Aptroot* 19080 (ABL).

***Astrothelium purpurascens* (Müll. Arg.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816728

*Heufleria purpurascens* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 384 (1885).—*Cryptothelium purpurascens* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* **1**: 522 (1922); type: Cuba, *Wright* s. n. (G—holotype, not seen; NY!—isotype; Müller, *Verr. Cub.* 116b).

*Cryptothelium rhodotitthon* R. C. Harris, *Acta Amazon. (Suppl.)* **14**: 65 ('1984') [1986]; type: Brazil, Roraima, along Manaus-Boa Vista Road, *Buck* s. n. (NY!—isotype).

(Fig. 37L)

**Thallus** corticate, olive-green to yellowish or reddish, uneven to bullate.

**Ascomata** astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, 0.7–1.5 mm diam., immersed, completely covered by thallus except for protruding, dark red ostiole. **Hamathecium** clear. **Ascospores** 8 per ascus, densely muriform, fusiform, 100–130 × 25–30 µm, median septum thickened, hyaline, IKI–.

**Chemistry.** Thallus UV–, K–; ascomata with red, K+ green-reacting isohypocrellin.

**Distribution.** Neotropical (Brazil and Cuba).

***Astrothelium pustulatum* (Vain.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816729

*Pseudopyrenula pustulata* Vain., in Hiern, *Cat. Afr. Pl.* **2**(2): 456 (1901).—*Trypethelium pustulatum* (Vain.) Zahlbr., *Catal. Lich. Univ.* **1**: 499 (1922); type: Angola, Ambriz, *Welwitsch* 190 (TUR-Vain 30791!—holotype; BM!—isotype).

(Fig. 21G)

*Thallus* corticate, olive-green, uneven- verrucose, pseudogall-inducing.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic; pseudostromata 1–2 mm diam., prominent, completely covered by thallus, internally with yellow pigment, chiefly around the ostiolar region. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 5–9-septate, 180–220 × 40–45 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances.

*Distribution.* African palaeotropical (Angola).

*Discussion.* In the original description a red pigment was mentioned, which is absent from the type material. The type of *Trypethelium lageniferum* Ach. also contains this taxon but additionally a species of *Pyrenula*, on which most of the description was based.

***Astrothelium pyrenastrosulphureum*  
Aptroot & Lücking nom. nov.**

Mycobank No.: MB 816730

*Pyrenastrum sulphureum* Eschw., in Martius, *Icon. Pl. Cryptog.*: 17 (1828).—*Astrothelium sulphureum* (Eschw.) Müll. Arg., *Flora* 68: 255 (1885) nom. illeg. non *Astrothelium sulphureum* Nyl., *Ann. Sci. Nat., Bot., sér. 4* 20: 260 (1863); type: Brazil, Amazonas, Martius s. n. (M!—holotype).

*Pyrenodium hypoxylon* Fée, *Essai Crypt. Écorc. Suppl.*: 69 (1837).—? *Astrothelium hypoxylon* (Fée) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 141 (1857); type not indicated.

*Pyrenastrum sulphureum* subsp. *plicatum* Eschw., in Martius, *Flora Brasil.* 1: 145 (1833); type: Brazil, Amazonas, Martius s. n. (M—holotype, not seen).

*Astrothelium sulphureum* var. *subpallescens* Nyl., *Bull. Soc. Linn. Normand., sér. 2* 2: 133 (1868); type: New Caledonia, Lifu, *Deplanche* s. n. (H-Nyl—holotype, not seen).

(Fig. 28A)

*Thallus* corticate, olive-green to yellowish, uneven to bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata irregularly pseudostromatic;

pseudostromata 0.8–1.5 mm diam., erumpent to prominent, covered by thallus except for blackish ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 27–30 × 8–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances.

*Distribution.* Pantropical (Brazil, India and New Caledonia).

***Astrothelium robustum* Müll. Arg.**

*Bull. Soc. Roy. Bot. Belg.* 32(1): 164 (1893); type: Costa Rica, Puntarenas, Rio Naranjo, 1893, *Tonduz* s. n. (G!—holotype; BR—isotype).

*Astrothelium conigerum* Zahlbr., *Bull. Herb. Boissier, sér. 2* 8: 459 (1908); type: Brazil, Amazonas, Rio Juruá, *Ule* 356 (W—holotype, not seen).

(Fig. 30H & I)

*Thallus* corticate, olive-green to yellowish, uneven to bullate, sometimes pseudogall-inducing.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to irregularly confluent or diffusely pseudostromatic, 1–3 mm diam., erumpent to prominent, covered by thallus except for blackish ostiolar area. *Hamathecium* clear. *Ascospores* 8 per ascus, (3–)5–7(–9)-septate, fusiform, (70–)90–130 × 20–30 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Brazil and Costa Rica).

*New country records.* **Puerto Rico:** Ponce: Caribbean National Forest, 1989, *Aptroot & Aptroot* 25603, 25602 (ABL).—**Colombia:** Nariño: Tumaco, Estacion Forestal La Espriella, 1986, *Sipman & Velosa* 33054 (B). **Amazonas:** Araracuara, opposite Isla Mariñame, 240 m, 1988, *Sipman & Duivenvoorden* 28328 (B).

***Astrothelium rufescens* (Müll. Arg.)  
Aptroot & Lücking comb. et stat. nov.**

Mycobank No.: MB 816731



*Trypethelium catervarium* var. *rufescens* Müll. Arg., *Bot. Jahrb. Syst.* 6: 391 (1885); type: Cuba, *Wright* s. n. (G!—lectotype, designated here; FH-TUCK 3970!—isolectotype, designated here; Müller, *Verr. Cub.* 576).

(Fig. 18K & L)

*Thallus* corticate, olive-green to brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 0.5–1.5 mm broad, immersed, forming irregular, whitish lines that become fused and reticulate. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 17–27 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Cuba).

*Distribution.* This taxon belongs in the *Astrothelium nitidiusculum* aggregate, where it is characterized by its linear-reticulate, immersed, whitish pseudostromata.

***Astrothelium sanguinarium* (Malme)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816733

*Laurera sanguinaria* Malme, *Ark. Bot.* 19(1): 21 (1924).—*Meristosporium sanguinarium* Malme (1924) nom. inval; type: Brazil, Matto Grosso, Serra da Chapada da Burity, *Malme* 2253 (S!—lectotype, designated here).

(Fig. 32G)

*Thallus* corticate, olive-green to yellowish, smooth to uneven to shallowly bullate.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata 1–2 mm diam., erumpent to prominent, dark brown with pale brown ostioles, internally with bright to dark red pigment; pseudostromata up to 5 mm long and 2 mm broad. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, ellipsoid, (75–)90–130 × 15–25 µm, without strongly thickened median septum, hyaline, IKI+ violet.

*Chemistry.* Thallus UV–, K–; pseudostromata UV–, internally with red, K+ green-reacting isohypocrellin.

*Distribution.* Neotropical (Brazil).

*Discussion.* This taxon resembles a species of *Bathelium* but molecular data place it in *Astrothelium*. Specimens with whitish to pale cream-coloured pseudostromata represent an undescribed taxon labelled “*Laurera Formosa*” by R. C. Harris, the original material collected in Brazil by *Malme* (2514, S).

***Astrothelium santessonii* (Letr.-Gal.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816737

*Laurera santessonii* Letr.-Gal., *Rev. Bryol. Lichénol.* 37: 68 (1958); type: Ivory Coast, Mont Toukoui, cercle de Man, 14 August 1954, *Santesson* 10607d (UPS—holotype, not seen).

(Fig. 38B)

*Thallus* corticate, olive-green to brownish, smooth to uneven.

*Ascomata* pleurothelioid, with eccentric, separate ostioles, solitary to aggregate but not distinctly pseudostromatic, 0.7–1.5 mm diam., immersed-erumpent, covered by thallus except dark grey ostiolar area surrounded by irregular whitish rim. *Hamathecium* interspersed with red, K+ green droplets. *Ascospores* 8 per ascus, muriform, ellipsoid, 70–100 × 20–32 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–; hamathecium red, K+ green, with isohypocrellin.

*Distribution.* Pantropical (previously reported only from the Ivory Coast).

*New country record.* **Guyana:** *Upper Takutu:* Kuyuwini Landing, 1992, *Sipman* 58142 (B).

***Astrothelium saxicola* (Malme) Aptroot  
& Lücking comb. nov.**

Mycobank No.: MB 816738

*Cryptothelium saxicola* Malme, *Svensk Bot. Tidskr.* **30**: 246 (1936); type: Brazil, Matto Grosso, Serra da Chapada, Bocca da Serra, Malme 2314 (S!—holotype).

(Fig. 39I)

*Thallus* pale greenish grey to yellowish, smooth to uneven or rough.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, 1.0–1.8 mm diam., erumpent, applanately wart-shaped, completely covered by thallus, with upper part yellowish. *Hamathecium* clear. *Ascospores* 1 per ascus, densely muriform, ellipsoid, 215–230 × 60–80 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances.

*Distribution.* Neotropical (Brazil).

*Discussion.* This is one of the very few specimens of *Trypetheliaceae* encountered on rock, and one of the three species that seem restricted to rock; the others are *Astrothelium stramineum*, from the same locality, and *Pseudopyrenula saxicola*.

### ***Astrothelium scoria* (Fée) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816739

*Trypethelium scoria* Fée, *Essai Crypt. Écorc.*: 69 (1824).—*Pseudopyrenula scoria* (Fée) Vain., *Bol. Soc. Broteriana*, Ser. 2 **6**: 178 (1930); type: South America, “corticem Crotonis cascarillae” (G!—lectotype; Harris, *Lichenogr. Thomsoniana*: 147, 1998; G!, BM!—isolectotypes).

*Pyrenula myriocarpa* Fée, *Essai Crypt. Écorc.*: 74 (1824).—*Verrucaria myriocarpa* (Fée) Spreng., *Syst. Veget.* **4**(1): 245 (1827).—*Spermatodium myriocarpum* (Fée) Trevis., *Conspect. Verruc.*: 11 (1860).—*Trypethelium myriocarpum* (Fée) Müll. Arg., *Bot. Jahrb. Syst.* **6**: 391 (1885); type: South America, s. col. (G!—holotype).

*Trypethelium scoria* var. *sordidius* Nyl., *Flora* **52**: 126 (1869); type: Brazil, Rio de Janeiro, Glaziou 1961 (H—holotype, not seen; M!—isotype).

*Trypethelium dichroum* Makhija & Patw., *J. Hattori Bot. Lab.* **73**: 195 (1993); type: India, Andaman Islands, North Andaman, Diglipue Range, Millangram, 3 January 1986, Nagarkar & Patwardhan AMH 86.250 (ABL—*isotype*).

*Trypethelium indicum* Makhija & Patw., *J. Hattori Bot. Lab.* **73**: 199 (1993); type: India, Meghalaya, Willoe, 30 October 1977, Patwardhan & Nagarkar AMH 77.1130 (ABL—*isotype*).

*Trypethelium meghalayense* Makhija & Patw., *J. Hattori Bot. Lab.* **73**: 201 (1993); type: India, Meghalaya, near Sohararaim, on road to Cherapunji, 28 October 1977, Patwardhan & Nagarkar AMH 86.862 (ABL—*isotype*).

(Fig. 18C–E)

*Thallus* corticate, olive-green to yellowish or brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic, 0.3–0.5 mm diam., erumpent, laterally covered by thallus but upper portion blackish brown with whitish rim. *Hamathecium* interspersed. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 15–27 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (e.g. Puerto Rico, El Salvador, Guyana, French Guiana, Ecuador, Brazil, Zaire, India, China, Hong Kong, Papua New Guinea, Solomon Islands, New Caledonia).

*Discussion.* The epithet *scoria* is the oldest for the specimens with hamathecium interspersed of the complex previously known as *Trypethelium nitidiusculum*. As defined here, *Astrothelium scoria* is still heterogeneous and might comprise several species, but due to the limited material available we were unable to assess the variation of potential lineages represented by the synonyms listed here. The thallus of the newly synonymized *Trypethelium indicum* is an unspecific UV+ pinkish, not yellow as mentioned in the protologue.

*New country records.* **El Salvador:** Ahuachapán: Parque Nacional El Imposible, 1998, Sipman et al. 44570 (B).—**Puerto Rico:** Aguadilla: Guajataca, 1989, Aptroot & Aptroot 25737 (ABL).—**Guyana:** Upper Takutu: Dadanawa ranch, 1992, Sipman 57985 (B).—**French Guyana:** Regina: Camp Aratai, 2003, Sipman 50699 (B).—**Ecuador:** Napo: Archidona, 1982, Aptroot & Hensen 10328 (ABL).—**Zaire:** Kivu: Equateur, Kalamba, 450 m, 1991, Müller s. n. (DR).—**China:** Yunnan: Xishuangbanna, 2003, Aptroot 57283 (ABL).—**Hong Kong:** Lantau: Ngong Ping, 2000, Aptroot 48638 (ABL).—**Papua New Guinea:** Madang: 11 km W of Brahman Mission, 1995, Sipman 38912 (B).—**Solomon Islands:** Santa Isabel: Tatamba, 1965, Hill 11170 (ABL, BM).—**New Caledonia:** Vieillard s. n. (BM).

***Astrothelium scorioides* Nyl.**

*Ann. Sci. Nat., Bot., sér. 5* 7: 348 (1867); type: Colombia, Rio Negro, Lindig 132 (H-Nyl 120!—holotype; BM!—isotype).

(Fig. 27F & G)

*Thallus* corticate, pale greenish to yellowish, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to confluent, 0.3–0.5 mm diam., erumpent, conical with flattened top, covered by thallus and upper part with yellow-orange pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 33–45 × 10–17 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; ascomata with yellow to orange, K+ purple, UV+ red anthraquinone.

*Distribution.* Pantropical (previously reported from Venezuela, Colombia, Brazil and Seychelles).

*New country records.* **Guiana:** *Upper Mazaruni:* Mount Latipu, Sipman & Aptroot 19072 (ABL, B).—**French Guiana:** Saül, 1985, Aptroot 15442 (ABL, B).

***Astrothelium scoriophilum* Aptroot & Lücking nom. nov.**

Mycobank No.: MB 816740

*Trypethelium scorioides* Leight., *Trans. Linn. Soc. London* 25: 459 (1866) non *Astrothelium scorioides* Nyl. (1867); type: Brazil, Amazonas, Spruce s. n. (BM!—holotype).

*Pseudopyrenula infuscatula* var. *tecomae* Vain., *Ann. Acad. Sci. Fenn., ser A* 6(7): 197 (1915).—*Trypethelium infuscatulum* var. *tecomae* (Vain.) Zahlbr., *Catal. Lich. Univ.* 8: 128 (1931); type: Guadeloupe, Près du Camp-Jacob, Duss 1501 (TUR-Vain 30780!—holotype).

(Fig. 20C)

*Thallus* corticate, olive-green, uneven- verrucose.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata

irregular, 0.7–1.7 mm broad, immersed to erumpent, exposed and blackish, with ostioles only visible by their pale rings. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 36–39 × 11–12 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances.

*Distribution.* Neotropical (reported from Guadeloupe, Venezuela and Colombia).

***Astrothelium scorizum* (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816741

*Trypethelium scorizum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 389 (1885).—*Trypethelium scorizum* Nyl. (1876) nom. nud.; type: Cuba, Wright s. n. (G!—holotype; BM!—isotype; Müller, *Verr. Cub.* 166a).

(Fig. 28C & D)

*Thallus* corticate, light olive-green to pale brownish, smooth to uneven-rugulose.

*Ascomata* pleurothelioid, with eccentric, separate ostioles, pseudostromatic; pseudostromata 0.7–1.5 mm diam., immersed-erumpent, forming irregular, in part confluent groups or lines, with the individual ascomata exposed and dark brown. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 20–26 × 8–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances.

*Distribution.* Neotropical (Cuba and Brazil).

*New country record.* **Brazil:** *São Paulo:* Pratânia, Fazenda Palmeira da Serra, 2009, Lücking 29814 (B, F).

***Astrothelium sepultum* Mont.**

*Ann. Sci. Nat., Bot., sér. 2* 19: 74 (1843).—*Cryptothelium sepultum* (Mont.) A. Massal., *Atti I. R. Istiut. Veneto, Ser. 3* 5: 335 (1860).—*Heufleria sepulta* (Mont.) Trevis., *Flora* 44: 23 (1861).—*Laurera sepulta* (Mont.) O. E. Erikss., *Op. Bot.* 60: 50 (1981); type: French Guiana, Leprieur s. n. (BR, PC—syntypes).



*Trypethelium commivens* Nyl., *Mém. Soc. Acad. Maine-et-Loire* 4: 79 (1858).—*Bathelium commivens* (Nyl.) Trevis., *Flora* 44: 21 (1861).—*Laurera commivens* (Nyl.) Zahlbr., *Catal. Lich. Univ.* 1: 503 (1922); type: Peru, *s. col.* (H-Nyl—holotype, not seen; PC!—isotype).

(Fig. 36H)

*Thallus* corticate, greyish green to pale yellowish brown (lichexanthone colour), smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to confluent but not distinctly pseudostromatic, 1.0–1.8 mm diam., erumpent, covered by thallus but with upper part whitish and ostiole dark. *Hamathecium* clear. *Ascospores* 2 per ascus, densely muriform, fusiform, 150–250 × 30–65 µm, with distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and usually also ascomata UV+ yellow, with lichexanthone.

*Distribution.* Neotropical (reported from Costa Rica, Guyana, French Guiana, Surinam, Brazil and Peru).

***Astrothelium sierraleonense***  
(C. W. Dodge) Aptroot & Lücking  
comb. nov.

Mycobank No.: MB 816742

*Tremotylium sierraleonense* C. W. Dodge, *Nova Hedwigia, Beih.* 12: 104 (1964); type: Sierra Leone, Kori, Njala, *Deighon* M5693C (FH-DODGE!—holotype).

(Fig. 32C)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, dispersed to confluent but not distinctly pseudostromatic, 0.8–1.5 mm diam., erumpent, laterally covered by thallus but upper part conspicuously black and flattened, surrounded by an irregular whitish rim, internally with pockets of red crystals. *Hamathecium* clear. *Ascospores* 4 per ascus, muriform, ellipsoid, *c.* 80 × 14 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata externally UV–, K–; ascomata internally with red, K+ purple anthraquinone crystals.

*Distribution.* African palaeotropical (Sierra Leone).

***Astrothelium sikkimense*** (Makhija & Patw.) Aptroot & Lücking comb. nov.

Mycobank No.: MB 816743

*Laurera sikkimensis* Makhija & Patw., *Mycotaxon* 31: 580 (1988); type: India, Sikkim, Gangtok, Near Tangshi View Point, 17 September 1977, *Patwardhan & Nagarkar* AMH 77.1970 (ABL!—isotype).

(Fig. 33L)

*Thallus* corticate, brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 1–2 mm diam., immersed to erumpent, covered by thallus except black ostiole surrounded by whitish rim. *Hamathecium* inspersed. *Ascospores* 6–8 per ascus, muriform, ellipsoid, 120–140 × 25–30 µm, with somewhat thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (India).

***Astrothelium spectabile*** (Aptroot & Ferraro) Aptroot & Lücking comb. nov.

Mycobank No.: MB 817086

*Trypethelium spectabile* Aptroot & Ferraro, *Kurtziana* 31: 59 (2005); type: Argentina, Misiones, Iguazú, 2003, *Ferraro & Popoff* 6602 (CTES!—holotype; ABL!—isotype).

(Fig. 21L)

*Thallus* corticate, light green, smooth.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.7–1.2 mm diam., immersed, completely covered by thallus. *Hamathecium* clear. *Ascospores* 8 per ascus, 11–19-septate, fusiform, 140–190 × 20–25 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Argentina).

***Astrothelium sphaerioides* (Mont.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816744

*Trypethelium sphaerioides* Mont., *Ann. Sci. Nat., Bot., sér. 2* 19: 73 (1843).—*Bathelium sphaerioides* (Mont.) Trevis., *Spighe e Paglie*: 20 (1861).—*Laurera sphaerioides* (Mont.) Zahlbr., *Catal. Lich. Univ.* 1: 506 (1922); type: French Guiana, Leprieur 80 (PC!—lectotype, designated here; H-Nyl!—isolectotype).

(Fig. 35H)

*Thallus* corticate, olive-green to brownish, smooth to uneven.

*Ascomata* trypethelioid to pleurothelioid, with apical to eccentric, separate ostioles, distinctly pseudostromatic; pseudostromata irregular, 0.5–1.5 mm broad, erumpent to prominent, whitish and black ostioles. *Hamathecium* clear. *Ascospores* 2–4 per ascus, muriform, ellipsoid, 80–175 × 25–50 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical; previously reported from Colombia (Isla de Providencia), French Guiana, Brazil and India.

*New country records.* **El Salvador:** *Ahuachapán:* Parque Nacional El Imposible, 1998, Welz s. n. (B).—**Costa Rica:** *Guanacaste:* 5 km NNW of Tilarán, 650 m, 2004, Aptroot 60659 (ABL, INB).—**Panama:** *Veraguas:* Bahía Honda, 2001, Cabrera & Etayo 18583 (ABL, hb. Etayo).—**Puerto Rico:** *Mayagüez:* Reserva Forestal Maricao, 800 m, 1989, Aptroot & Aptroot 24948, 24943 (ABL).—**Guyana:** *Upper Takutu:* Rupununi Savannah, Karanambo Ranch, 1992, Sipman 57321 (B).—**Ecuador:** *Zamora-Chinchipec:* Estacion Científico San Francisco, 40 km S of Loja, 2004, Sipman 52367 (B).

***Astrothelium stramineum* (Malme)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816745

*Thelenella straminea* Malme, *Ark. Bot.* 22A(1): 7 (1928).—*Clathroporina straminea* (Malme) Zahlbr., *Catal. Lich. Univ.* 8: 111 (1931).—*Laurera straminea* (Malme) P. M. McCarthy, *Lichenologist* 27: 348 (1995); type: Brazil, Matto Grosso, Serra da Chapada, Bocca da Serra, 15 March 1884, Malme 2550 (S!—holotype).

(Fig. 31D)

*Thallus* saxicolous, corticate, yellowish white, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary, 0.4–0.6 mm diam., hemispherical, covered by thallus. *Hamathecium* inspersed. *Ascospores* (2–)4(–6) per ascus, densely muriform, fusiform, 40–80 × 15–24 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus UV+ yellow, K–, with lichexanthone; ascomata UV–, K–.

*Distribution.* Neotropical (Brazil).

*Discussion.* This is one of the very few species of *Trypetheliaceae* ever encountered on rock, and one of three species that seem restricted to rock; the others are *A. saxicola*, from the same locality, and *Pseudopyrenula saxicola*.

***Astrothelium straminicolor* (Nyl.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816746

*Trypethelium straminicolor* Nyl., *Lich. Japon.* 115 (1890); type: Malaysia, Labuan, Almqvist s. n. (H-Nyl 174!—lectotype, designated here; S!—isolectotype).

*Trypethelium stramineum* Kremp., *Nuov. Giorn. Bot. Ital.* 7: 56 (1875), non *Astrothelium stramineum* (Malme) Aptroot & Lücking, see above; type: Sarawak, Beccari 212 (M!—lectotype, Makhija & Patwardhan, *Int. J. Mycol. Lichenol.* 5: 246, 1992).

*Astrothelium subvariolosum* Makhija & Patw., *Bioivigyanam* 15: 64 (1989); type: India, Nicobar Islands, Great Nicobar, Campbell Bay to Laful Bay, 2 January 1987, Patwardhan & Nagarkar AMH 87-70 (ABL!—isotype).

(Fig. 27J–L)

*Thallus* corticate, olive-green to yellowish brown, uneven to shallowly bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic; pseudostromata 1–2 mm diam., erumpent to prominent, covered by thallus except for blackish upper part surrounded by a thin, whitish rim, with blackish ostiolar areas often arranged in lobate fashion. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 20–25 × 7–9 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (India and Malaysia, including Sarawak).

### ***Astrothelium subaequans* Müll. Arg.**

*Bot. Jahrb. Syst.* 6: 383 (1885); *Astrothelium subaequans* Nyl. (1876) nom. nud.; type: Cuba, *Wright* s. n. (G!—holotype; H-Nyl 108!—isotype; Müller, *Verr. Cub.* 146).

(Fig. 37H)

*Thallus* corticate, olive-green to yellowish, uneven to shallowly bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed, 1–2 mm diam., erumpent, covered by thallus except dark, protruding and papilliform ostiole, thinly covered with yellow-orange pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, submuriform, fusiform, (45–)72–83 × 15–25 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; ascomata with yellow-orange, K+ purple, UV+ red anthraquinone.

*Distribution.* Neotropical (previously reported from Costa Rica and Cuba).

*New country records.* **Venezuela:** *Bolívar:* Cerro Guaiquinima, 1200 m, 1990, *Sipman* 26848 (B).—**Guyana:** *Upper Mazaruni:* N of Paruima Mission, Aymatoi savannah, 1000 m, 1997, *Sipman* 39806 (B). *Potaro-Siparuni:* Kaieteur Falls, around airstrip, 400 m, 1996, *Sipman* 40408 (B).

### ***Astrothelium subcatervarium* (Malme) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816747

*Trypethelium subcatervarium* Malme, *Ark. Bot.* 19(1): 29 (1924); type: Brazil, Matto Grosso, Serra da Chapada, Buriti, *Malme* s. n. (S!—holotype).

(Fig. 15L)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to confluent or diffusely pseudostromatic, 0.4–0.6 mm diam., erumpent, whitish and dark brown ostiolar area thinly covered with yellow-orange pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 27–33 × 10–12 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV+ orange, K+ red, with anthraquinone.

*Distribution.* Neotropical (reported from Cuba and Brazil). Incorrectly reported from Costa Rica: the specimen (*Breuss* 21057 in LI) proved to have K– pseudostromata.

### ***Astrothelium subclandestinum* Leight.**

*Trans. Linn. Soc. London* 25: 460 (1866); type: Brazil, Amazonas, São Gabriel, *Spruce* 242 (BM!—holotype).

(Fig. 29L)

*Thallus* corticate, olive-green to yellowish, uneven to shallowly bullate.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata diffusely pseudostromatic; pseudostromata 1.0–1.5 mm diam., erumpent, laterally covered by thallus but apically greyish. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 5-septate, fusiform, 50–75 × 14–22 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (previously reported from Costa Rica, Brazil and Australia).



*New country records.* **Venezuela:** Bolivar: National Park Canaima, 2003, *Berger* 18510 (ABL, hb. Berger).—**Guyana:** Demerara-Berbice: Mabura Hill, 1985, *Cornelissen* 486 (ABL).—**Papua New Guinea:** Madang: Foothills of Finisterre Range, 1992, *Aptroot* 33209 (ABL).

***Astrothelium subdiscretum* (Nyl.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816748

*Trypethelium subdiscretum* Nyl., *Flora* 52: 73 (1869).—*Bathelium subdiscretum* (Nyl.) Müll. Arg., *Bot. Jahrb. Syst.* 6: 395 (1885).—*Laurera subdiscreta* (Nyl.) Zahlbr., *Catal. Lich. Univ.* 1: 506 (1922); type: India, West Bengal, *Kurz* s. n. (H-Nyl 322!—holotype; M! —isotype).

*Bathelium phaeomelodes* Müll. Arg., *Bot. Jahrb. Syst.* 6: 394 (1885).—*Trypethelium phaeomelodes* Nyl. (1876) nom. nud.—*Laurera phaeomelodes* (Müll. Arg.) Zahlbr., in Engler & Prantl, *Natürl. Pflanzenfamil.* 1(1\*): 71 (1903); type: Cuba, *Wright* s. n. (Gl—holotype; BM!—isotype; Müller, *Verr. Cub.* 170).

*Laurera nigeriensis* C. W. Dodge, *Ann. Missouri Bot. Gard.* 40: 297 (1953); type: Nigeria, Abadan, 1951, *Thorold* 165 (FH-Dodge—holotype, not seen).

*Laurera subphaeomelodes* Upreti & Ajay Singh, *Bull. Jard. Bot. Nat. Belg.* 57: 382 (1987); type: India, West Bengal, Howrah, Sibpur, *Roychaudhury* 649 (CAL—holotype, not seen).

*Laurera verrucoaggregata* Makhija & Patw., *Mycotaxon* 31: 586 (1988); type: India, Andaman Islands, North Andaman, Lamia Bay, 5 January 1986, *Nagarkar & Sethy* AMH 86.550 (ABL—*isotype*).

*Laurera fusispora* Makhija & Patw., *Mycotaxon* 31: 576 (1988); type: India, Karnataka, Anamod ghat, Anamod-Goa Road, 10 December 1974, *Patwardhan & Prabhu* AMH 74.2499 (ABL—*isotype*).

(Fig. 33A–E)

*Thallus* corticate, olive-green to brownish, uneven to verrucose-rugulose.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 0.8–1.5(–2.0) mm broad, immersed-erumpent, irregular to linear and often confluent and reticulate, with ascomata exposed and black. *Hamathecium* inspersed, clear. *Ascospores* 8 per ascus, small muriform, ellipsoid, 35–50 × 12–18 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (previously reported from Cuba, Costa Rica, Nigeria, India and Thailand).

*New country records.* **Netherlands Antilles:** Bonaire: Ceru Kammia, 1977, *van Slageren* 8406-b (ABL).—**Dominican Republic:** La Altagracia, Bayahibe, 1981, *Buck* 5141 (NY, hb. Kalb).—**Colombia:** Caqueta, Araracuara, opposite airstrip, 250 m, 1988, *Sipman & Duivenvoorden* 27909 (B).—**Venezuela:** Bolivar: Cerro Guaiquinima, along Rio Carapo, 800 m, 1990, *Sipman* 26942 (B).—**Guyana:** between Karanambo and Kwaimatta, 1988, *Maas et al.* 7709d (ABL).—**Sri Lanka:** Anuradhapura: Wipattu, *Santesson* 26185 (S).—**Singapore:** Pulau Ubin Island: 2000, *Sipman & Tan* 46340 (B).

***Astrothelium subdisjunctum* (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816749

*Bottaria subdisjuncta* Müll. Arg., *Bot. Jahrb. Syst.* 6: 395 (1885).—*Laurera subdisjuncta* (Müll. Arg.) R. C. Harris, *Acta Amazon. (Suppl.)* 14: 66 ('1984') [1986]; type: Cuba, *Wright* s. n. (Gl—holotype; Müller, *Verr. Cub.* II: 676).

*Laurera dodgei* Letr.-Gal., *Rev. Bryol. Lichénol.* 27: 71 (1958); type: Costa Rica, Puntarenas, Rio Sandalo, Galjo Dulce, Peninsula de Osa, 0–10 m, 23 August 1936, *Dodge & Goeger* 10063 (FH-DODGE!—holotype).

*Clathroporina waimiana* Zahlbr., *Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Classe* 111(1): 364 (1902); type: Brazil, Rio de Janeiro, *Höhmel* 151 (W—holotype, not seen).

(Fig. 35I & J)

*Thallus* corticate, olive-green to brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 0.7–1.5 mm broad, immersed-erumpent, irregular to linear and often confluent and reticulate, with ascomata exposed and black. *Hamathecium* clear. *Ascospores* 4 per ascus, densely muriform, fusiform, 120–175 × 30–45 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from the USA, Cuba, Costa Rica, Guyana, Venezuela and Brazil).

*New country records. French Guiana: Cayenne:* Cayenne, along forest track called Risque tout, 50 m, 1985, *Aptroot* 15126 (ABL, B). *Saint-Laurent-du-Maroni:* Saül, 1985, *Aptroot* 15440 (ABL, B); Saül, 1986, *Montfoort & Ek* 290 (ABL).

***Astrothelium subdissocians* (Nyl. ex Vain.) Aptroot & Lücking comb. et stat. nov.**

Mycobank No.: MB 816750

*Pseudopyrenula ochroleuca* var. *subdissocians* Nyl. ex Vain., *Bot. Tidskr.* **29**: 147 (1909).—*Trypethelium ochroleucum* var. *subdissocians* (Vain.) Hue (1892) nom. nud.—*Trypethelium pallescens* var. *subdissocians* Nyl. (1864) nom. nud; type: Thailand, Koh Chang, *Schmidt* 11 (TUR-Vain 30761!—holotype).

(Fig. 28L)

*Thallus* corticate, light olive-green to yellowish brown, smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed to irregularly confluent, 0.4–0.6 mm diam., erumpent to prominent, with complete whitish cover. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 20–25 × 7–9 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Palaeotropical (reported from Thailand).

***Astrothelium subfuscum* Kremp.**

*Nuovo Giorn. Bot. Ital.* **7**: 64 (1875); type: Singapore, *Beccari* 236 (M!—holotype).

(Fig. 28H & I)

*Thallus* corticate, olive-green to brownish, rather thick, uneven to bullate-folded.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata confluent to diffusely pseudostromatic; pseudostromata 0.7–1.3 mm diam., erumpent, irregular in outline, laterally

covered by thallus but upper part of ascomata exposed, blackish and groups of ascomata bordered by thin, whitish line. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 21–27 × 8–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (previously reported from India, Singapore, Sabah, New Caledonia and Papua New Guinea). Reports from the Neotropics refer probably to *Astrothelium crassum*.

*New country records. China: Hong Kong:* New Territories, Tai Po Kau Nature Reserve, 1998, *Aptroot* 43290 (ABL).—**Philippines:** *Luzon:* Sorsogon, Irosin, 1916, *Elmer* 17111 (B).

***Astrothelium superbum* (Fr.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816751

*Trypethelium superbum* Fr., *Syst. Orb. Veget.* **1**: 287 (1825).—*Campylothelium superbum* (Fr.) Müll. Arg., *Flora* **68**: 251 (1885); type: Indonesia, *s. col.* (UPS—holotype, not seen).

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* pleurothelioid, with eccentric, separate ostioles, solitary to irregularly grouped, 1–2 mm diam., immersed-erumpent, covered by thallus. *Hamathecium* clear. *Ascospores* 8 per ascus, densely muriform, fusiform, 130–165 × 35–45 µm, without distinctly thickened median septum, hyaline or becoming yellowish, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from India and Indonesia).

***Astrothelium tenue* (Aptroot) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816752

*Campylothelium tenue* Aptroot in Aptroot *et al.*, *Biblioth. Lichenol.* **98**: 53. (2008); type: Costa Rica, Alajuela, Volcán Tenorio National Park, surroundings of Pílon Biological Station, *Sipman* 51867 (B!—holotype).

(Fig. 38K & L)

*Thallus* corticate, olive-green, smooth to uneven.

*Ascomata* pleurothelioid, with eccentric, separate ostioles, 0.4–0.7 mm diam., erumpent, completely covered by thallus. *Hamathecium* clear. *Ascospores* 4–8 per ascus, muriform, fusiform, 95–115 × 20–28 µm, with distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Possibly pantropical (so far reported only from Costa Rica).

*Discussion.* This species is characterized by the fusiform distoseptate ascospores, in which the stellate primary locules remain recognizable in the mature ascospores.

*New country records.* **Guyana:** Demerara-Berbice: Mabura Hill, 1988, *Bleij & Biesmeijer* (ABL).—**Singapore:** Nee Soon, 2000, *Sipman et al.* 46164 & 46159 (B).

***Astrothelium thelotremoides* (Nyl.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816753

*Verrucaria thelotremoides* Nyl., *Ann. Sci. Nat., Bot., sér. 5* **7**: 346 (1867).—*Pseudopyrenula thelotremoides* (Nyl.) Müll. Arg., *Flora* **66**: 248 (1883).—*Trypethelium thelotremoides* (Nyl.) R. C. Harris, *Lichenogr. Thomsoniana*: 148 (1986); type: Colombia, Rio Negro, *Lindig* 51 (H-Nyl 1113!—lectotype, designated here; BM!—isolectotype).

(Fig. 14D & E)

*Thallus* corticate, olive-green to brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent,

0.5–0.8 mm diam., erumpent, covered by thallus with ostiolar area dark greyish with thin whitish rim, internally with red pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 50–65 × 15–21 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–; ascomata internally K+ purple, with an anthraquinone.

*Distribution.* Neotropical (previously reported only from Colombia).

*Discussion.* The type sheet contains three specimens; two are *Ocellularia* species and the third specimen is designated here as lectotype.

*New country record.* **Brazil:** Bahia: Entre Rios, 1981, *Boom & Mori* 1010 (hb. Kalb, NY).

***Astrothelium trypethelizans* (Nyl.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816754

*Verrucaria trypethelizans* Nyl., in Crombie, *J. Linn. Soc. London, Bot.* **20**: 60 (1883).—*Pseudopyrenula trypethelizans* (Nyl.) Zahlbr., *Catal. Lich. Univ.* **1**: 359 (1922).—*Trypethelium trypethelizans* (Nyl.) R. C. Harris, *Lichenogr. Thomsoniana*: 148 (1998); type: Malaysia, Malacca, Tanjong, *Maingay* 149 (BM!—lectotype; Harris, *Lichenogr. Thomsoniana*: 148, 1998).

(Fig. 21D)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, dispersed to largely confluent, 0.3–0.5 mm diam., erumpent with flattened top, brownish black. *Hamathecium* clear. *Ascospores* 8 per ascus, 7–9-septate, fusiform, 32–38 × 10–11 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from Malaysia).



***Astrothelium tuberculosum* (Vain.)  
Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816755

*Pseudopyrenula annularis* var. *tuberculosa* Vain., *Ann. Acad. Sci. Fenn., ser. A* 6(7): 196 (1915).—*Trypethelium crassum* var. *tuberculosum* (Vain.) Zahlbr., *Catal. Lich. Univ.* 8: 128 (1932).—*Trypethelium tuberculosum* (Vain.) R. C. Harris, *Acta Amazon. (Suppl.)* 14: 76 (1984) [1986]; type: Guadeloupe, Safraga, Duss 1415 (TUR-Vain 30778!—holotype).

(Fig. 20L)

*Thallus* corticate, olive-green to brownish, strongly bullate.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic; pseudostromata 1–2 mm diam., prominent to sessile, irregular, fully covered by thallus except dark ostioles surrounded by whitish rim. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 48–65 × 17–20 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Guadeloupe, Trinidad, Tobago, Costa Rica, Guyana, French Guiana, Venezuela, Galapagos and Colombia).

*New country record.* **Brazil:** São Paulo: Campos de Jordão, 1800 m, 1997, Sipman 41127 (SP, B).

***Astrothelium ubianense* (Vain.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816756

*Pseudopyrenula ubianensis* Vain., *Ann. Acad. Sci. Fenn., ser. A* 15(6): 353 (1921).—*Trypethelium ubianense* (Vain.) Zahlbr., *Catal. Lich. Univ.* 8: 129 (1932); type: Philippines, Ubian, Merrill 5403 p.p. (TUR-Vain 30798!—holotype).

(Fig. 21C)

*Thallus* corticate, light olive-green to yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata irregular, 0.8–1.5 mm broad, basally covered by thallus but otherwise whitish, with the

ostioles areas of individual ascomata black and strongly contrasting. *Hamathecium* clear. *Ascospores* 8 per ascus, 5–11-septate, fusiform, 30–36(–49) × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances reported.

*Distribution.* Eastern palaeotropical (reported from India and the Philippines).

***Astrothelium variatum* (Nyl.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816757

*Trypethelium variatum* Nyl., *Ann. Sci. Nat., Bot., sér.* 5 7: 347 (1867).—*Laurea variata* (Nyl.) Zahlbr., *Catal. Lich. Univ.* 1: 507 (1922); type: Colombia, Rio Negro, Lindig s. n. (H-Nyl!—holotype).

*Heufleria subvariata* Müll. Arg., *Bot. Jahrb. Syst.* 6: 384 (1885).—*Trypethelium subvariatum* Nyl. (1876) nom. nud.—*Cryptothelium subvariatum* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* 1: 523 (1922); type: Cuba, Wright s. n. (G!—holotype; Müller, *Verr. Cub.* 164).

(Fig. 35A & B)

*Thallus* corticate, olive-green, smooth to uneven or shallowly rugose.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic; pseudostromata 0.7–1.4 mm diam., prominent, irregular, covered by thallus except dark ostioles. *Hamathecium* clear. *Ascospores* 8 per ascus, small muriform, fusiform, 24–35 × 11–13 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Cuba and Colombia).

*New country record.* **Venezuela:** Amazonas: Alto Orinoco, 15 km W of Esmeralda, 110 m, 1997, Hafellner & Komposch 209-3-7 (GZU).

***Astrothelium variolosum* (Ach.) Müll. Arg.**

*Flora* 68: 255 (1885).—*Trypethelium variolosum* Ach., *Synops. Lich.*: 104 (1814); type: “ad corticem Chinchonae flavae” (H-ACH 877!—holotype; S!—isotype).

*Trypethelium papillosum* Ach., *Synops. Lich.*: 104 (1814) non Knight (1886).—*Bathelium papillosum* (Ach.) C. W. Dodge, *Ann. Missouri Bot. Gard.* **40**: 288 (1953); type: Guinea, s. col. (H-ACH 878A!—holotype; S!—isotype).

*Pyrenula epapillata* Fée, *Essai Crypt. Écorc.*: 78 (1824).—*Spermatodium epapillatum* (Fée) Trevis., *Conspect. Verruc.*: 11 (1860); type (PC—syntypes, not seen).

*Trypethelium papillosum* var. *fusum* Müll. Arg., *Flora* **68**: 255 (1885); type: French Guiana, Leprieur 467 p.p. (G!—holotype).

(Fig. 24A–D)

*Thallus* corticate, pale greenish grey to pale yellowish brown (lichexanthone colour), smooth to uneven.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata pseudostromatic; pseudostromata 0.7–1.5 mm broad, erumpent to prominent, irregular in outline, covered by thallus but often paper to whitish, with dark ostioles. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 20–26 × 7–9 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV+ yellow, K–, with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone).

*Distribution.* Pantropical (previously reported from the continental USA, Bahamas, Cuba, Trinidad, Costa Rica, French Guiana, Venezuela, Colombia, Brazil, Bolivia, Sri Lanka, Thailand, Guam, Northern Mariana Islands and Australia).

*Discussion.* Further synonyms in the genera *Verrucaria* and *Spermatodium* are mentioned by Zahlbruckner (1922), but not cited here as the species was used in a different sense at that time and the material has not been checked. *Astrothelium variolosum* is accepted here in a very much more restricted sense than by Harris (1995), who included specimens with or without lichexanthone, with apical or eccentric ostioles, with simple or aggregated ascomata and with or without hamathecium inspersion, each of which are species characters in our concept. Specimens which differ only in an inspersed hamathecium are known from, for example, Guyana (*Sipman* 58039, 39954, and 39969). A new

species is not described for them because it cannot be ruled out that one of the taxa that have been synonymized with *A. variolosum* has an inspersed hamathecium.

*New country records.* **Puerto Rico:** *Aguadilla:* Bosque Estatal de Guajataca, 1989, *Aptroot & Aptroot* 25730 (ABL).—**Guyana:** *Upper Demerara-Berbice:* Mabura Hill, 1994, *DePriest et al.* 9086 (B).—**Indonesia:** *Java:* Malang, 1932, *Groenhart* 412 (ABL, L).—**Papua New Guinea:** *Madang:* Madang, 1992, *Aptroot* 30078 (ABL).

### ***Astrothelium versicolor* Müll. Arg.**

*Flora* **71**: 495 (1888); type: Puerto Rico, *Sintenis* 6 (G!—holotype).

(Fig. 23C)

*Thallus* corticate, whitish to pale yellowish, strongly bullate-folded.

*Ascomata* astrothelioid, several chambers joined with eccentric, fused ostioles; joined ascomata dispersed but dense, 0.2–0.4 mm diam., completely immersed in thallus folds and warts, visible only by their darker ostioles thinly furnished with yellow-orange pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, fusiform-ellipsoid, 3-septate, 28–35 × 10–15 µm, hyaline, IKI–.

*Chemistry.* Thallus UV+ yellow, K–, with lichexanthone; ascomata apically K+, UV+ red, with anthraquinone.

*Distribution.* Pantropical (previously reported from the USA, Bahamas, Cuba, Puerto Rico, Trinidad, Costa Rica, Guyana, French Guiana, Venezuela, Brazil, Bolivia, Philippines and New Caledonia).

*New country record.* **Papua New Guinea:** *Central:* Varirata National Park, 1995, *Aptroot* 39772 (ABL).

### ***Astrothelium vezdae* (Makhija & Patw.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816758

*Laurera vezdana* Makhija & Patw., *Mycotaxon* **31**: 587 (1988) [as '*vezdae*']; type: India, Maharashtra, Vishalgarh, Amba-Gajapur Road, 6 December 1974, *Nagarkar & Prabhu* AMH 74.2183 (ABL!—isotype).

(Fig. 32K)

*Thallus* corticate, olive-green to brownish, uneven-rugulose.

*Ascomata* trypethelioid to pleurothelioid, with apical to eccentric, separate ostioles, pseudostromatic; pseudostromata 1.0–1.3 mm diam., erumpent to prominent, covered by thallus but thinly covered with orange pigment. *Hamathecium* clear. *Ascospores* 2–4 per ascus, muriform, ellipsoid, 80–175 × 25–50 µm, without distinctly thickened median septum, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV+ reddish, K+ purple, with orange anthraquinone.

*Distribution.* Possibly pantropical (previously reported only from India).

*New country record.* **Guyana:** *Upper Takutu*: c. 35 km S of Aishalton, 250 m, 1992, *Sipman* 51722 (B).

### **Bathelium** Ach.

*Methodus*: 111 (1803); type: *Bathelium mastoideum* Ach. (holotype).

*Riddlea* C. W. Dodge, *Annals of the Missouri Botanical Garden* 40: 287 (1953); type: *Riddlea papillosa* C. W. Dodge (= *Bathelium* cf. *madreporiforme*, holotype).

*Thallus* corticate, olive-green to brownish or greyish.

*Ascomata* with apical ostioles, solitary to grouped or mostly pseudostromatic, prominent to sessile, brown-black or rarely whitish pruinose, with a peripheral layer

of compressed cells. *Hamathecium* clear, hyaline, filaments thin, anastomosing paraphysoids. *Ascospores* 1–8 per ascus, transversely septate to muriform, with thin septa and more or less angular lumina, fusiform with acute or rounded ends, not constricted at the median septum, hyaline, IKI–, surrounded by a gelatinous sheath.

*Conidiomata* unknown.

*Chemistry.* Anthraquinones often present internally in pseudostromata, lichexanthone occasionally present.

*Discussion.* A genus of currently 11 species, all tropical epiphytes, which are phylogenetically separate from *Astrothelium*. *Bathelium* is morphologically characterized by the usually prominent pseudostromata not covered by thallus, superficially somewhat similar to those of *Trypethelium* s. str. and like the latter usually with internal pigment granules, and the apparently thin-walled ascospores with a reduced endospore, best seen in species with transversely septate ascospores. The genus was first properly recognized by Harris (1995), who also included some species now shown to belong in *Astrothelium*, such as *A. degenerans* and *A. endochryseum* (Lücking *et al.* 2016a). Harris (1995) therefore did not note the lack of an endospore in species of this genus but instead mentioned hamathecium inspersion as a character of taxa with muriform ascospores. However, all *Bathelium* species have a clear hamathecium except for the ostiolar region, which is inspersed in many *Trypetheliaceae*.

### **Key to the species of *Bathelium***

- |      |  |                                      |
|------|--|--------------------------------------|
| 1    | Ascospores transversely septate. . . . .   | 2                                    |
|      | Ascospores muriform . . . . .  | 7                                    |
| 2(1) | Ascospores 13–17-septate, 65–105 µm long; ostiolar area UV+ yellow, with lichexanthone (Flakus <i>et al.</i> 2016; Fig. 40A) . . . . . | <b><i>Bathelium flavostiolum</i></b> |
|      | Ascospores 3–9-septate, 18–40 µm long; UV–, no substances. . . . .   | 3                                    |
| 3(2) | Ascospores 3(–5)-septate, 18–25(–30) µm long. . . . .  | 4                                    |
|      | Ascospores 5–9-septate, 25–40 µm long . . . . .  | 6                                    |



- 4(3) Internal pseudostroma pigment yellow, K+ persistently yellow; ascomata distinctly pseudostromatic (this synopsis; Fig. 40B) . . . . . **Bathelium carolinianum**  
Internal pseudostroma pigment yellow-orange to reddish brown, K+ orange-red or purple-violet; ascomata variable . . . . . 5
- 5(4) Internal pseudostroma pigment yellow-orange, K+ purple-violet; ascospores 18–21 × 6–7 µm long; ascomata pseudostromatic (this synopsis) . . . . . **Bathelium austroafricanum**  
Internal pseudostroma pigment reddish brown, K+ orange-red; ascospores 20–30 × 6–7 µm long; ascomata solitary to irregularly confluent (Lücking *et al.* 2016b; Fig. 40C & D) . . . . . **Bathelium porinosporum**
- 6(3) Ostioles usually white-pruinose; ascospores 5–7-septate, 25–32 µm long (this synopsis; Fig. 40E) . . . . . **Bathelium albidoporum**  
Ostioles non-pruinose, black; ascospores 5–9-septate, 30–40 µm long (this synopsis; Fig. 40F–H) . . . . . **Bathelium nigroporum**
- 7(1) Thallus and pseudostromata UV+ yellow, with lichexanthone . . . . . 8  
Thallus and pseudostromata UV– or UV+ red when pigment is present, lichexanthone absent . . . . . 9
- 8(7) Hamathecium inspersed; ascospores 45–50 × 15–17 µm (this synopsis; Fig. 40I) . . . . . **Bathelium pruinolucens**  
Hamathecium clear; ascospores 45–70 × 13–20 µm (Flakus *et al.* 2016; Fig. 40J) . . . . . **Bathelium pruinorum**
- 9(7) Internal pigment of pseudostromata dark red, K+ green . . . . . 10  
Internal pigment of pseudostromata yellow-orange, K+ purple . . . . . 11
- 10(9) Pseudostromata erumpent, covered with orange pigment and with dark ostioles surrounded by paler rim (Flakus *et al.* 2016; Fig. 40K) . . . . . **Bathelium mirabile**  
Pseudostromata prominent to sessile, dark brown and with strongly contrasting, whitish ostiolar area (Flakus *et al.* 2016; Fig. 40L) . . . . . **Bathelium boliviense**
- 11(9) Ascospores 40–80 µm long . . . . . 12  
Ascospores 100–200 µm long . . . . . 15
- 12(11) Hamathecium fully inspersed (Flakus *et al.* 2016; Fig. 41A) . . . . . **Bathelium inspersionmastoideum**  
Hamathecium clear except for ostiolar area . . . . . 13
- 13(12) Ascospores (50–)60–80 µm long (this synopsis; Fig. 41B) . . . **Bathelium mastoideum**  
Ascospores 40–55 µm long . . . . . 14
- 14(13) Thallus smooth to uneven (this synopsis; Fig. 41C–G) . . . . . **Bathelium madreporiforme**  
Thallus verrucose-bullate (this synopsis; Fig. 41H–J) . . . . . **Bathelium tuberculorum**
- 15(11) Ascospores 100–120 µm long (this synopsis; Fig. 41K) . . . . . **Bathelium lineare**  
Ascospores 130–200 µm long (this synopsis; Fig. 41L) . . . **Bathelium sphaericum**

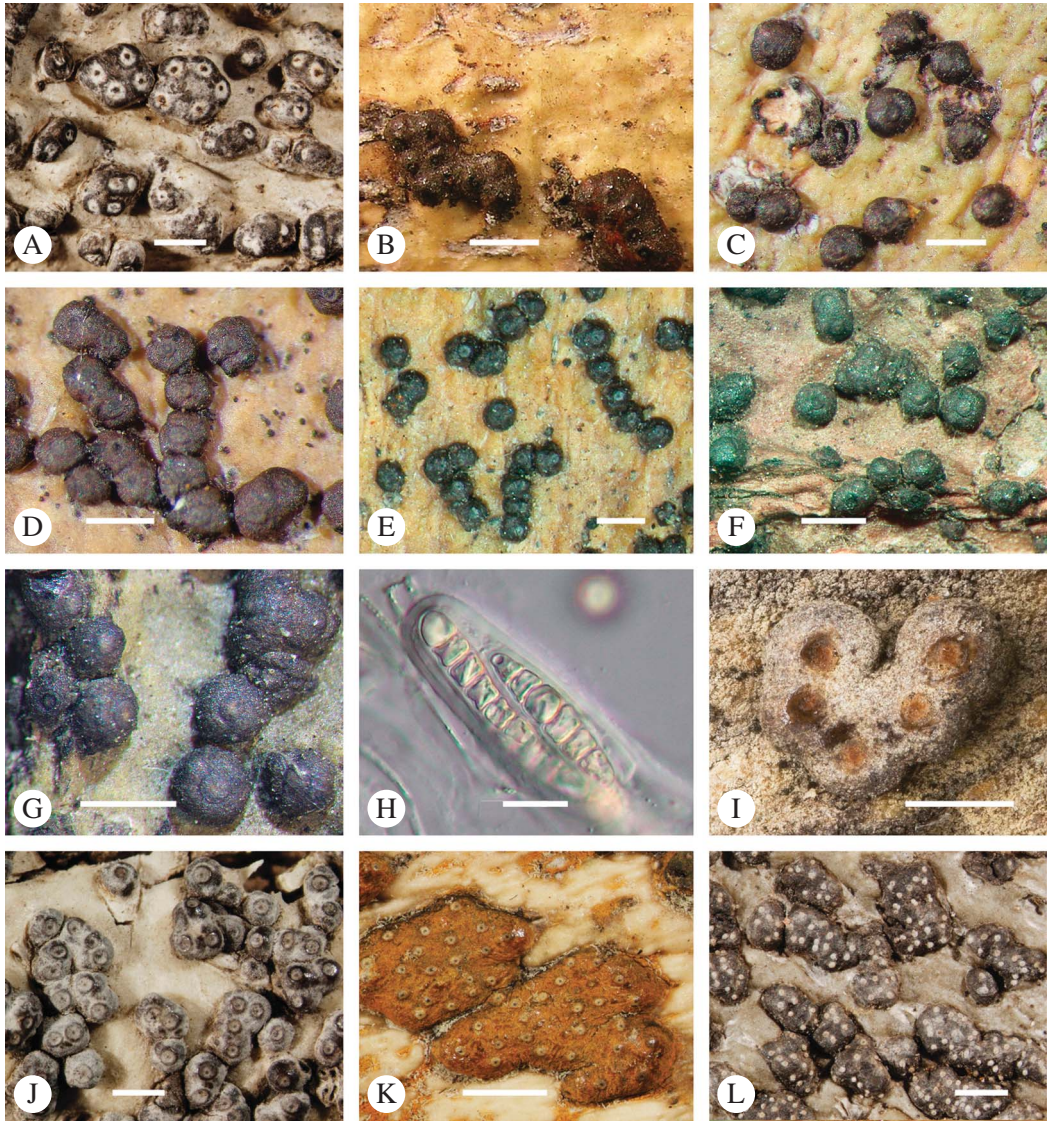


FIG. 40. Habitus and ascospores of *Bathelium* species. A, *B. flavostiolatum* (Bolivia, holotype); B, *B. carolinianum* (USA, South Carolina, isolectotype); C & D, *B. porinosporum* (Vietnam, holotype); E, *B. albidoporum* (Papua New Guinea, Aptroot 32903); F–H, *B. nigroporum* (India, isotype); I, *B. pruinosum* (Brazil, lectotype); J, *B. pruinosum* (Bolivia, holotype); K, *B. mirabile* (Bolivia, holotype); L, *B. boliviense* (Bolivia, holotype). Scales: A–G, I–L = 1 mm; H = 10  $\mu$ m.

***Bathelium albidoporum* (Makhija & Patw.) R. C. Harris**

*More Florida Lichens*: 116 (1995).—*Trypethelium albidoporum* Makhija & Patw., *Internat. J. Mycol. Lichenol.* 5: 238 (1992); type: Vietnam, Tu-phap, *Balansa* s. n. (BM!—holotype).

(Fig. 40E)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent,



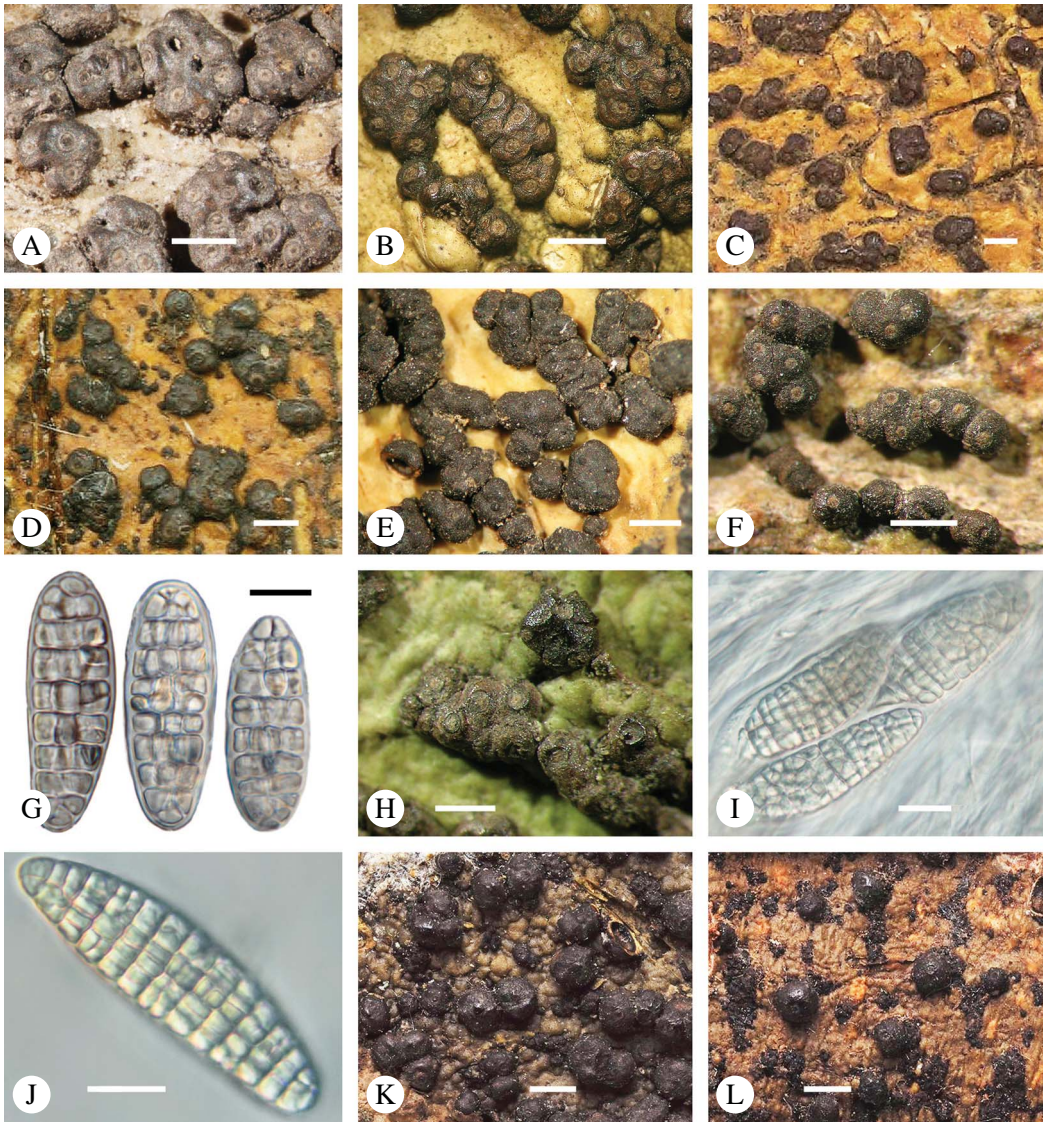


FIG. 41. Habitus and ascospores of *Bathelium* species. A, *B. inspersomastoideum* (Bolivia, holotype); B, *B. mastoideum* (Costa Rica, Buck 43891); C–G, *B. madreporiforme* (C, Brazil, lectotype; D, South Africa, holotype of *Trypethelium marginatum*; E, Sierra Leone, holotype of *Riddlea papillosa*; F, Brazil, Cáceres 258; G, USA, Johnson 6057); H–J, *B. tuberculosum* (India, Lumbsch 1973j); K, *B. lineare* (Sierra Leone, isotype); L, *B. sphaericum* (Sierra Leone, isotype). Scales: A–F, H, K & L = 1 mm; G, I & J = 10  $\mu$ m.

0.6–1.0 mm diam., prominent to sessile, blackish brown, often with white-pruinose ostioles, internally with orange-brown, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 5–7-septate, fusiform, 25–32  $\times$  6–9  $\mu$ m, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; ascomata UV–, internally K+ red, with anthraquinone.

*Distribution.* Eastern palaeotropical (previously reported from Thailand, Vietnam and Myanmar).



*New country records.* **China:** Yunnan: Xishuangbanna, Menglun, 2002, *Aptroot* 57020 (ABL).—**Indonesia:** Java: Bay of Serang, S of Bliter, 1937, *Groenhart* 5813, 5826 (ABL, L).—**Papua New Guinea:** Madang: S side of Ramu River, Brahman Mission, 1995, *Aptroot* 38525 (ABL); Gogol Valley, Tgubi logging site, 1992, *Aptroot* 32903 (ABL).

***Bathelium austroafricanum* (Zahlbr.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816759

*Trypethelium austroafricanum* Zahlbr., *Ann. Cryptog. Exot.* **5**: 204 (1932); type: South Africa, Cape Region, Knysna, *van der Byl* 918 (W—holotype, not seen; BM!—isotype).

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 0.8–1.5 mm diam. (individual ascomata 0.5–0.9 mm diam.), prominent to sessile, blackish brown, internally with yellow-orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 6–8 per ascus, 3-septate, fusiform, 18–21 × 6–7 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV–, internally K+ purple-violet, with anthraquinone.

*Distribution.* African Palaeotropics (reported from South Africa).

***Bathelium carolinianum* (Tuck.)  
R. C. Harris**

*More Florida Lichens:* 116 (1995); *Trypethelium carolinianum* Tuck., *Amer. J. Sci. Arts, ser. 2* **25**: 429 (1858); type: USA, South Carolina, *Ravenel* 298 (FH-TUCK—lectotype; Harris, *More Florida Lichens:* 117, 1995, not seen; S!—isolectotype).

(Fig. 40B)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 0.8–1.5 mm diam. (individual ascomata 0.5–0.8 mm diam.), prominent to sessile, blackish

brown, internally with yellow, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 18–28 × 6–9 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV–, internally K+ yellow, with anthraquinone.

*Distribution.* South-eastern North America.

***Bathelium lineare* (C. W. Dodge)  
R. C. Harris**

*More Florida Lichens:* 117 (1995).—*Polyblastiopsis linearis* C. W. Dodge, *Ann. Missouri Bot. Gard.* **40**: 276 (1953).—*Laurera linearis* (C. W. Dodge) Letr.-Gal., *Rev. Bryol. Lichénol.* **36**: 253 (1957); type: Sierra Leone, Njala, *Deighton* M4634 (BM!—isotype).

(Fig. 41K)

*Thallus* corticate, olive-green to yellowish brown, uneven to shallowly verrucose.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.9–1.2 mm diam., prominent to sessile, blackish brown, internally with yellow-orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, fusiform, 100–120 × 13–20 µm, central septum not strongly thickened, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; ascomata UV–, internally K+ purple, with anthraquinone.

*Distribution.* Possibly pantropical (reported from Costa Rica, Senegal, Mozambique and Sierra Leone).

***Bathelium madreporiforme* (Eschw.)  
Trevis.**

*Flora* **2**: 21 (1861).—*Trypethelium madreporiforme* Eschw., *Syst. Lich.*: 24 (1824).—*Laurera madreporiformis* (Eschw.) Riddle, in Howe, *Torreya* **16**: 50 (1916); type: Brazil, Serra dos Montes Altos, *Martius* s. n. (M-0207125!—lectotype, designated here).

?*Riddlea papillosa* C. W. Dodge, *Annals of the Missouri Botanical Garden* **40**: 287 (1953); type: Sierra Leone, Njala (Kori), *Deighton* M4624 (FH!—holotype).

*Laurera kundaraensis* Upreti & Ajay Singh, *Bull. Jard. Bot. Nat. Belg.* **57**: 375 (1987); type: India, Kerala,

Quilon, Kundara, Singh & Ranjan s. n. (LWG—holotype, not seen).

(Fig. 41C–G)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 1–2 mm broad (individual ascomata 0.7–1.0 mm diam.), prominent to sessile, blackish brown, internally with yellow-orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, small muriform, fusiform-ellipsoid, 40–55 × 11–17 μm, central septum not strongly thickened, hyaline, IKI–.

**Chemistry.** Thallus UV–, K–; pseudostromata UV–, internally K+ purple, with anthraquinone. TLC also revealed terpenoid-like spots but these are probably from the bark.

**Distribution.** Pantropical (previously reported from the USA, Mexico, Costa Rica, French Guiana, Colombia, Venezuela, Brazil, Paraguay, Bolivia, Ivory Coast, India, Thailand, Myanmar and Australia).

**Discussion.** The type of *Riddlea papillosa* contains only immature ascospores without septa. The size of these (c. 30 × 10 μm) agrees with immature ascospores of *Bathelium madreporiforme*, as does the external morphology of the pseudostromata, and hence *R. papillosa* is tentatively listed here as a synonym of *B. madreporiforme*. However, there is a possibility that *R. papillosa* is conspecific with *B. mastoideum*, which has larger ascospores but is more common in tropical Africa.

**New country record.** **Guyana:** Upper Takutu: Rupununi Savannah, Dadanawa ranch, 1992, *Sipman* 57387 (B).

### ***Bathelium mastoideum* Ach.**

**Methodus:** 111 (1803).—*Trypethelium mastoideum* (Ach.) Ach., *Lichenogr. Univers.*: 307 (1810); type: Sierra Leone, *Afzelius* s. n. (S!—lectotype, Harris, *More Florida Lichens*: 117, 1995; H-ACH 879E!—isolectotype).

*Trypethelium marginatum* Fée, *Ann. Sci. Nat. Bot.* **23**: 433 (1831).—*Laurera marginata* (Fée) C. W. Dodge, *Ann. Missouri Bot. Gard.* **40**: 297 (1953); type: Senegal, Presque-Ile du Cap Vert, *Perrottet* s. n. (G!—holotype; BM!—isotype).

*Thelenella elegans* Vain., *Bull. Soc. Broteriana, ser. 2* **6**: 174 (1930).—*Laurera elegans* (Vain.) Zahlbr., *Catal. Lich. Univ.* **10**: 103 (1938); type: Mozambique, Palma, *Pires de Lima* 84 (TUR-Vain 34704—holotype, not seen).

*Laurera submadreporiformis* Abbayes, *Bull. Inst. Franç. Afr. Noire* **15**: 52 (1953); type: Equatorial Guinea, *des Abbayes* s. n. (type probably lost).

*Polyblastiopsis pyriformis* C. W. Dodge, *Ann. Missouri Bot. Gard.* **40**: 276 (1953).—*Laurera pyriformis* (C. W. Dodge) Letr.-Gal., *Rev. Bryol. Lichénol.* **26**: 252 (1957); type: Sierra Leone, Njala, *Deighton* M4404 (BM!—isotype).

(Fig. 41B)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 1–2(–3) mm broad (individual ascomata 0.8–1.2 mm diam.), prominent to sessile, blackish brown, internally with yellow-orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, fusiform, 50–80 × 13–20 μm, central septum not strongly thickened, hyaline, IKI–.

**Chemistry.** Thallus UV–, K–; pseudostromata UV–, internally K+ purple, with anthraquinone.

**Distribution.** Pantropical (previously reported from Costa Rica, Colombia, Brazil, Seychelles, Senegal, Mozambique and Sierra Leone). Wrongly reported from many other areas, such as the Galapagos.

**New country records.** **China:** Yunnan: Xishuangbanna, Menglun, 2002, *Aptroot* 57033 (ABL).

### ***Bathelium nigroporum* (Makhija & Patw.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816760

*Trypethelium nigroporum* Makhija & Patw., *J. Hattori Bot. Lab.* **73**: 202 (1993); type: India, Nagaland, Dimapur-Kohima Road, 7 November 1977, *Padwardhan & Nagarkar* AMH 77.1381 (ABL!—isotype).

(Fig. 40F–H)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.7–1.0 mm diam., prominent to sessile, blackish brown, internally with orange-brown, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 5–9-septate, fusiform, 30–40 × 6–9 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; *ascomata* UV–, internally K+ red, with anthraquinone.

*Distribution.* Palaeotropical (reported from Gambia and India).

***Bathelium pruinosum* Aptroot & Lücking nom. et stat. nov.**

Mycobank No.: MB 816761

*Laurera madreporiformis* var. *pruinosa* Malme, *Ark. Bot.* 19(1): 23 (1924); type: Brazil, Matto Grosso, Cuyaba, Malme, Regn. Lich. 2560A (S!—lectotype, Harris, *More Florida Lichens*: 117, 1995).

(Fig. 40I)

*Thallus* corticate, olive-grey, whitish pruinose, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 1–2 mm broad (individual *ascomata* 0.7–1.0 mm diam.), prominent to sessile, blackish brown but whitish pruinose, internally with yellow-orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 4 per ascus, small muriform, fusiform, 45–50 × 15–17 µm, central septum not strongly thickened, hyaline, IKI–.

*Chemistry.* Thallus UV+ yellow, K–; pseudostromata UV+ yellow, internally K+ purple; with lichexanthone and anthraquinone.

*Distribution.* Neotropical (reported from Brazil).

*Discussion.* Rather than elevating the epithet *pruinum* to the species level, we

introduce the new name *pruinolucens* to emphasize the presence of lichexanthone, unusual for this genus, thus reserving the epithet *pruinum* for a new species described from Bolivia (Flakus *et al.* 2016).

***Bathelium sphaericum* (C. W. Dodge) R. C. Harris**

*More Florida Lichens*: 118 (1995).—*Polyblastiopsis sphaerica* C. W. Dodge, *Ann. Missouri Bot. Gard.* 40: 277 (1953).—*Laurera sphaerica* (C. W. Dodge) Letr.-Gal., *Rev. Bryol. Lichénol.* 26: 254 (1957); type: Sierra Leone, Njala, Deighton M4795 (BM!, F!—isotypes).

(Fig. 41L)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 1–3 mm broad (individual *ascomata* 1.0–1.3 mm diam.), prominent to sessile, blackish brown, internally with yellow-orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, fusiform, 130–200 × 13–20 µm, central septum not strongly thickened, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata UV–, internally K+ purple, with anthraquinone.

*Distribution.* African palaeotropical (reported from Sierra Leone).

***Bathelium tuberculosum* (Makhija & Patw.) R. C. Harris**

*More Florida Lichens*: 118 (1995).—*Laurera tuberculosa* Makhija & Patw., *Mycotaxon* 31: 584 (1988); type: India, Karnataka, Sirsi-Kumtha Roas, Kulkarni 74.2689 (LWG—holotype, not seen).

(Fig. 41H–J)

*Thallus* corticate, olive-green to yellowish brown, verrucose-bullate.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata 1–2 mm broad (individual *ascomata* 0.8–1.0 mm diam.), prominent to sessile, blackish



brown, internally with yellow-orange, dusty granular pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, small muriform, fusiform-ellipsoid,  $40\text{--}50 \times 12\text{--}17 \mu\text{m}$ , central septum not strongly thickened, hyaline, IKI-.

*Chemistry.* Thallus UV-, K-; pseudotromata UV-, internally K+ purple, with anthraquinone.

*Distribution.* Eastern palaeotropical (reported from India).

### **Bogoriella Zahlbr.**

*Ann. Cryptog. Exotique* 1928(1): 111 (1928); type: *Bogoriella subpersicina* Zahlbr. [= *Bogoriella decipiens* (Müll. Arg.) Aptroot & Lücking, holotype].

*Ornatopyrenis* Aptroot, *Biblioth. Lichenol.* 44: 128 (1991); type: *Ornatopyrenis queenslandica* (Müll. Arg.) Aptroot [= *Bogoriella queenslandica* (Müll. Arg.) Aptroot & Lücking, holotype].

*Thallus* ecorticate, endoperidermal, or non-lichenized, usually forming whitish or pinkish patches, sometimes bordered by dark prothallus lines, sometimes indistinct and not discolouring the bark surface.

*Ascomata* with apical or rarely eccentric ostioles, solitary or irregularly confluent, usually exposed and black. *Wall* carbonized, dimidiate, often with basal fringe, originating subepidermally but becoming exposed, sometimes with only ostiole exposed, sometimes becoming sessile due to erosion of surrounding bark, carbonized parts in thin section dark (reddish) brown, K+ more or less strongly olivaceous. *Hamathecium* clear or rarely inspersed, IKI-, with *c.*  $2 \mu\text{m}$  wide, sparsely septate, branched and anastomosing filaments, hardly branched at ascus level, supposed to be pseudoparaphyses. *Asci* clavate to subcylindrical, I-, wall gradually thickening towards the tip, with small ocular chamber *c.* 1/4 of ascus width. *Ascospores* 8 per ascus or, inconstantly in somewhat reduced number, olivaceous grey, becoming brownish with age, with one (sub)central euseptum, where they are constricted and a torus ring can sometimes be seen, rarely 3-septate; internally an endospore layer can be seen against the spore wall in certain

stages of the spore development; the endospore may protrude into the locule and form rings or transverse or occasionally longitudinal septa; outer surface covered with a more or less distinct gelatinous sheath (halo), usually at some stage verruculose or spinulose; lower cell usually smaller than upper cell.

*Pycnidia* absent in some species, common in others, often concentrated along the hypothallus border lines.

*Discussion.* The genus *Bogoriella* is reinstated here to accommodate most of the tropical lichen species that have so far been united with some temperate non-lichenized fungi in the genus *Mycomicrothelia* Keissl. The phylogenetic position of only a small number of species has been confirmed so far; several others that cluster separately in the family *Trypetheliaceae* are united below in the new genera *Distothelia* and *Novomicrothelia*. Many of the almost 40 species placed here in *Bogoriella* differ from related ones mainly in ascospore shape and size; therefore measurements are very important for the identification, but also comparison with published ascospore drawings in Hawksworth (1986) and Aptroot (1991, 1995). Much information on this group, under the name *Mycomicrothelia*, was given by Sipman & Aptroot (2005) and its accompanying internet key (Sipman 2005), but descriptions, type citations and full synonymy, partly taken from Hawksworth (1986), are given here for all species of *Bogoriella*.

*Mycomicrothelia willeyana* (Müll. Arg.) D. Hawks. was reported from Florida (Harris 1995), based on clearly lichenized specimens (Lücking *et al.* 2011), although the type appears to be a non-lichenized fungus (no thallus formed) from temperate North America (Massachusetts). After restudy of the (sub-)tropical Florida material, we noticed that the specimens have partially grouped ascomata and are better identified with *Bogoriella socialis*, a tropical, lichenized taxon known from Puerto Rico and Ecuador. This name is therefore added as a new country record below.

**Key to the species of *Bogoriella* and *Novomicrothelia*  
(with references to *Distothelia*)**

- 1 Foliicolous, with a subcuticular, lobed thallus (this synopsis; Fig. 42A) . . . . .  
     . . . . . ***Bogoriella striguloides***  
 On bark or rarely on wood . . . . . 2
- 2(1) Ascomata grouped with lateral, fused ostioles; ascospores 3-septate, 34–38 × 11–  
 13 µm (this synopsis; Fig. 42B) . . . . . ***Bogoriella collospora***  
 Ascomata solitary or rarely confluent, with apical or rarely lateral, always separate  
 ostioles; ascospores 1-septate, of variable size . . . . . 3
- 3(2) Hymenium inspersed . . . . . 4  
 Hymenium clear . . . . . 6
- 4(3) Spores under 28 µm long; pycnidia absent; lichexanthone absent (this synopsis;  
 Fig. 42C) . . . . . ***Novomicrothelia oleosa***  
 Spores mostly over 30 µm long; pycnidia present; lichexanthone usually present . . . 5
- 5(4) Ascomata *c.* 0.5–0.7 mm wide (this synopsis) . . . . . ***Bogoriella xanthonica***  
 Ascomata *c.* 0.7–1.1 mm wide (this synopsis) . . . . . ***Bogoriella macrocarpa***
- 6(3) Excipulum K+ crimson red, pigment dissolving (this synopsis) . . . . .  
     . . . . . ***Bogoriella leuckertii***  
 Excipulum K+ olivaceous or K–, pigment not dissolving or with yellow solution . . . 7
- 7(6) Ostiole lateral; asci cylindrical, up to *c.* 10 µm wide, with uniseriate spores . . . . . 8  
 Ostiole apical; asci clavate, over 10 µm wide, with (sub-)biseriate spores . . . . . 9
- 8(7) Ascospores over 24 µm long (this synopsis; Fig. 42D) . . . ***Bogoriella triangularis***  
 Ascospores under 24 µm long (this synopsis; Fig. 42E) . . . . ***Bogoriella lateralis***  
     If mature ascospores with strongly thickened, distal walls, see *Distothelia angulata* (this synopsis)
- 9(7) Ascospores small, mostly under 22 µm long . . . . . 10  
 Ascospores large, mostly over 22 µm long . . . . . 31
- 10(9) Ascospores mostly under 16 µm long . . . . . 11  
 Ascospores mostly over 16 µm long . . . . . 21  
     If mature ascospores with strongly thickened, distal walls, 15–17 × 6–7 µm, see *Distothelia angulata*  
     (this synopsis)
- 11(10) Pycnidia present . . . . . 12  
 Pycnidia absent . . . . . 14
- 12(11) Thallus brownish, with dark border lines with many pycnidia (this synopsis;  
 Fig. 42F) . . . . . ***Bogoriella punctata***  
 Thallus without border lines with pycnidia; pycnidia between the ascomata . . . 13
- 13(12) Ascomata in groups of (1–)2–6; thallus whitish to pale grey or pinkish (this synopsis;  
 Fig. 42G) . . . . . ***Bogoriella socialis***

	Ascomata single; thallus whitish (this synopsis; Fig. 42H) . . . . .	<b>Bogoriella fumosula</b>
14(11)	Ascomata (incl. fringe) under 0.5 mm wide . . . . .	15
	Ascomata (incl. fringe) over 0.5 mm wide (this synopsis) . . . . .	<b>Bogoriella alata</b>
15(14)	Ascomata (incl. fringe) under 0.3 mm wide . . . . .	16
	Ascomata (incl. fringe) 0.3–0.5 mm wide . . . . .	18
16(15)	Ascomata without fringe (this synopsis; Fig. 42I) . . . . .	<b>Bogoriella exigua</b>
	Ascomata with distinct fringe . . . . .	17
17(16)	Thallus with distinct border lines; paraphyses <i>c.</i> 2.5 $\mu$ m thick (this synopsis; Fig. 42H) . . . . .	<b>Bogoriella fumosula</b>
	Thallus without border lines; paraphyses 1.0–1.5 $\mu$ m thick (this synopsis; Fig. 42J) . . . . .	<b>Bogoriella minutula</b>
18(15)	Thallus without border lines, indistinct to whitish . . . . .	19
	Thallus with border lines, whitish to pinkish or pale brownish . . . . .	20
19(18)	Spores mostly below 15 $\mu$ m long (this synopsis; Fig. 42J) . . . . .	<b>Bogoriella minutula</b>
	Spores mostly over 15.5 $\mu$ m long (this synopsis; Fig. 42K) . . . . .	<b>Bogoriella nonensis</b>
20(18)	Spores often under 15 $\mu$ m long, with slightly unequal loculi; ascomata without fringe usually under 250 $\mu$ m wide (this synopsis; Fig. 42L) . . . . .	<b>Bogoriella subfallens</b>
	Spores rarely under 15 $\mu$ m long, with strongly unequal loculi; ascomata without fringe usually over 250 $\mu$ m wide (this synopsis; Fig. 43A) . . . . .	<b>Bogoriella miculiformis</b>
21(10)	Pycnidia present . . . . .	22
	Pycnidia absent . . . . .	23
22(21)	Ascomata mostly single, <i>c.</i> 0.4–0.7 mm wide incl. fringe (this synopsis; Fig. 42F) . . . . .	<b>Bogoriella punctata</b>
	Ascomata mostly in groups of (1–)2–6, under 0.3 mm wide incl. fringe (this synopsis; Fig. 42G) . . . . .	<b>Bogoriella socialis</b>
23(21)	Thallus border lines present . . . . .	24
	Thallus border lines absent . . . . .	28
24(23)	Asci over 80 $\mu$ m long . . . . .	25
	Asci under 80 $\mu$ m long . . . . .	26
25(24)	Asci under 22 $\mu$ m wide (this synopsis; Fig. 43B) . . . . .	<b>Bogoriella conothelena</b>
	Asci over 22 $\mu$ m wide (this synopsis; Fig. 43C) . . . . .	<b>Bogoriella thelena</b>
26(24)	Ascocarps conical, without distinct fringe, over 150 $\mu$ m high (this synopsis; Fig. 43D) . . . . .	<b>Bogoriella captiosa</b>
	Ascocarps flattened, with distinct fringe, usually under 150 $\mu$ m high . . . . .	27



- 27(26) Ascomata 0.4–0.5 mm wide (this synopsis; Fig. 43A) . . . **Bogoriella miculiformis**  
 Ascomata 0.5–0.9 mm wide (this synopsis) . . . . . **Bogoriella alata**
- 28(23) Perithecium fringe 50–100 µm wide (this synopsis) . . . . . **Bogoriella annonacea**  
 Perithecium fringe under 50 µm wide . . . . . 29
- 29(28) Ascospores under 18 µm long (this synopsis) . . . . . **Bogoriella nonensis**  
 Ascospores mostly over 18 µm long . . . . . 30
- 30(29) Ascomata flattened, not over 100 µm tall (this synopsis; Fig. 43E) . . . . .  
 . . . . . **Bogoriella modesta**  
 Ascomata conical (this synopsis) . . . . . **Bogoriella pachytheca**
- 31(9) Ascospores submuriform (this synopsis; Fig. 43F & G) . . . **Bogoriella decipiens**  
 Ascospores transversely, usually 1-septate . . . . . 32
- 32(31) Ascospores mostly under 30 µm long . . . . . 33  
 Ascospores mostly over 31 µm long . . . . . 38
- 33(32) Most ascospores under 9 µm wide . . . . . 34  
 Most ascospores over 9 µm wide . . . . . 35
- 34(33) Ascomata 0.8–1.0 mm wide, with 200–400 µm wide fringe (this synopsis; Fig. 43H)  
 . . . . . **Bogoriella confluens**  
 Ascomata 0.4–0.5 mm wide, without distinct fringe (this synopsis; Fig. 43I) . . . . .  
 . . . . . **Bogoriella hemisphaerica**
- 35(33) Asci under 20 µm wide . . . . . 36  
 Asci over 20 µm wide . . . . . 37  
 If ostioles with red anthraquinone pigment and mature ascospores with strongly thickened, terminal  
 walls, 23–29 × 11–14 µm, see *Distothelia rubrostoma* (this synopsis)
- 36(35) Most ascospores under 23 µm long, with rounded ends (this synopsis; Fig. 43B) . . .  
 . . . . . **Bogoriella conothelena**  
 Most ascospores over 24 µm long, with attenuated ends (this synopsis; Fig. 43J) . . .  
 . . . . . **Bogoriella apposita**
- 37(35) Thallus with border lines (this synopsis; Fig. 43C) . . . . . **Bogoriella thelena**  
 Thallus without border lines (this synopsis) . . . . . **Bogoriella obovata**
- 38(32) Most ascospores under 13 µm wide (this synopsis; Fig. 43K) . . . . .  
 . . . . . **Bogoriella megaspora**  
 Most ascospores over 13 µm wide (this synopsis; Fig. 43L) . . . . .  
 . . . . . **Bogoriella queenslandica**

**Bogoriella alata (Groenh. ex Aptroot)**  
**Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816762

*Mycromicrothelia alata* Groenh. ex Aptroot, *Biblioth. Lichenol.* 44: 130 (1991); type: Indonesia, Java, East Java, Semaru Lands, ravine of the Glidik River near Tempur Sewu estate, *Groenhart* 1681 (L!—holotype).

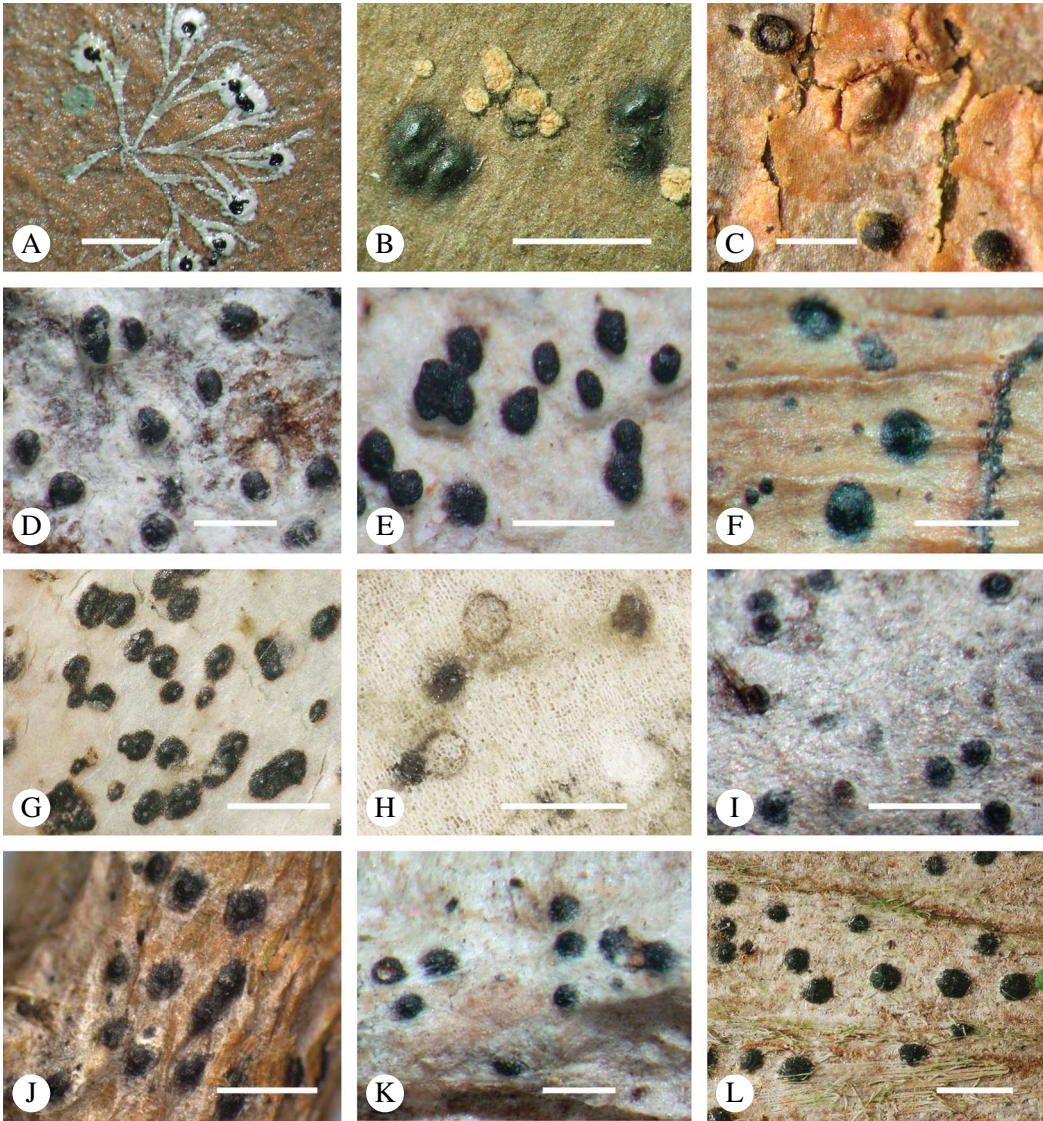


FIG. 42. Habitus of *Bogoriella* and *Novomicrothelia* species. A, *Bogoriella striguloides* (New Zealand, isotype); B, *B. collospora* (Japan, holotype); C, *Novomicrothelia oleosa* (Brazil, Cáceres & Aptroot 11967); D, *Bogoriella triangularis* (Puerto Rico, isotype); E, *B. lateralis* (Australia, isotype); F, *B. punctata* (Papua New Guinea, holotype); G, *B. socialis* (USA, Florida, Lücking 26733); H, *B. fumosula* (China, isotype); I, *B. exigua* (Brazil, Menezes s. n.); J, *B. minutula* (Argentina, Ferraro 8776); K, *B. nonensis* (Ecuador, Arvidsson 6614); L, *B. subfallens* (USA, Florida, Lücking 26772). Scales = 1 mm.

*Thallus* pinkish grey, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, 0.5–0.9 mm wide and 0.1–0.2 mm high, erumpent, with fringe. *Wall* to 150  $\mu$ m thick.

*Asci* 60–80  $\times$  10–15  $\mu$ m. *Ascospores* 8 per ascus, 14–17  $\times$  4.0–6.5  $\mu$ m, with slightly larger upper locule, with rounded ends, verruculose.

*Pycnidia* absent.



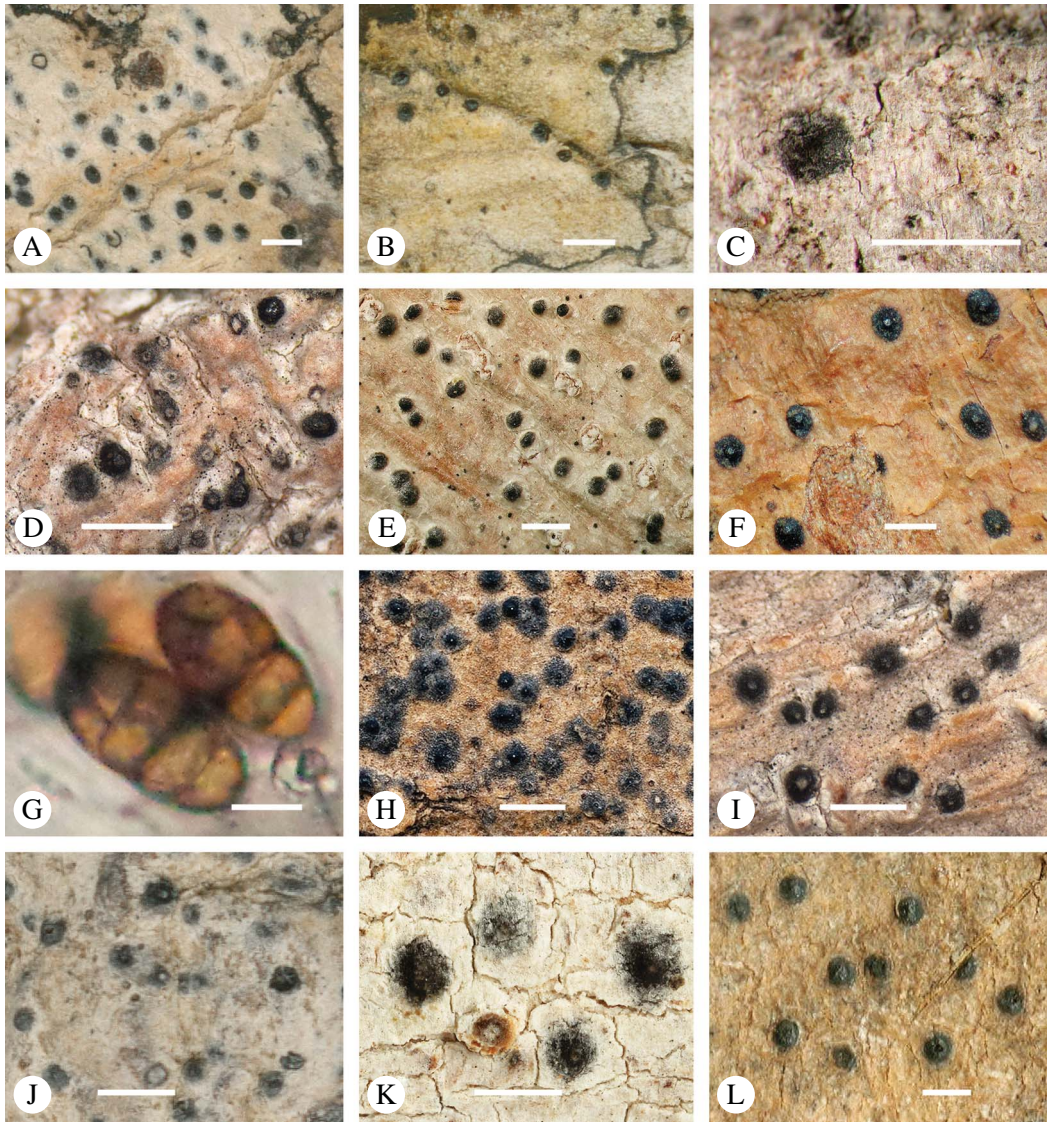


FIG. 43. Habitus and ascospores of *Bogoriella* species. A, *B. miculiformis* (Cuba, holotype); B, *B. conothelena* (India, lectotype); C, *B. thelena* (Brazil, Cáceres & Aptroot 11903); D, *B. captiosa* (Argentina, Moncada s. n.); E, *B. modesta* (Costa Rica, Lücking 15253); F & G, *B. decipiens* (Indonesia, holotype of *Bogoriella subpersicina*); H, *B. confluens* (South Africa, holotype); I, *B. hemisphaerica* (Argentina, Michlig 544); J, *B. apposita* (Colombia, holotype); K, *B. megaspora* (Brazil, Cáceres & Aptroot 11920); L, *B. queenlandica* (Australia, lectotype). Scales: A–F, H–L = 1 mm; G = 10 µm.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from Indonesia).

***Bogoriella annonacea* (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816763



*Microthelia ammonacea* Müll. Arg., *Hedwigia* **34**: 145 (1895).—*Mycomicrothelia ammonacea* (Müll. Arg.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* **14**: 67 (1986) [‘1985’]; type: Venezuela, Caracas, *Ernst* s. n. (G!—holotype).

*Thallus* indistinct.

*Ascomata* with apical ostioles, solitary, 0.4–0.5 mm diam. and 0.10–0.17 mm high, erumpent, with 50–100 µm wide fringe, only ostiole exposed. *Wall* 30–50 µm thick. *Ascospores* (15.5–)17.0–19.0(–23.0) × 5–7 µm, with equal locules, with rounded ends, verruculose, olivaceous brown.

*Pycnidia* absent.

*Chemistry.* Thallus and *ascomata* UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Venezuela, Ecuador and Costa Rica) and also from Hawai’i.

***Bogoriella apposita* (Nyl.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816764

*Verrucaria apposita* Nyl., *Ann. Sci. Nat. Bot., sér. 4* **20**: 254 (1863).—*Arthopyrenia apposita* (Nyl.) H. Oliv., *Exp. Lich. Ouest Fr.* **2**: 258 (1902).—*Microthelia apposita* (Nyl.) Boistel, *Nouv. Fl. Lich.* **2**: 288 (1903).—*Mycomicrothelia apposita* (Nyl.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* **14**: 68 (1986) [‘1985’]; type: Colombia, Choachi, *Lindig* 815 (H-Nyl 702!—holotype).

(Fig. 43J)

*Thallus* whitish, without prothallus lines.

*Ascomata* with apical ostioles, solitary, c. 0.4 mm diam. and 0.15–0.20 mm high, erumpent. *Wall* 40–80 µm thick. *Asci* 90–120 × 14–16 µm. *Ascospores* (22.0–)24.0–28.0(–29.5) × (8.5–)9.0–11.5(–12.5) µm, with larger upper locule, with attenuated ends, verruculose, reddish brown.

*Pycnidia* absent.

*Chemistry.* Thallus and *ascomata* UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Colombia).

*Discussion.* *Bogoriella apposita*, *B. obovata* and *B. thelena* are very similar and possibly conspecific. In that case the earliest name would be *B. thelena*.

***Bogoriella captiosa* (Kremp.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816765

*Verrucaria captiosa* Kremp., *Flora* **59**: 524 (1876).—*Microthelia captiosa* (Kremp.) Müll. Arg., *Bot. Jahrb. Syst.* **6**: 416 (1885).—*Mycomicrothelia captiosa* (Kremp.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* **14**: 73 (1986) [‘1985’]; type: Brazil, Rio de Janeiro, *Glaziou* 5057a (M—lectotype, Hawksworth, *Bull. Br. Mus. Nat. Hist. (Bot.)* **14**: 73 (1986) [‘1985’], not seen).

*Microthelia flavicans* Müll. Arg., *Bull. Soc. Roy. Bot. Belgique* **32**: 170 (1894); type: Costa Rica, *Tonduz* s. n. (G—holotype, not seen; *Pittier, Pl. Costaric. Exs.* 6307).

(Fig. 43D)

*Thallus* whitish rose, with black prothallus lines.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam. and 0.15–0.25 mm high, erumpent, conical, without distinct fringe. *Wall* 50–65 µm thick. *Asci* (55–)65–73 × (12–)13–14 µm. *Ascospores* (13.5–)17.0–19.0(–21.0) × (5.5–)6.5–7.5(–8.5) µm, with equal locules or larger upper locule, with rounded (–attenuate) ends, verruculose, olivaceous brown.

*Pycnidia* absent.

*Chemistry.* Thallus and *ascomata* UV–, K–. TLC: no substances detected.

*Distribution.* Possibly pantropical (reported from Brazil, Costa Rica, Colombia, Guyana and Hawai’i).

***Bogoriella collospora* (Vain.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816766

*Pyrenula collospora* Vain., *Bot. Mag. Tokyo* **32**: 162 (1918).—*Mycomicrothelia collospora* (Vain.) Aptroot, in Kashiwadani *et al.*, *Biblioth. Lichenol.* **99**: 249 (2009); type: Japan, Honshu, *Tsunoda* s. n. (TUR-Vain 31241!—holotype; TNS!—isotype).

(Fig. 42B)

*Thallus* dark olive-brown, nearly absent.

*Ascomata* with lateral, fused ostioles, 2–10 together in dense groups, exposed and black. *Ascospores* 8 per ascus, brown, ellipsoid to clavate with rounded ends, granularly ornamented, 3-septate,  $34\text{--}38 \times 11\text{--}13 \mu\text{m}$ , wall not thickened but surrounded by a hyaline gelatinous sheath.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern temperate (reported from Japan).

***Bogoriella confluens* (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816767

*Microthelia confluens* Müll. Arg., *Flora* 68: 333 (1885).—*Verrucaria confluens* (Müll. Arg.) Stizenb., *Ber. Tät. St. Gall. Naturw. Ges.* 1889–1890: 217 (1891), non (Weber) Hoffm. (1790).—*Mycomicrothelia confluens* (Müll. Arg.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 75 (1986) [‘1985’]; type: South Africa, Cape of Good Hope, s. col. (G!—holotype).

(Fig. 43H)

*Thallus* indistinct.

*Ascomata* in groups of 2–8 with common fringe, 0.8–1.0 mm diam. and 0.12–0.17 mm high, with 200–400  $\mu\text{m}$  wide fringe. *Wall* 60–100  $\mu\text{m}$  thick. *Ascospores* (21–)22–25  $\times$  7.5–9.0(–10.5)  $\mu\text{m}$ , with equal locules or larger upper locule, with rounded ends, verruculose, golden brown.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Costa Rica, South Africa and Fiji Islands).

***Bogoriella conothelena* (Nyl.) Aptroot  
& Lücking comb. nov.**

Mycobank No.: MB 816768

*Verrucaria conothelena* Nyl., *Bull. Soc. Linn. Normandie* 2, 7: 180 (1873).—*Microthelia conothelena* (Nyl.) Zahlbr., *Catal. Lich. Univ.* 1: 258 (1921).—*Mycomicrothelia conothelena* (Nyl.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 81 (1986) [‘1985’]; type: India, Andaman Islands, Kurz 54 (H-Nyl 704!—lectotype, Hawksworth, *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 81 (1986) [‘1985’]).

*Verrucaria conothelena* var. *errans* Nyl., *Bull. Soc. Linn. Normandie* 2, 7: 180 (1873).—*Microthelia conothelena* var. *errans* (Nyl.) Zahlbr., *Catal. Lich. Univ.* 1: 258 (1921); type: India, Andaman Islands, Kurz 78 (H-Nyl 710!—holotype).

(Fig. 43B)

*Thallus* pale brown, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, c. 0.4 mm diam. and 0.20–0.25 mm high. *Wall* 30–50(–70 below)  $\mu\text{m}$  thick. *Asci* 80–100  $\times$  10–20  $\mu\text{m}$ . *Ascospores* 19–23(–27)  $\times$  (7.5–)9.0–11.0(–12.0)  $\mu\text{m}$ , with larger upper locule, with rounded ends, verruculose, golden brown.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (previously reported from India).

*New country record.* **Sri Lanka:** Eastern Province: Ampara, 2013, Weerakoon s. n. (ABL, F).

***Bogoriella decipiens* (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816769

*Anthracotheceum decipiens* Müll. Arg., *Bot. Jahrb. Syst.* 6: 415 (1885).—*Mycomicrothelia decipiens* (Müll. Arg.) R. C. Harris, *Mem. New York. Bot. Gard.* 49: 78 (1989); type: Cuba, Wright 130 (G!—holotype).

*Bogoriella subpersicina* Zahlbr., *Ann. Cryptog. Exotique* 1928(1): 111 (1928); type: Indonesia, Java, Bogor, van Overeem 45 (W!—holotype).

*Ornatopyrenis muriformis* Aptroot in Aptroot et al., *Biblioth. Lichenol.* 64: 123 (1997); type: Papua New Guinea, Madang Prov., Gogol Valley, c. 30 km W of Madang, Tgubi logging site, Sipman 35978 (B!—holotype).

(Fig. 43F &amp; G)

*Thallus* pale brownish to whitish, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, 0.7–0.9 mm diam. and *c.* 0.2 mm high, with wide fringe. *Asci c.* 100 × 28 µm. *Ascospores* 4–8 × (1–)2–4 loculate, 25–35 × 12–15 µm, with rounded ends, smooth, grey.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (previously reported from Cuba, Guyana, Philippines, Indonesia and Papua New Guinea).

*New country record. Mexico:* Yucatán: Chichén Itzá, 1993, Hensen s. n. (ABL).

***Bogoriella exigua* (Müll. Arg.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816770

*Microthelia exigua* Müll. Arg., *Bot. Jahrb. Syst.* 6: 416 (1885).—*Verrucaria microthelena* Nyl., *Flora* 59: 364 (1876), nom. inval.—*Mycomicrothelia exigua* (Müll. Arg.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 84 (1986) [‘1985’]; type: Cuba, Müller, *Verr. Cub.* 14 (G—holotype, not seen).

*Microthelia intermedia* Müll. Arg., *Bot. Jahrb. Syst.* 6: 416 (1885); type: Cuba, Wright s. n. (G—holotype, not seen).

(Fig. 42I)

*Thallus* pale creamy brown, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, 0.20–0.25 mm diam. and 0.08–0.11 mm high, without fringe. *Wall* 25–45 µm thick. *Asci* 42–60 × 8.5–12.0 µm. *Ascospores* 12.5–14.0(–15.5) × 4.0–5.5 µm, with equal locules or larger upper locule, with rounded ends, weakly constricted, weakly verruculose, pale olivaceous brown.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Cuba, Papua New Guinea and Australia).

***Bogoriella fumosula* (Zahlbr.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816771

*Microthelia fumosula* Zahlbr., in Handel-Mazzetti, *Symbol. Sin.* 3: 18 (1930).—*Mycomicrothelia fumosula* (Zahlbr.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 85 (1986) [‘1985’]; type: China, Kweishou, Dodjje, *Handel-Mazzetti* 10728 (W—holotype, not seen; S-L1444!—isotype).

(Fig. 42H)

*Thallus* whitish, with distinct border lines.

*Ascomata* with apical ostioles, solitary, with purplish basal fringe, 0.2–0.3 mm diam. and 0.07–0.11 mm high. *Wall* 25–40 µm thick. *Asci* 55–65 × 10–14 µm. *Paraphyses c.* 2.5 µm thick. *Ascospores* (11–)12–15(–17) × (5.0–)5.5–6.5(–7.5) µm, with larger upper locule, with rounded to weakly attenuated ends, verruculose, pale brown to golden brown.

*Pycnidia* usually present. *Conidia* unknown.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Ecuador, Guyana, China, Japan and Australia).

***Bogoriella hemisphaerica* (Müll. Arg.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816772

*Microthelia hemisphaerica* Müll. Arg., *Bot. Jahrb. Syst.* 6: 47 (1885).—*Mycomicrothelia hemisphaerica* (Müll. Arg.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 86 (1986) [‘1985’]; type: Cuba, Wright s. n. (G—lectotype, Hawksworth, *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 86 (1986) [‘1985’], not seen; Müller, *Verr. Cub.* 66).

*Microthelia intercedens* Müll. Arg., *Bull. Soc. Roy. Bot. Belgique* 32: 171 (1894); type: Costa Rica, Boruca, Tonduz s. n. (G—lectotype; BR—isolectotype, Hawksworth, *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 86 (1986) [‘1985’], not seen; Pittier, *Pl. Costaric. Exs.* 6304).

*Didymosphaeria philippina* Vain., *Ann. Acad. Sci. Fenn., ser. A* 15(6): 348 (1921); type: Philippines, Luzon, Nueva Vizcaya, Dupax, McGregor, Bureau of Science 14308 (TUR-Vain 32528!—holotype).

(Fig. 43I)

*Thallus* whitish, without prothallus lines.



*Ascomata* with apical ostioles, solitary, 0.4–0.5 mm diam. and 0.15–0.18 mm high, without distinct fringe. *Wall* 35–60 µm thick. *Asci* 75–90 × 12–18 µm. *Ascospores* (21–)24–28(–30) × 5–9(–11) µm, with equal locules or slightly larger upper locule, with rounded ends, verruculose, sometimes with 2 pseudosepta, olivaceous brown.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (previously USA, Cuba, Costa Rica, Colombia, Guyana, Ecuador, Brazil, Philippines and Hawai'i).

*New country record. Malaysia:* Sarawak: Gunung Mulu, Coppins 5127 (E, ABL).

***Bogoriella lateralis* (Sipman) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816773

*Mycromicrothelia lateralis* Sipman, in Sipman & Aptroot, *Lichenologist* 37: 309 (2005); type: Norfolk Island, Mt Pitt Reserve, track from Red Road to Mt Bates, Streimann 34411 (B!—holotype).

(Fig. 42E)

*Thallus* whitish, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, usually oval, without fringe, 0.4–0.5 mm diam. and c. 0.15 mm high, with lateral ostiole. *Asci* c. 130 × 10 µm. *Ascospores* 18–22 × 6–7 µm, with equal locules or slightly larger upper locule, with rounded ends, verruculose, grey.

*Pycnidia* near the border lines, c. 0.3 mm wide. *Conidia* bacilliform, simple, hyaline, c. 3.0 × 0.5 µm.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from Norfolk Island).

***Bogoriella leuckertii* (D. Hawksw. & J. C. David) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816774

*Mycromicrothelia leuckertii* D. Hawksw. & J. C. David, *Biblioth. Lichenol.* 57: 98 (1995); type: Mauritius, Plaines Wilhelms, Vacoas, Hawksworth (IMI 400619!—holotype).

*Thallus* pinkish white, becoming whitish grey, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, with fringe, c. 0.5–0.7 mm diam. and 0.1–0.2 mm high; *exciple* K+ crimson red, colour dissolving. *Asci* 45–80 × 11–14(–16) µm. *Ascospores* 17–22 × (6.0–)7.0–10.5 µm, with upper locule about twice as large as lower locule, with rounded ends, minutely punctate-verruculose, olivaceous brown to red-brown.

*Pycnidia* mainly near the border lines, c. 50 µm wide. *Conidia* bacilliform, simple, hyaline, 2.5–3.5 × 1.0–1.5 µm.

*Chemistry.* Thallus UV–, K–; excipulum K+ crimson red, with anthraquinone.

*Distribution.* Possibly pantropical (reported from Costa Rica and Mauritius).

***Bogoriella macrocarpa* (Komposch, Aptroot & Hafellner) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816775

*Mycromicrothelia macrocarpa* Komposch *et al.*, *Lichenologist* 34: 226 (2002); type: Venezuela, Estado Amazonas, Alto Orinoco c. 15 km W of La Esmeralda, plot of tower crane on the W riverbank of Surumoni, Hafellner & Komposch 3095 (GZU!—isotype).

*Thallus* creamy white, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, with wide fringe, c. 0.7–1.1 mm diam. and 0.3–0.4 mm high. *Hamathecium* with oil droplets, these mainly restricted to the centre and margins. *Asci* c. 140–190 × 20–24 µm. *Ascospores* c. 30–45 × 10–15 µm, with slightly larger upper locule, with rounded ends, verruculose, olivaceous brown.

*Pycnidia* 75–125 µm wide; *conidia* bacilliform with submedian enlargement, simple, hyaline, c. 15–21(–26) × 0.4 µm, at enlargement c. 0.8 µm.

*Chemistry.* Thallus UV+ yellow, K–, with lichexanthone.

*Distribution.* Neotropical (reported from Venezuela).

**Bogoriella megaspora (Aptroot & M. Cáceres) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 817004

*Mycomicrothelia megaspora* Aptroot & M. Cáceres, *Lichenologist* 45: 768 (2014); type: Brazil, Rondônia, Estação Ecológica de Cuniã, km 760 on road BR 319 NNE of Porto Velho, 2012, Cáceres & Aptroot 15747 (ISE!—holotype; ABL!—isotype).

(Fig. 43K)

*Thallus* pinkish to whitish grey, smooth to uneven, surrounded by a black prothallus line.

*Ascomata* with apical ostioles, solitary, 0.5–0.9 mm diam., erumpent to prominent, conical, exposed and black. *Hamathecium* clear, hyaline. *Ascospores* 8 per ascus, 1-septate, clavate, often constricted at the septum, 27–40 × 8–12 µm, brown, often surrounded by a gelatinous layer 6–15 µm thick.

*Pycnidia* not observed.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Brazil).

*Discussion.* This species has among the largest 1-septate ascospores of all the species now placed in *Bogoriella*, *Distothelia*, and *Novomicrothelia*. Only two species in *Bogoriella* have 1-septate ascospores that are in the same size class, viz. *B. macrocarpa* and *B. xanthonica* (see above). Both differ by the interspersed hamathecium and the presence of lichexanthone.

**Bogoriella miculiformis (Nyl. ex Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816776

*Microthelia miculiformis* Nyl. ex Müll. Arg., *Bot. Jahrb. Syst.* 6: 417 (1885).—*Verrucaria miculiformis* Nyl., *Flora*

59: 364 (1876) nom. inval.—*Mycomicrothelia miculiformis* (Nyl. ex Müll. Arg.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 99 (1986) [‘1985’]; type: Cuba, Wright s. n. (H-Nyl 678!—holotype; BM!—isotype; Müller, *Verr. Cub.* 68).

*Microthelia miculiformis* var. *detincta* Müll. Arg., *Bot. Jahrb. Syst.* 6: 417 (1885).—*Verrucaria miculiformis* var. *detincta* Nyl., *Flora* 59: 364 (1876) nom. inval.—*Verrucaria miculiformis* var. *detincta* Nyl. ex Hue, *Nouv. Arch. Mus. Paris* 3, 4: 126 (1892) nom. inval.—*Didymosphaeria detincta* (Müll. Arg.) Vain., *Ann. Acad. Sci. Femm., ser. A* 6(7): 211 (1915); type: Cuba, Wright s. n. (H-Nyl 683!—holotype; BM!—isotype; Müller, *Verr. Cub.* 87).

*Didymosphaeria coccifera* Vain., *Ann. Acad. Sci. Femm., ser. A* 15(6): 349 (1921); type: Philippines, Luzon, Laguna, Banajao, Robinson, Bureau of Science 9828 (TUR-Vain 32526!—holotype).

(Fig. 43A)

*Thallus* whitish to pale brown, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, with fringe, 0.4–0.5 mm diam. and (0.08–)0.10–0.1 mm high. *Wall* 35–45 µm thick. *Asci* 65–80 × 12–15 µm. *Ascospores* 14.5–17.5 (–19.0) × 6.0–7.5 µm, with upper locule about twice as large as lower locule, with rounded ends, verruculose, brown.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Cuba, Costa Rica, Brazil, Philippines and Papua New Guinea).

**Bogoriella minutula (Zahlbr.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816777

*Microthelia minutula* Zahlbr., in Handel-Mazzetti, *Symbol. Sin.* 3: 18 (1930).—*Mycomicrothelia minutula* (Zahlbr.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 102 (1986) [‘1985’]; type: China, Yunnan, Loping, Handel-Mazzetti 10428 (W—holotype, not seen).

(Fig. 42J)

*Thallus* indistinct, without prothallus lines.

*Ascomata* with apical ostioles, solitary, c. 0.3 mm diam. and 0.06–0.11 mm high. *Wall* 14–35 µm thick. *Paraphyses* 1.0–1.5 µm thick. *Asci* 55–65 × 12–14 µm. *Ascospores* (12.5–)

13.5–15.0(–16.0) × (5.5–)6.0–6.5(–7.0) μm, with larger upper locule, with rounded ends, verruculose, olivaceous brown.

*Pycnidia* absent.

**Chemistry.** Thallus and ascomata UV–, K–. TLC: no substances detected.

**Distribution.** Eastern palaeotropical (reported from China).

**Bogoriella modesta (Müll. Arg.)  
Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816778

*Microthelia modesta* Müll. Arg., *Bull. Herb. Boissier* 2: 93 (1894).—*Mycomicrothelia modesta* (Müll. Arg.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 104 (1986) [‘1985’]; type: Mexico, Jalisco, *Eckfeldt* 182 (G—holotype, not seen).

(Fig. 43E)

**Thallus** olivaceous, without prothallus lines.

**Ascomata** with apical ostioles, solitary, 0.2–0.4 mm diam. and 0.07–0.09(–0.10) mm high. **Wall** 20–35 μm thick. **Asci** 63–67 × 17–20 μm. **Ascospores** (17.5–)19.0–22.0(–23.0) × (8.0–)8.5–10.0(–10.5) μm, with equal locules or slightly larger upper locule, with rounded ends, verruculose, olive brown.

*Pycnidia* absent.

**Chemistry.** Thallus and ascomata UV–, K–. TLC: no substances detected.

**Distribution.** Pantropical (reported from Mexico, Costa Rica, South Korea and Japan).

**Discussion.** Part of the material identified as *Bogoriella modesta* from Costa Rica has consistently 4-spored asci. It remains to be seen whether this material represents a species.

**Bogoriella nonensis (Stirt.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816779

*Verrucaria nonensis* Stirt., *Proc. Phil. Soc. Glasgow* 11: 320 (1879).—*Microthelia nonensis* (Stirt.) Zahlbr., *Catal.*

*Lich. Univ.* 1: 264 (1921).—*Mycomicrothelia nonensis* (Stirt.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 105 (1986) [‘1985’]; type: India, Kerala, Nilghiri Hills, *Watt* (BM!—isotype).

(Fig. 42K)

**Thallus** whitish, without prothallus lines.

**Ascomata** with apical ostioles, solitary, 0.3–0.4 mm diam. and 0.12–0.15 mm high. **Wall** 30–40 μm thick. **Asci** 50–60 × 8–15 μm. **Ascospores** (14–)16–18 × (6.0–)6.5–7.5 μm, with equal locules or somewhat larger upper locule, with rounded ends, smooth to verruculose, olivaceous brown.

*Pycnidia* absent.

**Chemistry.** Thallus and ascomata UV–, K–. TLC: no substances detected.

**Distribution.** Pantropical (reported from Ecuador and India).

**Bogoriella obovata (Stirt.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816780

*Verrucaria obovata* Stirt., *Trans. Proc. Roy. Soc. Victoria* 17: 74 (1881).—*Pyrenula obovata* (Stirt.) Shirley, *Lich. Fl. Queensland* 4: 176 (1890).—*Microthelia obovata* (Stirt.) Müll. Arg., *Rep. Australas. Soc. Advancem. Sci.* 6: 454 (1895).—*Mycomicrothelia obovata* (Stirt.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 106 (1986) [‘1985’]; type: Australia, Queensland, Brisbane, *Bailey* 125 (BM!—holotype).

*Microthelia alba* Müll. Arg., *Rep. Australas. Soc. Advancem. Sci.* 6: 455 (1895); type: Australia, Queensland, Brisbane, *Knight* s. n. (G!—holotype).

*Microthelia brisbanensis* Müll. Arg., *Rep. Australas. Soc. Advancem. Sci.* 6: 455 (1895); type: Australia, Queensland, Brisbane, *Bailey* s. n. (G!—holotype).

*Didymosphaeria tetraspora* Masee, *Kew Bull.* 1907: 124 (1907); type: Malaysia, Sarawak, *Ridley* s. n. (K!—holotype).

*Didymosphaeria thelenoides* Vain., *Ann. Acad. Sci. Fenn. ser. A* 6(7): 211 (1915); type: Dominica, Mt. Conliabon, *Elliot* 1533 (TUR-Vain 32530!—lectotype, Aptroot, *Nova Hedwigia* 60: 352, 1995).

**Thallus** pinkish white, border lines.

**Ascomata** with apical ostioles, solitary, 0.5–0.6 mm diam. and 0.2–0.3 mm high. **Wall** 45–60 μm thick. **Asci** (65–)75–90 × 20–30 μm. **Ascospores** (21–)22–28(–30) × (8.5–)



9.0–11.0(–12.0)  $\mu\text{m}$ , with slightly larger upper locule, with rounded ends, often with 2 pseudosepta and seemingly 3-septate, verruculose, brown.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from Borneo, Philippines, Papua New Guinea and Australia).

**Bogoriella pachythea (Sacc. & Syd.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816781

*Didymosphaeria pachythea* Sacc. & Syd. in Sydow & Sydow, *Bull. Herb. Boissier* 8: 79 (1900).—*Mycomicrothelia pachythea* (Sacc. & Syd.) Aptroot, *Nova Hedwigia* 60: 352 (1995); type: Brazil, Isla S. Francisco, Ule 403 (S!—holotype).

*Thallus* indistinct.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., conical. *Ascospores* 21–22  $\times$  8  $\mu\text{m}$ , with rounded upper and attenuated lower ends, verruculose.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Brazil).

**Bogoriella punctata (Aptroot) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816782

*Mycomicrothelia punctata* Aptroot, *Biblioth. Lichenol.* 44: 134 (1991); type: Papua New Guinea, Morobe Prov., Huon Peninsula, Honzeukngon Village S of Derim in Timbe Valley, Aptroot 17994 (ABL!—holotype).

(Fig. 42F)

*Thallus* brownish, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary or in groups of 1(–3), with fringe, 0.4–0.7 mm

diam. and 0.1–0.3 mm high, completely exposed. *Wall* to 100  $\mu\text{m}$  thick. *Asci* 80–90  $\times$  10–15  $\mu\text{m}$ . *Ascospores* (12–)15–18 (–21)  $\times$  (6–)7–8  $\mu\text{m}$ , with larger, rounded upper locule, and much smaller, often attenuated lower locule, smooth.

*Pycnidia* mainly near the border lines, c. 0.1 mm wide; *conidia* not known.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical, mostly at c. 2000–3000 m (previously reported from Costa Rica, Philippines and Papua New Guinea).

*New country records.* **Ecuador.** *Azuay:* Road Cuenca-Girón, 1977, *Andersson et al.* s. n. (UPS, ABL).—**Malaysia:** *Sarawak:* Borneo, Sandakan, *Elmer* 20019 (L, ABL).—**Fiji:** Vanua Levi, 1970, *Degelius* s. n. (UPS).

**Bogoriella queenslandica (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816783

*Microthelia queenslandica* Müll. Arg., *Rep. Australas. Assoc. Advancem. Sci.* 6: 455 (1895).—*Ornatopyrenis queenslandica* (Müll. Arg.) Aptroot, *Biblioth. Lichenol.* 44: 128 (1991).—*Mycomicrothelia queenslandica* (Müll. Arg.) Sipman & Aptroot, *Lichenologist* 37: 309 (2005); type: Australia, Queensland, *Knight* 71 (G!—lectotype, Hawksworth, *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 161 (1986) [‘1985’]).

(Fig. 43L)

*Thallus* whitish, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, 0.8–1.1 mm diam. and c. 0.2–0.3 mm high. *Asci* 110–130  $\times$  30  $\mu\text{m}$ . *Ascospores* 35–45  $\times$  13–15  $\mu\text{m}$ , with equal locules or slightly larger upper locule, with rounded ends, often with 2 pseudosepta and seemingly 3-septate, verruculose, grey.

*Pycnidia* between the ascomata and near the border lines. *Conidia* not seen.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Costa Rica, Colombia, Indonesia, Papua New Guinea and Australia).

**Bogoriella socialis (Zahlbr.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816784

*Microthelia socialis* Zahlbr., *Mycologia* 22: 69 (1930).—*Mycomicrothelia socialis* (Zahlbr.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 110 (1986) [‘1985’]; type: Puerto Rico, Yauco, *Fink* 1459a (W 1925/9360—holotype, not seen).

(Fig. 42G)

*Thallus* whitish grey (to pale pink), without prothallus lines.

*Ascomata* in groups of (1–)2–6, with wide fringe to 100 µm, *c.* 0.15–0.20 mm diam. (groups to *c.* 1 mm diam.) and 0.08–0.12 mm high, only ostiole exposed. *Wall* 10–15(–29) µm thick. *Asci* 45–60 × 15–24 µm. *Ascospores* 15–20 × 6–9 µm, with equal locules, with rounded or somewhat attenuated ends, delicately verruculose, brown.

*Pycnidia* between the ascomata, 50–75 µm wide; *conidia* bacilliform, simple, hyaline, 12–15 × 0.5–1.0(–1.5) µm.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (previously reported from Puerto Rico and Ecuador).

*New country record. USA:* material previously reported as *Mycomicrothelia willeyana* (Lücking *et al.* 2011).

**Bogoriella striguloides (Sérus. & Aptroot) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816785

*Mycomicrothelia striguloides* Sérus. & Aptroot, *Bryologist* 101: 145 (1998); type: New Zealand, North Island, near Orewa, 30 km N of Auckland, *Bartlett* (ABL!—isotype).

(Fig. 42A)

*Thallus* foliicolous, hypocuticular and lobed.

*Ascomata* in groups of 1–8, 0.1–0.2 mm diam. and 0.1 mm high. *Asci* 40–50

(–55) × 10–12(–15) µm. *Ascospores* *c.* 14 × 4 µm, smooth, dark brown.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from New Zealand).

**Bogoriella subfallens (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816786

*Microthelia subfallens* Müll. Arg., *Bot. Jahrb. Syst.* 6: 416 (1885).—*Verrucaria subfallens* Nyl., *Flora* 59: 364 (1876) nom. inval.—*Mycomicrothelia subfallens* (Müll. Arg.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* 14: 111 (1986) [‘1985’]; type: Cuba, *Wright* s. n. (G—holotype, not seen; Müller, *Verr. Cub.* 5).

*Didymosphaeria baccharidis* Starbäck, *Bih. K. Svenska Vetensk.-Akad. Handl.* 25, 3(1): 59 (1879) [as ‘*bacharidis*’]; type: Brazil, Rio Grande do Sul, Santo Angelo near Cachoeira, *Regnell* 257 [‘251’ in publication] (S—holotype).

*Didymosphaeria coccifera* var. *cineaeonubricosa* Vain., *Ann. Acad. Sci. Fenn., ser. A* 15(6): 349 (1921); type: Philippines, Polillo, *Robinson*, Bureau of Science 9090 (TUR-Vain 32527—holotype).

(Fig. 42L)

*Thallus* whitish to pale pink or brownish and nearly absent, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, with *c.* 50 µm wide fringe, 0.4–0.5 mm diam. and 0.06–0.10 mm high. *Wall* 25–50 µm thick. *Asci* 50–65 × 12–14 µm. *Ascospores* 13.5–16.0 × 6–7 µm, with upper locule almost twice as large as lower locule, with rounded ends, verruculose, golden brown.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (previously reported from Cuba, Costa Rica, Venezuela, Guyana, Ecuador, Brazil, Philippines, Singapore, Taiwan, Papua New Guinea, Australia and Hawai’i). Introduced on *Dracaena* in the Netherlands.

*New country record. Solomon Islands:* *Santa Cristobal Island:* 1965, *Hill* 8936 (BM).

**Bogoriella thelena (Ach.) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816787

*Verrucaria thelena* Ach., *Syn. Lich.*: 92 (1814).—*Microthelia thelena* (Ach.) Trev., *Consp. Verruc.*: 10 (1860).—*Mycomicrothelia thelena* (Ach.) D. Hawksw., *Bull. Br. Mus. Nat. Hist. (Bot.)* **14**: 112 (1986) [‘1985’]; type: South America, s. col. (H-ACH 692B!—holotype).

*Microthelia albidella* Müll. Arg., *Flora* **66**: 272 (1883); type: Brazil, Apiaty, Puggari 349 (G—holotype, not seen).

*Microthelia thelena* var. *subtriseptata* Vain., *Acta Soc. Fauna Fl. Fenn.* **7**(2): 232 (1890); type: Brazil, Caraca, Vainio s. n. (BM!—isotype; Vainio, *Lich. Brasil.* 715).

*Microthelia leucothallina* Vain., *Ann. Acad. Sci. Fenn., ser. A* **6**(7): 210 (1915); type: Danish West Indies, Boergesen s. n. (TUR-Vain 32469—holotype, not seen).

*Didymosphaeria palaquii* Vain., *Ann. Acad. Sci. Fenn., ser. A* **15**(6): 348 (1921); type: Philippines, Mindanao, Zamboanga, Merrill 5006 (TUR-Vain 32529!—holotype).

(Fig. 43C)

*Thallus* creamy or whitish or indistinct, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, with or without fringe, c. 0.5 mm diam. and 0.10–0.25 mm high. *Wall* 30–70 µm thick. *Asci* 80–90(–100) × (23–)26–31 µm. *Ascospores* (17.5–)21.0–24.0(–26.0) × (7.5–)9.0–11.5(–13.0) µm, with larger upper locule, with rounded ends, verruculose, deep golden brown.

*Pycnidia* absent.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Costa Rica, West Indies, Colombia, Ecuador, Brazil, Philippines and Hawai’i).

**Bogoriella triangularis (Aptroot) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816788

*Mycomicrothelia triangularis* Aptroot in Sipman & Aptroot, *Lichenologist* **37**: 309 (2005); type: Puerto Rico, Mayagüez, Reserva Forestal Maricao, N of Sabana Grande, along road 120, km 16–17, *Aptroot & Aptroot* 24949 (B!—holotype).

(Fig. 42D)

*Thallus* whitish, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, usually oval to triangular, with conspicuous fringe, 0.4–0.5 mm diam. and c. 0.2 mm high, with lateral ostiole. *Asci* c. 120 × 15 µm. *Ascospores* 25–37 × 7–10 µm, with equal locules or slightly larger upper locule, with rounded ends, roughly verruculose with warts sometimes in lines, brown.

*Pycnidia* near the border lines, c. 0.1 mm wide; *conidia* not observed.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Puerto Rico).

**Bogoriella xanthonica (Komposch, Aptroot & Hafellner) Aptroot & Lücking comb. nov.**

MycoBank No.: MB 816789

*Mycomicrothelia xanthonica* Komposch *et al.*, *Lichenologist* **34**: 224 (2002); type: Venezuela, Estado Amazonas, Alto Orinoco c. 15 km WSW of La Esmeralda, plot of tower crane on the W riverbank of Surumoni, *Hafellner & Komposch* 3399 (GZU!—isotype).

*Thallus* whitish to creamy, with dark prothallus lines.

*Ascomata* with apical ostioles, solitary, with wide fringe, c. 0.5–0.7(–0.8) mm diam. and 0.15–0.20 mm high. *Hamathecium* with oil droplets, these often restricted to less fertile parts. *Asci* c. 130–160 × 20–30 µm. *Ascospores* c. 30–40 × 10–14 µm, with slightly larger upper locule, with rounded ends, verruculose, olivaceous brown.

*Pycnidia* 75–125 µm wide; *conidia* bacilliform with submedian enlargement, simple, hyaline, c. 12–15 × 0.4 µm, at enlargement 0.8 µm wide.

*Chemistry.* Thallus UV+ (sometimes weakly), K–. TLC: lichexanthone.

*Distribution.* Neotropical (reported from Venezuela).



**Constrictolumina Lücking *et al.***

In Lücking *et al.*, *Lichenologist* **48**: 756 (2016); type: *Constrictolumina cinchonae* (Ach.) Lücking, M. P. Nelsen & Aptroot (holotype).

*Thallus* not corticate.

*Ascomata* single, roughly conical, not in pseudostroma, but sometimes fused sideways. *Ostiole* apical. *Hamathecium* hyaline, completely clear, filaments thick at the base, much thinner above, but not anastomosing. *Asci* clavate. *Ascospores* 1–3-septate, rarely submuriform, with irregular endospore formation, sometimes with pseudosepta, often one or two cells pinched in the middle, smooth or ornamented, hyaline, rarely becoming brown, often becoming granular ornamented.

*Pycnidia* sometimes present.

*Discussion.* This group of species has thus far been retained in the genus *Arthopyrenia*, a collective genus from which successively aberrant

groups have been split off. Species details have been given primarily by Harris (1975, 1995), either restricting the group to an even smaller number of species or using a wider concept, including the type of the genus *Arthopyrenia* and all synonym genera, viz. *A. analepta* (Ach.) Massal. The genus *Arthopyrenia* s. str. has now been restricted to a very small core group (Hyde *et al.* 2013). Regarding the species concept, the present treatment is heavily based on Harris's work and should be regarded as preliminary, since many taxa are not well sampled and molecular data are scarce. *Constrictolumina* unites c. 10 essentially tropical members, that is almost all tropical species that had remained in *Arthopyrenia* after the split-off of *Anisomeridium* (Harris 1975). Interestingly, the new genus is partly characterized by the unique hamathecium structure, a character which differs from almost all remaining *Trypetheliaceae*.

**Key to the species of *Constrictolumina***

- |      |  |                                     |
|------|--|-------------------------------------|
| 1    | Ascospores brown, 1-septate to submuriform (Flakus <i>et al.</i> 2016; Fig. 44A) . . . . . | <b>Constrictolumina chiquitana</b>  |
|      | Ascospores hyaline, 1–3-septate . . . . .  | 2                                   |
| 2(1) | Ascospores 2 per ascus (this synopsis; Fig. 44B–E) . . . . .                               | <b>Constrictolumina malaccitula</b> |
|      | Ascospores 4–8 per ascus . . . . .   | 3                                   |
| 3(2) | Ascospores generally over 29 µm long . . . . .   | 4                                   |
|      | Ascospores generally under 29 µm long . . . . .  | 5                                   |
| 4(3) | Ascospores 42–46 × 16–24 µm, 1-septate (this synopsis; Fig. 44F) . . . . .                 | <b>Constrictolumina porospora</b>   |
|      | Ascospores 27–37 × 10–12 µm, 1–3-septate (this synopsis; Fig. 44G–J) . . . . .             | <b>Constrictolumina majuscula</b>   |
| 5(3) | Ascospores 3-septate (this synopsis; Fig. 44K & L) . . . . .                               | <b>Constrictolumina leucostoma</b>  |
|      | Ascospores at least in majority 1-septate . . . . .  | 6                                   |
| 6(5) | Ascospores with granular ornamentation (this synopsis; Fig. 45A–C) . . . . .               | <b>Constrictolumina lyrata</b>      |
|      | Ascospores without ornamentation . . . . .   | 7                                   |
| 7(6) | Ascospores 17–23 × 5–7 µm (this synopsis; Fig. 45D) . . . . .                              | <b>Constrictolumina planorbis</b>   |
|      | Ascospores 20–30 × 7–11 µm . . . . .   | 8                                   |

- 8(7) Ascomata fused sideways to form pseudostromata (this synopsis; Fig. 45E) . . . . . **Constrictolumina esenbeckiana**  
 . . . . . **Constrictolumina esenbeckiana**  
 Ascomata mostly solitary (this synopsis; Fig. 45F–L) . . . . .  
 . . . . . **Constrictolumina cinchonae**

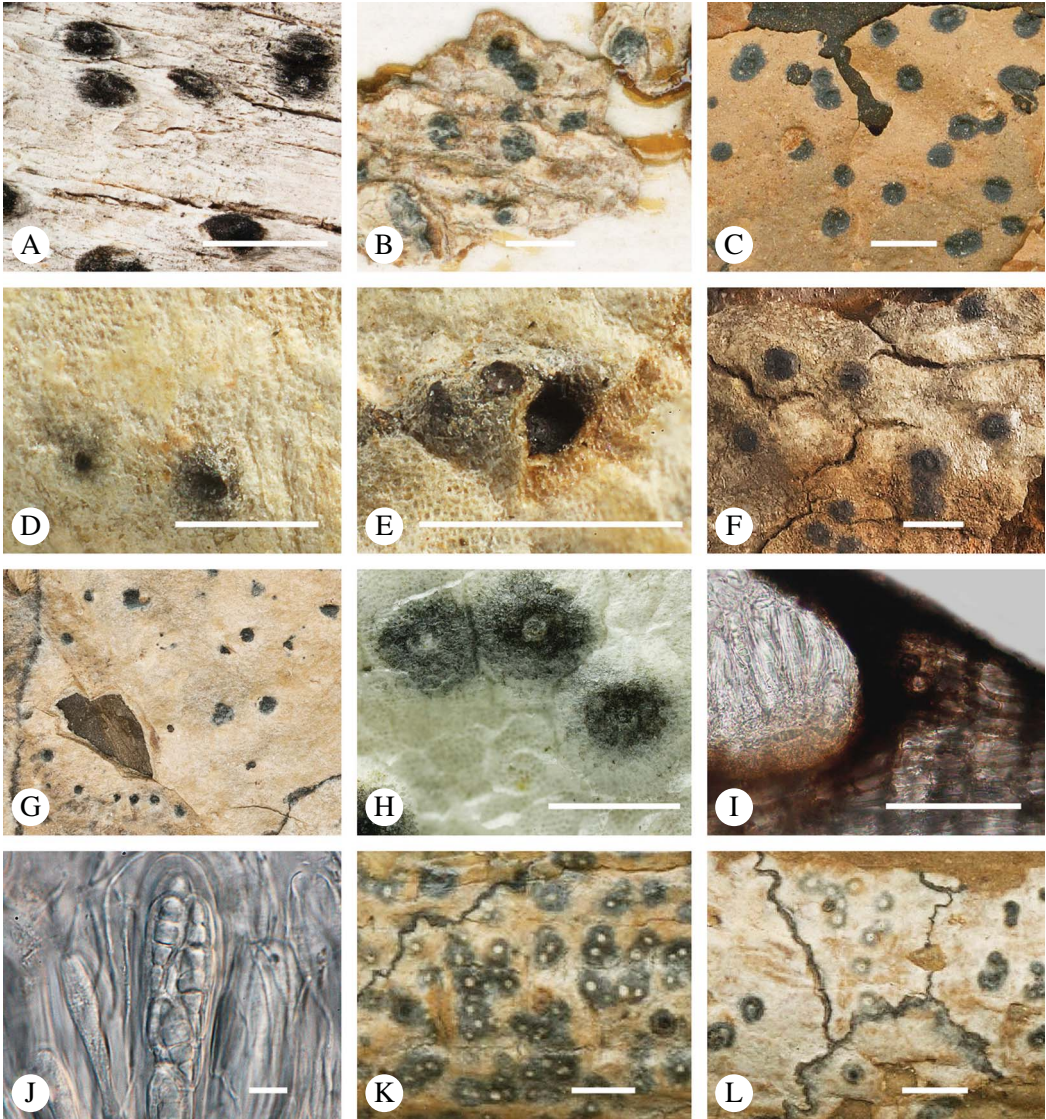


FIG. 44. Habitus of *Constrictolumina* species. A, *C. chiquitana* (Bolivia, holotype); B–E, *C. malaccitula* (B, Singapore, holotype; C, Malaysia, Borneo, lectotype of *Didymella gigantea*; D & E, Papua New Guinea, Aptroot 19093); F, *C. porospora* (Dominica, isotype); G–J, *C. majuscula* (G, Japan, holotype; H–J, Reunion, Schumm & Frahm 15483); K & L, *C. leucostoma* (unknown location, holotype). Scales: A–H, K & L = 1 mm; I = 100 µm; J = 10 µm. (Images D, E, H–J by F. Schumm).



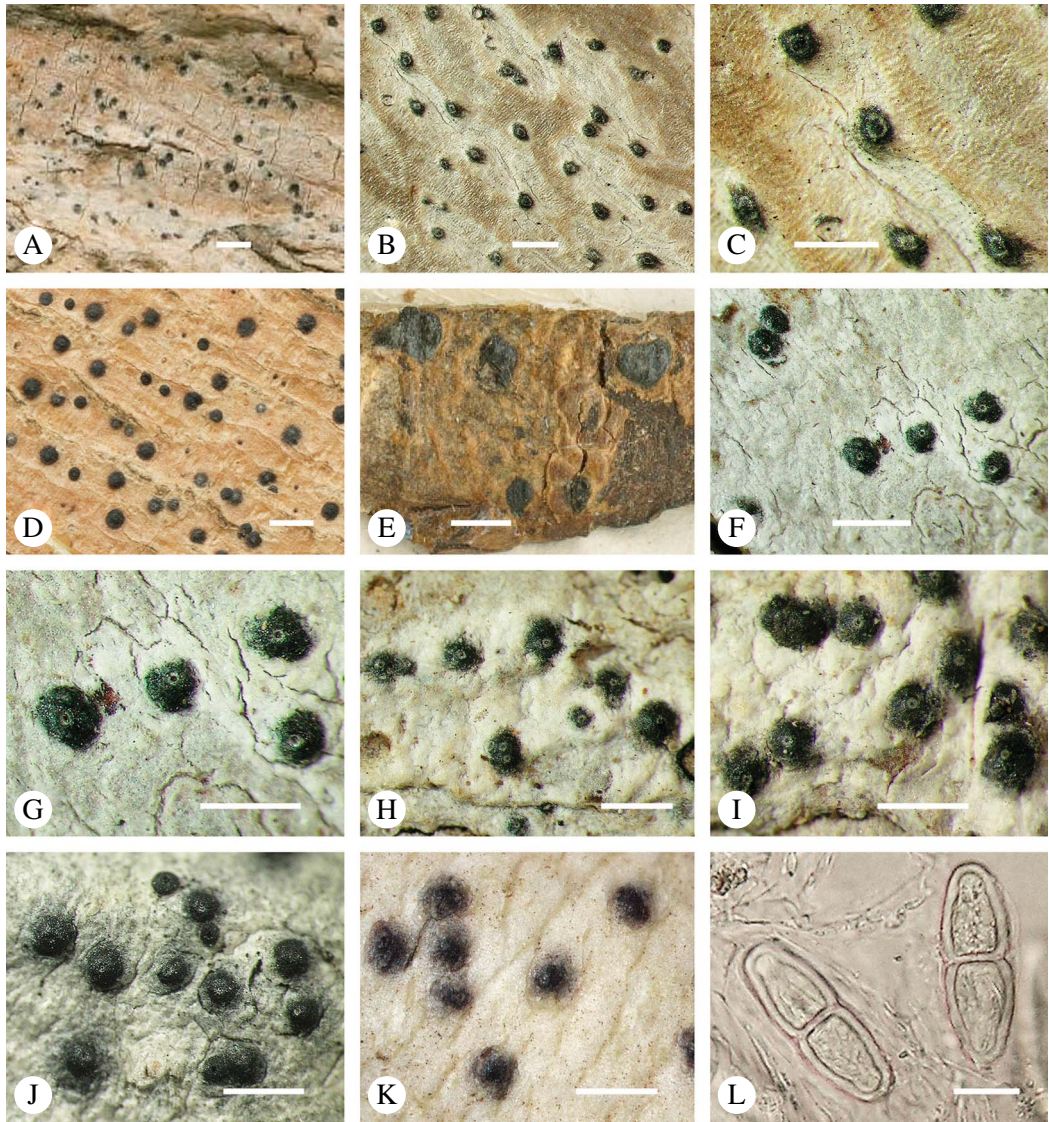


FIG. 45. Habitus and ascospores of *Constrictolumina* species. A–C, *C. lyrata* (A, USA, Florida, holotype; B & C, USA, Costa Rica, Lücking s. n.); D, *C. planorbis* (Cuba, lectotype); E, *C. esenbeckiana* (‘Antilles’, lectotype); F–L, *C. cinchonae* (F & G, Costa Rica, Lücking 45; H & I, Costa Rica, Lücking 44; J, Brazil, Câceres 2106; K, USA, Florida, Lücking 26787; L, Costa Rica, Brenes 188). Scales: A–K = 1 mm; L = 10  $\mu$ m.

***Constrictolumina cinchonae* (Ach.)  
Lücking et al.**

In Lücking et al., *Lichenologist* 48: 756 (2016); *Verrucaria cinchonae* Ach., *Synops. Lich.*: 90 (1814).—*Arthopyrenia cinchonae* (Ach.) Müll. Arg., *Flora* 66: 287 (1883); type: “cort. Cinchonae officinalis” (H-ACH 781B!—holotype).

*Verrucaria prostrans* Mont., *Ann. Sci. Nat. Bot.*, ser. 2 19: 53 (1843); type: French Guiana, Leprieur 215 (BM!—isotype).

*Verrucaria alboatra* var. *detergens* Nyl., *Flora* 52: 125 (1869); type: Brazil, Rio de Janeiro, Glaziou 1915 (H-Nyl 1662!—holotype; M— isotype, not seen).

*Verrucaria concamerata* Stirt., *Proc. Phil. Soc. Glasgow* 13: 192 (1881).—*Porina concamerata* (Stirton) Zahlbr.,



*Cat. Lich. Univ.* 1: 377 (1922); type: India, Assam, *Watt* s. n. (BM!—isotype).

*Arthopyrenia nieteriana* Müll. Arg., *Flora* 66: 288 (1883); type: Sri Lanka, *Nieter* 30 (G!—holotype).

*Arthopyrenia planipes* Müll. Arg., *Flora* 73: 345 (1890); type: Kenya, *Hamington* s. n. (G!—holotype; BM!—isotype).

(Fig. 45F–L)

*Thallus* thin, whitish.

*Ascomata* with apical ostioles, solitary, 0.4–0.6 mm diam., erumpent to prominent, hemispherical to flattened. *Wall* lacking below, often surrounded by a grey ring. *Asci* mostly narrowly obovate, rarely almost cylindrical, (85–)100–125 × 17–22 µm. *Ascospores* 4–8 per ascus, biseriata, narrow-ovate, 1-septate, lower cell occasionally slightly constricted in the middle; perispore well developed, 20–30 × 7–11 µm.

*Pycnidia* often present. *Conidia* rod-like, 4–5 × 1 µm.

*Chemistry.* Thallus and *ascomata* UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from the USA, Mexico, Bermuda, Bahamas, Cuba, Puerto Rico, Dominica, French Guiana, Ecuador, Brazil, Argentina, Kenya, Maldives, India, Sri Lanka, China, Indonesia (Java), Philippines, Papua New Guinea and Japan).

***Constrictolumina esenbeckiana* (Fée)  
Lücking, M. P. Nelsen & Aptroot  
comb. nov.**

MycoBank No.: MB 817006

*Melanotheca esenbeckiana* Fée, *Essai Crypt. Écorc. Suppl.* 71 (1837).—*Tomasellia esenbeckiana* (Fée) Müll. Arg., *Flora* 68: 257 (1883); type: Antilles, “cort. *Exostemmatis*” (G!—lectotype, Harris, *More Florida Lichens*: 81, 1995).

(Fig. 45E)

*Thallus* thin, whitish.

*Ascomata* with apical ostioles, solitary, 0.4–0.6 mm diam., erumpent to prominent, hemispherical to flattened, sideways confluent in

dense groups of 5–20. *Wall* lacking below. *Asci* mostly narrowly obovate, rarely almost cylindrical, c. 100–125 × 17–22 µm. *Ascospores* 4–8 per ascus, biseriata, subbiseriata or almost uniseriate, narrowly ovate, 1-septate, lower cell occasionally slightly constricted in the middle, perispore well developed, 22–27 × 7–10 µm.

*Pycnidia* often present. *Conidia* rod-like, 4–5 × 1 µm.

*Chemistry.* Thallus and *ascomata* UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from the Antilles and Brazil; mostly old reports, but also recently found in Sergipe State in Brazil).

***Constrictolumina leucostoma*  
(Müll. Arg.) Lücking, M. P. Nelsen &  
Aptroot comb. nov.**

MycoBank No.: MB 817010

*Tomasellia leucostoma* Müll. Arg., *Flora* 68: 257 (1883); *Arthopyrenia confluens* R. C. Harris, *More Florida Lichens*: 80 (1995), non *Arthopyrenia leucostoma* (Ach.) A. Massal. (1852); type: “cort. *Crotonis Cascarillae*, ex hb. Hampe”, 1877 (G!—holotype).

(Fig. 44K & L)

*Thallus* thin, whitish.

*Ascomata* with apical ostioles, solitary or grouped, 0.1–0.2 mm in diam., erumpent. *Wall* poorly developed, lacking below; tip of ascocarp surrounded by a broad, thin, black ring, 0.2–0.3 mm in width, often confluent with the rings of other *ascomata* forming groups of 2–10. *Ostioles* often depressed, surrounded by a whitish ring. *Asci* mostly narrowly ovate, rarely almost cylindrical, 60–105 × 16–26 µm. *Ascospores* 8 per ascus, irregularly arranged to biseriata, narrowly ovate to narrowly ellipsoidal, 3-septate, perispore well developed, 17–22 × 6–8 µm.

*Pycnidia* often present. *Conidia* linear, 6–9 × 1 µm.

*Chemistry.* Thallus and *ascomata* UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from the USA, Bahamas and Antilles).

**Constrictolumina lyrata (R. C. Harris)  
Lücking, M. P. Nelsen & Aptroot  
comb. nov.**

Mycobank No.: MB 817011

*Arthopyrenia lyrata* R. C. Harris, in Tucker & Harris, *Bryologist* 83: 6 (1980); type: USA, Florida, Daytona, 1911, Merrill s. n. (MSC!—holotype; BM!, NY!, US!—isotypes; Merrill, *Lich. Exs.* 2: 38).

(Fig. 45A–C)

*Thallus* thin, whitish.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., erumpent to prominent, less commonly immersed, hemispherical. *Wall* usually lacking below. *Asci* narrowly elliptical to elliptical, usually with a distinct ocular chamber, 75–120(–130) × 20–30 µm. *Ascospores* 4–8 per ascus, irregularly arranged to biserial, narrowly elliptical or narrowly ovate, 1-septate, with one or both cells weakly constricted near the middle, rarely becoming 3-septate; wall granular ornamented, perispore well developed, 18–30 × 7–12 µm (excluding perispore).

*Pycnidia* often present. *Conidia* linear, 6–9 × 1 µm.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from the USA, Mexico, Indonesia, Papua New Guinea and Australia).

**Constrictolumina majuscula (Nyl.)  
Lücking, M. P. Nelsen & Aptroot  
comb. nov.**

Mycobank No.: MB 817013

*Verrucaria majuscula* Nyl., *Ann. Sci. Nat. Bot., ser. 4* 20: 253 (1864).—*Arthopyrenia majuscula* (Nyl.) Zahlbr., *Cat. Lich. Univ.* 1: 332. 1922; type: Japan, Ogasawara-shoto (Bonin Islands), Wright s. n. (H-Nyl 824 p.p.!—lectotype: the left-hand specimens with cream/pink thallus, designated here; BM!—isolectotype).

(Fig. 44G–J)

*Thallus* thin, whitish.

*Ascomata* with apical ostioles, solitary, 0.4–0.9 mm diam., erumpent; *hymenium* flattened hemispherical. *Ostioles* surrounded by a broad, thin hyphal ring. *Wall* thin, lacking below. *Asci* narrowly obovate, (80–)105–125 × 25–30 µm. *Ascospores* 4–8 per ascus, irregularly arranged, narrowly elliptical to narrowly ovate, 1-septate, each cell partially subdivided by a flat-topped ring-like thickening of the wall, becoming 3-septate; wall strongly granular ornamented, perispore thick, up to 2 µm, 27–37 × 10–12 µm (excluding perispore).

*Pycnidia* often present. *Conidia* linear, 6–8 × 1 µm.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from the USA, Bahamas, Cuba, Puerto Rico, Chagos, Seychelles, Philippines and Japan).

**Constrictolumina malaccitula (Nyl.)  
Lücking, M. P. Nelsen & Aptroot  
comb. nov.**

Mycobank No.: MB 817014

*Verrucaria malaccitula* Nyl., *J. Linn. Soc., Bot.* 20: 61 (1883).—*Arthopyrenia malaccitula* (Nyl.) Zahlbr., *Cat. Lich. Univ.* 1: 284 (1921); type: Singapore, Malacca, Water Islands, Maingay 191 (H-Nyl 1706!—holotype; BM!—isotype).

*Arthopyrenia bifera* Zahlbr., *Ann. Mycol.* 33: 34 (1935); type: USA, Florida, Seminole County, Sanford, Rapp 80 [published as 86] (BM!—isotype).

*Didymella gigantea* Räsänen, *Arch. Soc. Zool. Bot. Fenn. "Vanamo"* 3: 89 (1949); type: Malaysia, Sarawak, Borneo, Sandakan, Myburgh, *Elmer* 20019, 1921 (H!—lectotype, designated here based on annotation label by R. C. Harris 1986; H!—isolectotype).

(Fig. 44B–E)

*Thallus* thin, whitish.

*Ascomata* with mostly eccentric ostioles, solitary, 0.2–0.4 mm diam., mostly immersed, subglobose to hemispherical. *Wall* thinner or lacking below. *Asci* narrowly elliptical to elliptical, 75–105(–120) × (20–)25–35 µm. *Ascospores* 2 per ascus, narrowly elliptical, 1-septate, with a slightly thickened area of the wall outlining a smaller

subchamber, ultimately becoming 3-septate; wall strongly granular ornamented, perispore well developed,  $37\text{--}48 \times 15\text{--}16 \mu\text{m}$  (excluding perispore).

*Pycnidia* often present. *Conidia* rod-like to linear,  $5\text{--}10 \times 1 \mu\text{m}$ .

*Chemistry.* Thallus and ascomata UV<sup>-</sup>, K<sup>-</sup>. TLC: no substances detected.

*Distribution.* Pantropical (reported from the USA, Singapore, Sarawak and Papua New Guinea).

**Constrictolumina planorbis (Ach.)  
Lücking *et al.***

In Lücking *et al.*, *Lichenologist* **48**: 756 (2016); *Verrucaria planorbis* Ach., *Synops. Lich.*: 92 (1814).—*Arthopyrenia planorbis* (Ach.) Müll. Arg., *Mem. Soc. Phys. Genève* **30**: 27 (1888); type: “cort. Crotonis Cascariillae” (H-ACH—holotype, not seen).

*Arthopyrenia planior* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 404 (1885); type: Cuba, Wright s. n. (G-G00290453!—lectotype, designated here; BM!—isolectotype; Müller, *Lich. Cub.*, Ser. II: 627a).

*Arthopyrenia planorbiculata* Müll. Arg., *Bot. Jahrb. Syst.* **6**: 405 (1885); type: Cuba, Wright s. n. (G-G00290457!, lectotype, designated here; BM!—isolectotype; Müller, *Verr. Cub.* 64).

(Fig. 45D)

*Thallus* thin, whitish.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, flattened to hemispherical. *Wall* usually extended outwards above, forming a broad shield up to 1 mm diam., lacking below. *Asci* narrowly elliptical,  $55\text{--}100 \times 12\text{--}17\text{--}(20) \mu\text{m}$ . *Ascospores* sub-biseriate to biseriate, narrowly ovate, 1-septate, rarely 3-septate; perispore thin,  $17\text{--}23 \times 5\text{--}7 \mu\text{m}$ .

*Pycnidia* often present. *Conidia* filiform, usually curved,  $20\text{--}27 \times 1 \mu\text{m}$ .

*Chemistry.* Thallus and ascomata UV<sup>-</sup>, K<sup>-</sup>. TLC: no substances detected.

*Distribution.* Pantropical (reported from the USA, Bahamas, Cayman Islands, Jamaica, Puerto Rico, Dominican Republic, Cuba, Papua New Guinea and Australia).

**Constrictolumina porospora (Vain.)  
Lücking, M. P. Nelsen & Aptroot  
comb. nov.**

Mycobank No.: MB 817015

*Arthopyrenia porospora* Vain., *J. Bot.* **24**: 296 (1896); type: Dominica, Morne Trois Pitons, 1892, Elliot s. n. (TUR-Vain—holotype, not seen; BM!—isotype).

(Fig. 44F)

*Thallus* thin, whitish.

*Ascomata* with apical ostioles, solitary, 0.8–1.2 mm diam., erumpent to prominent, hemispherical. *Wall* thin, lacking below. *Asci* narrowly obovate. *Ascospores* 8 per ascus, biseriate, narrowly elliptical to narrowly ovate, 1-septate, each cell partially subdivided by a flat-topped ring-like thickening of the wall, becoming 3-septate; wall strongly granular ornamented, perispore thick, up to  $2 \mu\text{m}$ ,  $42\text{--}46 \times 16\text{--}24 \mu\text{m}$  (excluding perispore).

*Chemistry.* Thallus and ascomata UV<sup>-</sup>, K<sup>-</sup>. TLC: no substances detected.

*Distribution.* Neotropical (reported from Dominica).

**Dictyomeridium Aptroot *et al.***

In Lücking *et al.*, *Lichenologist* **48**: 756 (2016); type: *Dictyomeridium propionens* (Nyl.) Aptroot, M. P. Nelsen & Lücking (holotype).

*Thallus* not corticate.

*Ascomata* single or a few aggregate, roughly conical to pyriform, not in pseudostroma. *Ostioles* eccentric. *Hamathecium* hyaline, clear. *Asci* with 2–8 ascospores. *Ascospores* muriform, hyaline, smooth, often IKI+ violet.

*Pycnidia* sometimes present.

*Discussion.* This species aggregate is kept separate here, as a split-off from *Polymeridium*, uniting seven muriform species that were mostly assigned to the genus *Polymeridium* before. This is done because these species are phylogenetically distant



from the core group of *Polymeridium*. The type and most common species was for a long time known under different names in the genus *Campylothelium*. Not much new information is reported here, as compared to

Aptroot *et al.* (2013*b*) and Aptroot & Cáceres (2014), but descriptions, type citations and full synonymy, partly taken from Harris (1993), are given for all species, as well as additional new synonyms.

### Key to the species of *Dictyomeridium*

- 1 Thallus UV+ yellow . . . . . 2  
Thallus UV- . . . . . 5
- 2(1) Ascomata deeply immersed in the bark, ascospores 2 per ascus, 45–70 × 17–25 µm (this synopsis; Fig. 46A & B) . . . . . **Dictyomeridium immersum**  
Ascomata erumpent, ascospores 8 per ascus . . . . . 3
- 3(2) Ascospores 25–35 × 12–17 µm (Flakus *et al.* 2016; Fig. 46C) . . . . .  
. . . . . **Dictyomeridium lueckingii**  
Ascospores over 35 µm long . . . . . 4
- 4(3) Ascospores 35–54 × 12–19 µm (this synopsis; Fig. 46D & E) . . . . .  
. . . . . **Dictyomeridium proponens**  
Ascospores 55–75 × 19–21 µm (this synopsis; Fig. 46F) . . . . .  
. . . . . **Dictyomeridium parapronens**
- 5(1) Ascospores 55–80 × 17–25 µm (this synopsis; Fig. 46G) . . . . .  
. . . . . **Dictyomeridium campylothelioides**  
Ascospores under 55 µm long . . . . . 6
- 6(5) Ostiole with red, K+ green pigment inside, ascospores 33–55 × 11–15 µm (this synopsis; Fig. 46H). . . . . **Dictyomeridium isohypocrellinum**  
Ostiole without red pigment, ascospores 33–55 × 12–21 µm (this synopsis; Fig. 46I)  
. . . . . **Dictyomeridium amylosporum**

**Dictyomeridium amylosporum (Vain.)  
Aptroot, M. P. Nelsen & Lücking  
comb. nov.**

(MICH-Fink 11252—lectotype, Harris, *Contr. Univ. Michigan Herb.* 11: 96, 1975, not seen).

(Fig. 46I)

MycoBank No.: MB 817017

*Thelenella amylospora* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 218 (1890).—*Polyblastiopsis amylospora* (Vain.) Zahlbr., *Catal. Lich. Univ.* 1: 347 (1922).—*Campylothelium amylosporum* (Vain.) R. C. Harris, in Tucker & Harris, *Bryologist* 83: 7 (1980).—*Polymeridium amylosporum* (Vain.) Aptroot, in Aptroot & Cáceres, *Nova Hedwigia* 98: 10 (2014); type: Brazil, Rio de Janeiro, Sepitiba, *Vainio* s. n. (M!, UPS—isotypes; Vainio, *Lich. Bras.* 419).

*Polyblastiopsis dealbens* Fink in Hedrick, *Mycologia* 25: 307 (1933); type: USA, South Carolina, *Green*

*Thallus* ecorticate, white, UV-.  
*Ascomata* pleurothelioid, with lateral ostioles, solitary, 0.4–0.6 mm diam., erumpent to prominent, black. *Hamathecium* clear, filaments profusely anastomosing. *Ascospores* 8 per ascus, IKI+ violet, muriform, 33–55 × 12–21 µm, with partly oblique septa, not ornamented, wall not thickened.

*Chemistry.* Thallus and ascomata UV-, K-. TLC: no substances detected.

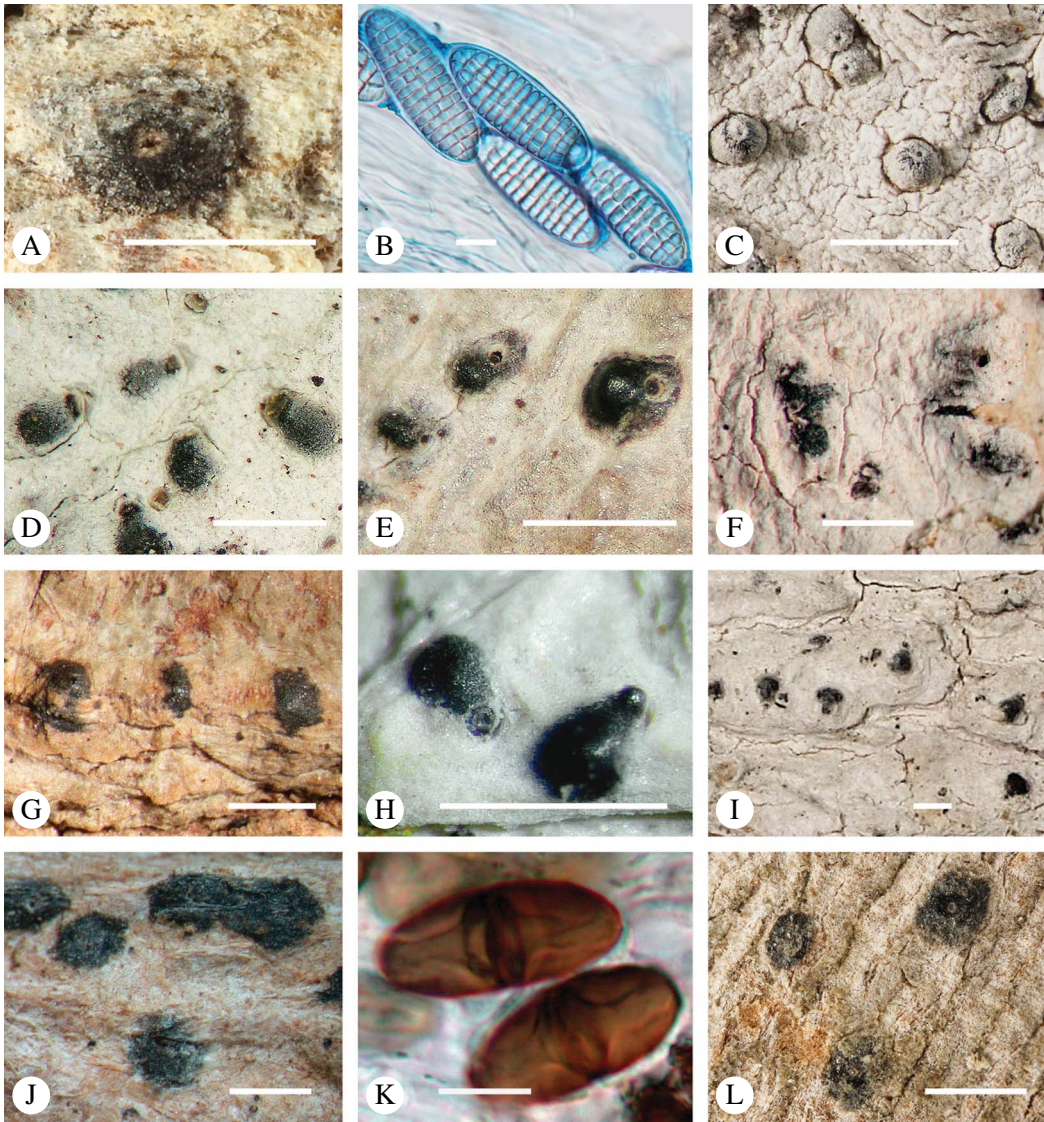


FIG. 46. Habitus and ascospores of *Dictyomeridium* and *Distothelia* species. A & B, *Dictyomeridium immersum* (Brazil, Caceres & Aptroot 11943); C, *D. lueckingii* (Bolivia, holotype); D & E, *D. proponens* (D, Cuba, Buck 23544; E, Venezuela, Lópes-Figueiras 22453); F, *D. paraproponens* (Brazil, isotype); G, *D. campylothelioides* (Indonesia, Java, Groenhart 5796); H, *D. isohypocrellinum* (Brazil, holotype); I, *D. amylosporum* (Brazil, isotype); J & K, *Distothelia rubrostoma* (Guadeloupe, isotype); L, *D. isthmospora* (China, isotype). Scales: A = 0.5 mm; C–J & L = 1 mm; B & K = 10  $\mu$ m. (Images A, B, J–L by F. Schumm).

*Distribution.* Pantropical (reported from Hawai'i, USA, Mexico, Puerto Rico, Costa Rica, Brazil, South Africa, Seychelles, Hong Kong, India, Fiji, New Caledonia, Papua New Guinea and Australia).

***Dictyomeridium campylothelioides***  
(Aptroot & Sipman) Aptroot,  
M. P. Nelsen & Lücking comb. nov.

MycoBank No.: MB 817018

*Polymeridium campylothelioides* Aptroot & Sipman, in Aptroot *et al.*, *Biblioth. Lichenol.* 57: 37 (1995); type: Papua New Guinea, Madang Prov., Laing Island in Hansa Bay near Bogia, Sipman 34767 (B!—holotype).

(Fig. 46G)

*Thallus* ecorticate, white, UV–.

*Ascomata* pleurothelioid, with lateral ostioles, solitary or two aggregated with common ostiole, 0.3–0.6 mm diam., erumpent, grey-black. *Hamathecium* clear, filaments profusely anastomosing. *Ascospores* 8 per ascus, IKI–, muriform, 55–80 × 17–25 µm, with partly oblique septa, not ornamented, wall not thickened.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Asian (previously reported from Taiwan and Papua New Guinea). Incorrectly reported from Venezuela (Komposch & Hafellner 1999).

*New country record.* **Indonesia:** Java: Bay of Tapen, S of Wlingi, 1939, Groenhart 5796 (ABL, L).

***Dictyomeridium immersum* (Aptroot, A. A. Menezes & M. Cáceres) Aptroot, M. P. Nelsen & Lücking comb. nov.**

Mycobank No.: MB 817019

*Polymeridium immersum* Aptroot *et al.*, in Aptroot *et al.*, *Lichenologist* 45: 546 (2013); type: Brazil, Rondônia, Porto Velho, UNIR Federal University campus S of city, on bark of tree, 100 m, 2012, Cáceres & Aptroot 11138 (ISE!—holotype; ABL!—isotype).

(Fig. 46A & B)

*Thallus* ecorticate, pale pinkish white, surrounded by a brown prothallus line.

*Ascomata* pleurothelioid, with lateral ostioles, solitary, 0.3–0.5 mm diam., immersed-erumpent, whitish. *Hamathecium* clear. *Ascospores* muriform, 2 per ascus, hyaline, IKI–, 9–15(–19) × 1–4-septate, ellipsoidal to fusiform, (45–)60–70 × 17–25 µm, outer wall generally constricted at the median septum.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropics (Brazil).

*Discussion.* This species differs from all other known *Dictyomeridium* species by the ascomata that are deeply immersed in the bark below the thallus. The species is easily taken for a sterile crust, because the ascomata are below the thallus in the bark and would escape notice when only a superficial section is made through the thallus at the ostiole. It is also the only species of *Dictyomeridium* with just two ascospores per ascus; all other species have 8 per ascus.

***Dictyomeridium isohypocrellinum* (Xavier-Leite *et al.*) Aptroot, M. P. Nelsen & Lücking comb. nov.**

Mycobank No.: MB 817021

*Polymeridium isohypocrellinum* Xavier-Leite *et al.*, in Aptroot *et al.*, *Lichenologist* 45: 548 (2013); type: Brazil, Paraíba, Reserve Muralha, on bark of tree, 2012, Xavier-Leite s. n. (ISE 15890!—holotype).

(Fig. 46H)

*Thallus* ecorticate, pale pinkish to cream-coloured, surrounded by a black prothallus line.

*Ascomata* pleurothelioid, with lateral ostioles, solitary or occasionally two with fused ostioles, 0.3–0.5 mm diam., erumpent to prominent, black; ostioles with red pigment inside. *Hamathecium* clear. *Ascospores* muriform, 8 per ascus, hyaline, IKI–, 9–15 × 1–3-septate, ellipsoidal, 33–47(–55) × 11–15 µm, not constricted.

*Chemistry.* Thallus UV–, red pigment in ostiole K+ green; isohypocrellin present in ostiole.

*Distribution.* Neotropical (reported from Brazil).

*Discussion.* This species differs from all other known *Dictyomeridium* species by the red, K+ green pigment in the ostiole. It has previously been found many times since its description, always in north-eastern Brazil.



**Dictyomeridium parapropionens**  
(Aptroot, *et al.*) Aptroot, M. P. Nelsen  
& Lücking comb. nov.

MycoBank No.: MB 817022

*Polymeridium parapropionens* Aptroot *et al.*, in Aptroot *et al.*, *Lichenologist* **45**: 548 (2013); type: Brazil, Rondônia, Porto Velho, UNIR Federal University campus S of city, on bark of tree, 100 m, 2012, Cáceres & Aptroot 11162 (ISE!—holotype; ABL!—isotype).

(Fig. 46F)

*Thallus* ecorticate, pale pinkish white, sometimes flaking off, surrounded by a broad brown prothallus line.

*Ascomata* pleurothelioid, with lateral ostioles, grouped together by two or three, 0.3–0.5 mm diam., erumpent to prominent, mostly covered by thallus, grey-black. *Hamathecium* clear. *Ascospores* muriform, 8 per ascus, hyaline, IKI–, 15–25 × 1–3-septate, long ellipsoidal, 55–75 × 19–21 µm, not constricted, surrounded by a gelatinous sheath 3 µm wide.

*Chemistry*. Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution*. Neotropical (reported from Brazil).

*Discussion*. This species differs from all other known *Dictyomeridium* species by the grouped ascomata with lateral, fused ostioles. It has been found already several times since its description, also in north-eastern Brazil.

**Dictyomeridium propionens (Nyl.)**  
Aptroot *et al.*

In Lücking *et al.*, *Lichenologist* **48**: 757 (2016); *Verrucaria propionens* Nyl., *Bull. Soc. Linn. Normandie, sér. 2* **2**: 130 (1868).—*Polyblastia propionens* (Nyl.) Müll. Arg., *Flora* **65**: 402 (1882).—*Campylothelium propionens* (Nyl.) Müll. Arg., *Hedwigia* **31**: 286 (1892).—*Polyblastiopsis propionens* (Nyl.) Zahlbr., *Catal. Lich. Univ.* **1**: 351 (1922).—*Polymeridium propionens* (Nyl.) R. C. Harris, *Bol. Mus. Paraense Emílio Goeldi, Ser. Bot.* **7**: 637 ('1991') [1993]; type: New Caledonia, Lifu, Loyalty Islands, Thiebaut s. n. (H-Nyl—holotype, not seen).

*Verrucaria anoista* Stirt., *Proc. Phil. Soc. Glasgow* **13**: 191 (1881).—*Anthracothecium anoistum* (Stirt.) Zahlbr., *Catal. Lich. Univ.* **1**: 458 (1922).—*Campylothelium anoistum* (Stirt.) Patw. & Makhija, *Biovigyanam* **7**: 44 (1981); type: India, Assam, Watt s. n. (BM!—lectotype, Patwardham & Makhija, *Biovigyanam* **7**: 44, 1981).

*Campylothelium album* Müll. Arg., *Bull. Soc. Roy. Bot. Belg.* **30**(1): 89 (1891); type: Costa Rica, Puntarenas, Baía de Salinas, 1890, Tonduz s. n. (G!—holotype; BR— isotype; Pittier, Pl. Costaric. Exs. 5173).

*Campylothelium nitidum* Müll. Arg., *Nuovo Giorn. Bot. Ital.* **23**: 401 (1891); type: Australia, Brisbane, Bailey 460 (G!—holotype).

(Fig. 46D & E)

*Thallus* ecorticate, white.

*Ascomata* pleurothelioid, with lateral ostioles, solitary, 0.4–0.6 mm diam., erumpent, grey-black. *Hamathecium* clear, filaments profusely anastomosing. *Ascospores* 8 per ascus, IKI+ violet, muriform, 33–54 × 12–19 µm, with partly oblique septa, not ornamented, wall not thickened.

*Chemistry*. Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution*. Pantropical (reported from USA, Mexico, Costa Rica, Puerto Rico, Venezuela, Guyana, Brazil, Canary Isles, Papua New Guinea, Australia and Hawai'i).

**Distothelia Aptroot**

In Seaward & Aptroot, *Bryologist* **108**: 284 (2005); type: *Distothelia isthmospora* Aptroot (holotype).

*Thallus* only causing a bleaching of the bark; algae only loosely associated with the thallus, chlorococcoid, c. 1.5 µm diam.

*Ascomata* single. *Ostioles* apical or lateral. *Hamathecium* hyaline, filaments only little branched or much anastomosing. *Ascospores* pale brown, essentially 1-septate, asymmetrically sole-shaped with the upper end widest; wall extremely thickened leaving two small reniform to halter-shaped lumina near the central septum.

*Pycnidia* sometimes present.

*Chemistry*. No substances detected.

*Discussion*: Only three species are known in this genus. Little new information is reported here as compared to Schumm & Aptroot

(2013), but it is the first time that this genus is considered to belong to the *Trypetheliaceae*, following the realization that much or most of

the species classified in *Mycomicrothelia*, to which *Distothelia* is probably close, belong in this family.

### Key to the species of *Distothelia*

- 1 Ostioles lateral; ascospore lumina reniform (this synopsis; Fig. 9C) . . . . . ***Distothelia angulata***  
 Ostioles apical; ascospore lumina halter-shaped . . . . . 2
- 2(1) Ostioles with red anthraquinone (this synopsis; Fig. 46J & K) . . . . . ***Distothelia rubrostoma***  
 Ostioles without pigment (this synopsis; Fig. 46L) . . . . . ***Distothelia isthmospora***

#### ***Distothelia angulata* Aptroot & Schumm**

In Schumm & Aptroot, *Flechten Madeiras, der Kanaren und Azoren* 2: 200 (2013); type: Portugal, Azores, Terceira, 430 m, 2008, Schumm 14061 (B!—holotype; ABL!—isotype).

(Fig. 9C)

*Thallus* only causing a bleaching of the bark or pinkish; *algae* only loosely associated with the thallus, chlorococcoid or *Trentepohlia*.

*Ascomata* emergent, 0.25–0.50 mm diam., black with grey covering. *Ostioles* black, strongly lateral. *Hamathecium* hyaline, IKI–, filaments only little branched, *c.* 1.5 µm wide. *Asci* cylindrical, IKI–, with 5–8 ascospores, ascus tips with long ocular chamber. *Ascospores* pale brown, IKI–, essentially 1-septate, asymmetrically sole-shaped with the upper end widest, with a submedian constriction, 14–21 × 5.5–9.5 µm; wall extremely thickened leaving two small reniform lumina near the central septum.

*Pycnidia* not observed.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Azores.

#### ***Distothelia isthmospora* Aptroot**

In Seaward & Aptroot, *Bryologist* 108: 284 (2005); type: China, Hong Kong Island, Hillside, Wright s. n. (FH!—holotype).

(Fig. 46L)

*Thallus* pinkish, UV+ whitish, mosaic-forming, *c.* 1–3 cm wide, with very thick

(up to 1 mm wide) dark brown border lines, seemingly associated with scattered *Trentepohlia* in the bark cells.

*Ascomata* regularly scattered, single, low-conical to hemispherical, *c.* 0.5–0.8 mm diam., and 0.1–0.2 mm high. *Ostioles* apical, 50–80 µm diam., black. *Wall* dark brown, in K blackish, *c.* 100 µm thick. *Hamathecium* clear, IKI–, filaments up to 1 µm wide, non-septate, anastomosing above the asci. *Asci* bitunicate, IKI– (but contents dextrinoid), *c.* 100–130 × 15–20 µm, tips without ocular chamber. *Ascospores* 8 per ascus, irregularly biseriate, 15–17 × 6–7 µm, elongate, reddish brown (in tap water), in K blackish grey, bilocular with unequal locules, upper locule wider and shorter than lower locule, conspicuously constricted at the septum, each locule with a halter-shaped lumen with a tiny isthmus (in tap water; unchanged in IKI or K) with rounded ends, surface smooth.

*Pycnidia* mostly near the border lines, *c.* 0.1–0.2 mm diam., wall dark brown, in K blackish, containing copious gel. *Conidia* fusiform, simple, hyaline, *c.* 4–5 × 0.8 µm, with pointed ends.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

#### ***Distothelia rubrostoma* (Aptroot) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816790

*Mycomicrothelia rubrostoma* Aptroot, *Biblioth. Lichenol.* 44: 135 (1991); type: Guadeloupe, Basse-Terre, Vieux Fort, trail above the town, Culberson & Culberson 14551 (NY!—holotype).

(Fig. 46K)

*Thallus* pinkish grey, without prothallus lines.

*Ascomata* single, with fringe, 1.0–1.3 mm wide and 0.2–0.6 mm high, young ostiole with red, K+ purple anthraquinone. *Wall* completely carbonized, to 80 µm thick. *Asci* c. 150 × 20 µm. *Ascospores* 23–29 × 11–14 µm, with equal locules, with rounded ends, walls much thickened with a halter-shaped endospore formation, verruculose.

*Pycnidia* 60–100 µm wide; *conidia* bacilliform, simple, hyaline, 6–8 × 0.3–0.5 µm.

*Chemistry.* Ostiole with anthraquinone.

*Distribution.* Neotropical (reported from Dominican Republic and Guadeloupe).

### **Marcelaria Aptroot *et al.***

*Glalia* 5(2): 3 (2013); type: *Marcelaria purpurina* (Nyl.) Aptroot, M. P. Nelsen & Parmen (holotype).

*Thallus* crustose, corticolous on tree trunks, in part endoperidermal, with a thin, prosoplectenchymatous, cartilaginous cortex. *Photobiont* *Trentepohlia*.

*Ascomata* abundant, perithecioid, sessile, in unilocular, solitary or aggregated warts but

not pseudostromatic, covered by bright (orange-)yellow or red pigment, usually with a split between the inner wall and the surrounding covering tissue; the covering tissue mostly formed by a thick, gelatinous inner cortex that becomes greenish in K. *Ostioles* apical. *Hamathecium* composed of thin, straight, branched and anastomosing paraphysoids embedded in a gelatinous matrix, IKI-. *Asci* bitunicate, with clearly discernible layers and a broad, flat ocular chamber, clavate with short stipe, IKI-. *Ascospores* hyaline, muriform, oblong-oval to ellipsoid or fusiform, without distinctly thickened median septum, with endospore and more or less rounded lumina.

*Pycnidia* with punctiform ostiole, internally brain-like lobate. *Conidia* hyaline, bacillar.

*Chemistry.* Several red, orange and/or yellow anthraquinones present (sometimes partly restricted to thallus or ascomata) and often also lichexanthone.

*Discussion.* The type and the other known species were for a long time known under different names in the genus *Laurera*. Much information has already been reported by Aptroot *et al.* (2013a).

### **Key to the species of *Marcelaria***

- 1      *Ascomata* (and often thallus) bright red, UV-; hamathecium clear; ascospores 110–170 µm long, amyloid; Neotropics and African Palaeotropics (this synopsis; Fig. 47A–H) ..... ***Marcelaria purpurina***
- Ascomata* (and often thallus) (orange-)yellow, UV+ yellow; hamathecium densely interspersed; ascospores 50–80 µm long, non-amyloid (rarely dextrinoid); eastern Palaeotropics ..... 2
- 2(1)    *Thallus* yellow-pruinose; ascospores 8 per ascus; ostiolar region narrow (this synopsis; Fig. 47I & J) ..... ***Marcelaria benguelensis***
- Thallus* non-pruinose; ascospores 2 per ascus; ostiolar region broad, flat (this synopsis; Fig. 47K & L) ..... ***Marcelaria cumingii***

### ***Marcelaria benguelensis* (Müll. Arg.) Aptroot *et al.***

*Glalia* 5(2): 4 (2013).—*Bathelium benguelense* Müll. Arg., *Flora* 68: 256 (1885).—*Laurera benguelensis* (Müll. Arg.) Zahlbr., *Cat. Lich. Univ.* 1: 503 (1922); type: India, *Kurz* 173 (G!—lectotype, Aptroot *et al.*, *Glalia* 5(2): 4, 2013).

*Laurera subbenguelensis* Upreti & Ajay Singh, *Bull. Jard. Bot. Nat. Belg.* 57: 380 (1987); type: India, *Singh & Ranjan* 102285 (BM!—isotype).

(Fig. 47I & J)



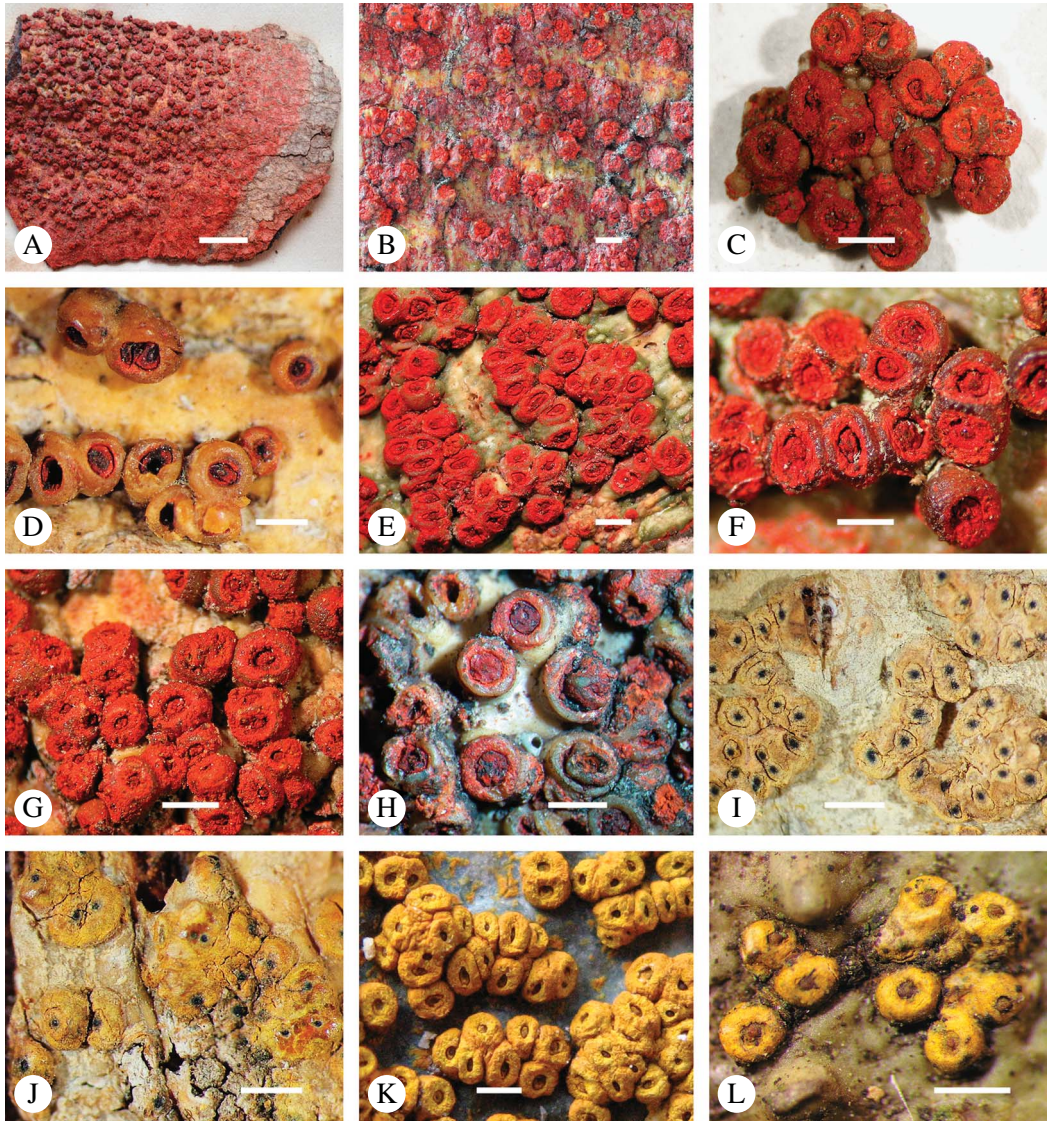


FIG. 47. Habitus of *Marcelaria* species. A–H, *M. purpurina* (A & B, Brazil, holotype; C, Brazil, isotype; D, Brazil, holotype of *Tremotylium sprucei*; E, Colombia, *Moncada* 3467; F, Brazil, *Brako* 7381; G, Bolivia, *van den Boom* 4107; H, DR Congo, *Ertz* 14840); I & J, *M. benguelensis* (India, lectotype); K & L, *M. cumingii* (K, Thailand, *Parmen* s. n.; L, Thailand, *Polyiam* s. n.). Scales = 1 mm. (Image K by W. Polyiam).

*Thallus* corticate, olive-green, often partly to completely (orange-)yellow pruinose (a different pigment compared to that of the ascomata), smooth to uneven.

*Ascomata* sessile with flattened top, solitary to irregularly grouped and confluent, covered with (orange-)yellow pigment

except for blackish ostiole, 0.6–1.0 mm diam., with groups up to 2.5 mm diam. *Hamathecium* densely and heavily interspersed. *Ascospores* 8 per ascus, muriform, fusiform-ellipsoid,  $50\text{--}80 \times 17\text{--}23 \mu\text{m}$ , hyaline, IKI–, surrounded by a gelatinous sheath  $3\text{--}12 \mu\text{m}$  thick.

*Conidia* 5 × 0.5 µm.

**Chemistry.** Thallus UV+ yellow, K– or K+ blood red where orange pigment is present as pruina or in the thin medulla; ascomata UV+ yellow, K+ blood red with purplish hue. TLC: two anthraquinones (parietin = physcione, teloschistin = fallacinol) plus lichexanthone.

**Distribution.** Eastern palaeotropical (India, Cambodia, Myanmar and Thailand).

**Marcelaria cumingii (Mont.) Aptroot et al.**

*Glalia* 5(2): 6 (2013).—*Trypethelium cumingii* Mont. in Hooker, *London J. Bot.* 4: 5 (1845).—*Bathelium cumingii* (Mont.) Trevis., *Flora* 44: 21 (1861).—*Trypethelium cumingianum* Stirt., *J. Linn. Soc. Bot.* 14: 473 (1875) [nom. illeg.].—*Melanotheca cumingiana* (Stirt.) Müll. Arg., *Bull. Herb. Boissier* 2(App. 1): 96 (1894) [nom. illeg.].—*Laurera cumingii* (Mont.) Zahlbr., *Catal. Lich. Univ.* 1: 503 (1922), also ‘*cumingii*’; type: Philippines, *Cuming* s. n. (BM!—holotype; H!—isotype).

(Fig. 47K & L)

**Thallus** corticate, olive-green to yellowish, smooth to uneven.

**Ascomata** sessile with flattened top, solitary to irregularly grouped and confluent, covered with (orange-)yellow pigment except for blackish ostiole, 0.5–0.8 mm diam., with groups up to 3 mm diam. *Hamathecium* densely and heavily inspersioned. *Ascospores* 2 per ascus, muriform, fusiform-ellipsoid, 50–70 × 14–22 µm, hyaline, IKI– or sometimes IKI+ brownish, surrounded by a gelatinous sheath 3–9 µm thick.

*Conidia* 4–5 × 0.5 µm.

**Chemistry.** Thallus UV+ yellow, K+ purple where medullary pigment is present; ascomata warts UV+ yellow, K+ purple. TLC: three anthraquinones (parietin = physcione, emodin, and a trace derivate) plus lichexanthone.

**Distribution.** Eastern Palaeotropics (India and the Philippines). Incorrectly reported from New Zealand.

**Marcelaria purpurina (Nyl.) Aptroot et al.**

*Glalia* 5(2): 9 (2013).—*Trypethelium purpurinum* Nyl. in Leighton, *Trans. Linn. Soc. London* 25: 459 (1866).—*Bathelium purpurinum* (Nyl.) Müll. Arg., *Linnaea* 63: 45 (1880).—*Laurera purpurina* (Nyl.) Zahlbr., *Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl.* 83: 93 (1909); type: Brazil, *Spruce* 236 (PC!—holotype; NY!—isotype).

*Tremotylum sprucei* Müll. Arg., *J. Linn. Soc., London* 30: 454 (1895); type: Brazil, *Spruce* 187 (G!—holotype).

(Fig. 47A–H)

**Thallus** corticate, olive-green but sometimes with patches of bright red pruina, smooth to uneven or shallowly bullate.

**Ascomata** sessile with flattened top, solitary to irregularly grouped and confluent, covered with red pigment, 0.7–1.2 mm diam., with groups up to 4 mm diam. *Hamathecium* clear. *Ascospores* 8 per ascus, muriform, fusiform-ellipsoid, 110–170 × 14–26 µm, hyaline, IKI+ violet, surrounded by a gelatinous sheath 5–10 µm thick.

*Conidia* not observed.

**Chemistry.** Thallus UV–, K+ purple where pigment is present; ascomata UV–, K+ purple. TLC: five anthraquinones (xanthorin = lauropurpurone, parietin = physcione, and three other orange anthraquinones, possibly secalonic acid derivatives).

**Distribution.** Neotropical and Africa (Colombia, Venezuela, Guyana, Brazil, Bolivia, Ivory Coast and DR Congo).

**Nigrovothelium Lücking et al.**

In Lücking et al., *Lichenologist* 48: 757 (2016); type: *Nigrovothelium tropicum* (Ach.), Lücking et al. (holotype).

**Thallus** corticate, olive-green to brownish.

**Ascomata** with apical ostioles, solitary but usually densely crowded, prominent to sessile, exposed and black. *Hamathecium* clear or inspersioned, hyaline, filaments thin, anastomosing paraphysoids. *Asci* clavate. *Ascospores* transversely 3-septate, astrothelioid, with diamond-shaped lumina, hyaline.

*Discussion.* The genus was established to accommodate the species that was until then known as *Trypethelium tropicum* and its relatives (Lücking *et al.* 2016a). Its ascoma morphology is unique, somewhat similar to that of

*Bathelium* species but with the ascomata black and the ascospores astrothelioid. *Nigrovothelium* is most closely related to *Polymeridium*, but differs from that genus in the corticate thallus and astrothelioid ascospores.

**Key to the species of *Nigrovothelium***  
(see also key to species of *Astrothelium*)

- 1 Hamathecium inspersed (Diederich *et al.*, in prep.) . . . . . ***Nigrovothelium* aff. *tropicum***  
Hamathecium clear . . . . . 2
- 1(2) Thallus smooth to uneven (this synopsis; Fig. 48A–E) . . . . ***Nigrovothelium tropicum***  
Thallus verrucose-bullate (Lücking *et al.* 2016b; Fig. 48F) . . . . ***Nigrovothelium bullatum***

***Nigrovothelium tropicum* (Ach.)  
Lücking *et al.***

In Lücking *et al.*, *Lichenologist* **48**: 757 (2016).—*Verrucaria tropica* Ach., *Lichenogr. Univ.*: 278 (1810).—*Sagedia tropica* (Ach.) A. Massal., *Ricerch. Auton. Lich.*: 161 (1852).—*Pyrenula tropica* (Ach.) Trevis., *Spighe e Paglie*: 17 (1853).—*Spermatodium tropicum* (Ach.) Trevis., *Conspect. Verruc.*: 11 (1860).—*Pseudopyrenula tropica* (Ach.) Müll. Arg., *Flora* **66**: 248 (1883).—*Trypethelium tropicum* (Ach.) Müll. Arg., *Bot. Jahrb. Syst.* **6**: 393 (1885); type: America, Swartz s. n. (H-ACH 707A!—lectotype; BM-ACH—isolectotype).

*Verrucaria gaudichaudii* Fée, *Essai Crypt. Écorc.*: 87 (1824).—*Pyrenula gaudichaudii* (Fée) Pers., in Freycinet, *Voyage Uranie, Bot.*: 182 (1826); type: (G—holotype, not seen).

*Verrucaria tristis* Hepp, in Zollinger, *Syst. Verzeichn. Ind. Archip. Ges. Pfl.*: 8 (1854); type: Indonesia, Java, Tjibodas, Zollinger s. n. (M!—lectotype, designated here).

*Trypethelium tropicum* var. *nigratum* Müll. Arg., *Rep. Australas. Assoc. Advancem. Sci.* **1895**: 460 (1895); type: Australia, Queensland, Bellenden Ker, Bailey s. n. (G!—holotype; BRI!—isostrate).

*Zignoella magnoliae* Tracy & Earle, *Bull. Torrey Bot. Club* **23**: 211 (1896); type: USA, Mississippi, Ocean Springs, Tracy s. n. (NY—holotype, not seen).

*Zignoella lichenoides* Höhn., *Sitzungsber. Kaiserl. Akad. Wiss., math.-naturwiss. Cl. Abt. 1*, **118**: 331 (1909); type: Indonesia, Java, Buitenzorg, von Höhnell s. n. (BPI!—isostrate; Rehm, *Ascomyceten* 1862).

*Pseudopyrenula pyrenuloides* Zahlbr., in Reehinger, *Denkschr. Kaiserl. Akad. Wiss., math.-naturwiss. Kl.* **88**: 12 (1911); type: Solomon Islands, Buka, Reehinger 4756 (W—holotype, not seen).

*Pseudopyrenula verrucosa* Vain., *Ann. Acad. Sci. Fenn., ser. A* **6**(7): 198 (1915).—*Trypethelium verrucosum* (Vain.) Zahlbr., *Catal. Lich. Univ.* **8**: 129 (1932) nom. illeg. non Fée (1824); type: Guadeloupe, Camp Jacob, Duss 1394 (TUR-Vain 30797—holotype, not seen).

*Zignoella nobilis* Rehm, *Leafl. Philipp. Bot.* **8**: 2950 (1916); type: Philippines, Luzon, Laguna, Mount Maquilung, Baker s. n. (BPI—isostrate; Baker, *Fungi Malayana* 200).

*Pseudopyrenula composita* Vain., *Bol. Soc. Broteriana ser. 2* **6**: 177 (1930).—*Trypethelium compositum* (Vain.) Zahlbr., *Catal. Lich. Univ.* **10**: 101 (1938).—*Bathelium compositum* (Vain.) C. W. Dodge, *Ann. Missouri Bot. Gard.* **40**: 289 (1953); type: Mozambique, Palma, *Pines de Lima* 310 (TUR-Vain—holotype, not seen).

*Pseudopyrenula bicincta* Zahlbr., *Repert. Spec. Nov. Regni Veg.* **31**: 200 (1933); type: Taiwan, Rengechi, *Asahina* F304 (W—holotype, not seen).

*Pseudopyrenula deightonii* C. W. Dodge, *Ann. Missouri Bot. Gard.* **40**: 279 (1953); type: Sierra Leone, Njala, Deighton M4340 (BM—isostrate).

*Massarina salicicola* var. *minor* Batista & Maia, *Brotéria Ci. Nat.* **29**: 134 (1960) [as '*Massaria salicicola*', illustrations sub '*Massarina salicicola*' and '*Massaria salicicola*']; type: Brazil, Bahia, Serrinha, Batista 11646 (URM 16277—holotype).

(Fig. 48A–E)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* with apical ostioles, solitary but usually densely crowded, 0.2–0.3 mm diam., prominent to sessile, subglobose to barrel-shaped with flattened top, exposed and black with ostiolar area greyish. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 20–25 × 7–10 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.



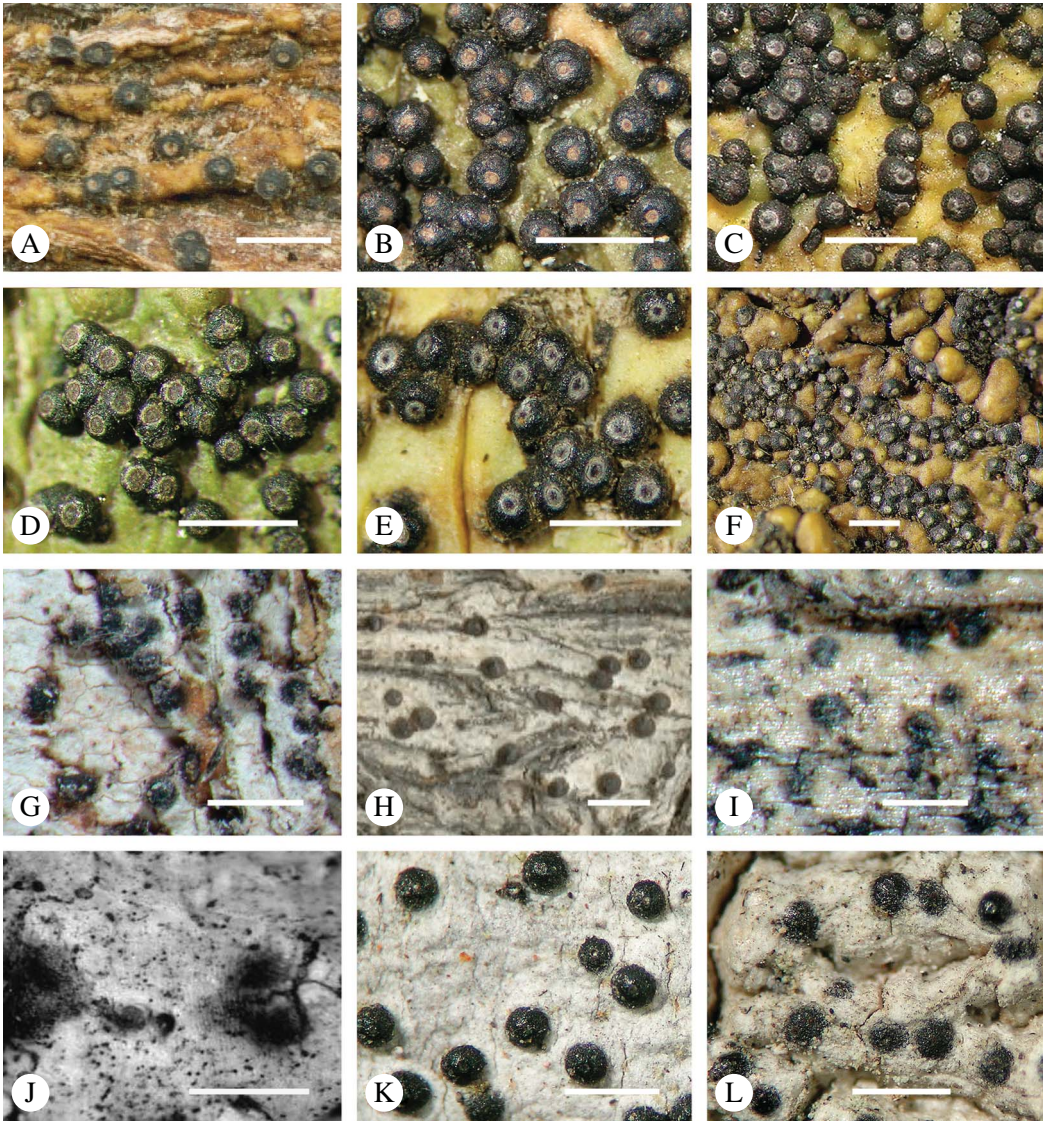


FIG. 48. Habitus of *Nigrovothelium* and *Polymeridium* species. A–E, *Nigrovothelium tropicum* ('South America', lectotype); F, *N. bullatum* (India, holotype); G, *Polymeridium subvirescens* (Brazil, Cáceres 11110); H, *P. pyrenuloides* ('South America', lectotype); I, *P. albidovarians* (Indonesia, isotype); J, *P. pyrenastroides* (Venezuela, holotype); K & L, *P. amyloideum* (J, Brazil, isotype; K, Brazil, *Brako* 6028). Scales = 1 mm.

*Distribution.* Pantropical (previously reported from the USA, Mexico, El Salvador, Cuba, Guadeloupe, Colombia, Venezuela, Guyana, French Guiana, Galapagos, Brazil, Argentina, Sierra Leone, Mozambique, Tanzania, Seychelles, India, Sri Lanka, China, Taiwan,

Hong Kong, Singapore, Thailand, Vietnam, Cambodia, Philippines, Indonesia, Papua New Guinea, Solomon Islands and Australia).

*New country records.* **Puerto Rico:** Mayagüez: Reserva Forestal Maricao, 1990, *Sipman* 25925 (B).—

**Madagascar:** *Tulear*: Ifaty, 1984, Aptroot & Hensen 12617 (ABL).—**Bangladesh:** *Dhaka*: Bhawal National Park, 2002, Hopman s. n. (ABL).

### **Novomicrothelia Aptroot et al.**

In Lücking et al., *Lichenologist* **48**: 757 (2016); type: *Novomicrothelia oleosa* (Aptroot) Aptroot, M. P. Nelsen & Lücking (holotype).

*Thallus* ecorticate, usually whitish.

*Ascomata* with apical ostioles, solitary, exposed and black. *Hamathecium* clear or interspersed, hyaline, clear, filaments thin, anastomosing paraphysoids. *Asci* clavate. *Ascospores* transversely 1-septate, with irregular endospore formation, becoming ornamented, brown, rather elongated.

*Pycnidia* sometimes present.

**Discussion.** The genus thus far accommodates a single tropical lichen species that was previously placed in the genus *Mycomicrothelia* Keissl. Its morphological distinction from the reinstated genus *Bogoriella* is not yet very clear, although it occupies a distinct phylogenetic position (Lücking et al. 2016a). Besides hamathecium inspersion, the formation of ascospore wall invaginations similar to those found in *Constrictolumina* (Fig. 8D) might be diagnostic (Harris 1995).

### **Novomicrothelia oleosa (Aptroot) Aptroot et al.**

In Lücking et al., *Lichenologist* **48**: 758 (2016); *Mycomicrothelia oleosa* Aptroot, *Biblioth. Lichenol.* **44**: 133 (1991); type: Trinidad and Tobago, Trinidad, Caroni, North Bank Road, Britton et al. 869 (NY!—holotype).

(Figs 8D, 42B)

*Thallus* ecorticate, whitish grey, smooth to uneven, without prothallus lines.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., erumpent to prominent, lens-shaped to hemispherical with spreading base (fringe), exposed and black. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 1-septate, ellipsoid-oval, not constricted at septum, 24–27 × 8–11 μm, with nearly equal locules, brown, verruculose.

*Pycnidia* absent.

**Chemistry.** Thallus and ascomata UV–, K–. TLC: no substances detected.

**Distribution.** Neotropical (Trinidad and Tobago, Colombia, Brazil and Guyana).

### **Polymeridium (Müll. Arg.) R. C. Harris**

In Tucker & Harris, *Bryologist* **83**: 12 (1980).—*Arthopyrenia* sect. *Polymeridium* Müll. Arg., *Flora* **46**: 317 (1883); type: *Polymeridium contendens* (Nyl.) R. C. Harris (holotype).

*Exiliseptum* R. C. Harris, *Acta Amazon. (Suppl.)* **14**: 65 ('1984') [1986]; type: *Exiliseptum ocellatum* (Müll. Arg.) R. C. Harris [= *Polymeridium ocellatum* (Müll. Arg.) Aptroot].

*Thallus* ecorticate except in two species, white to yellowish or grey.

*Ascomata* simple or fused with partly shared walls or only the ostioles fused, black, without pseudostromatic tissues, globose to pyriform, erumpent from the substratum. *Ostioles* apical to lateral, brown to black or with red anthraquinone. *Hamathecium* colourless, sometimes interspersed with hyaline or red (K+ green) oil droplets. *Ascospores* 4–8 per ascus, IKI– or rarely IKI+ violet, irregularly biseriolate, colourless, ellipsoid to fusiform with rounded to subacute ends, symmetrically 3–13-septate to muriform, not constricted at the septa, sometimes surrounded by a thin gelatinous sheath to 2–5 μm thick; septa not thickened; lumina rectangular, slightly rounded but not diamond-shaped.

*Conidiomata* rather rare.

**Chemistry.** Thallus occasionally with lichexanthone; anthraquinones rarely present in ostiole or hamathecium.

**Discussion.** Not much new information is reported here, as compared to Aptroot et al. (2013b) and Aptroot & Cáceres (2014), but descriptions, type citations and full synonymy, partly taken from Harris (1993), are given for all species. One species

aggregate, now united in the genus *Dictyomeridium*, is split off from *Polymeridium*. Both genera have their centre of diversity in north-eastern Brazil, and additional species continue to be reported from there (Cáceres *et al.* 2014).

### Key to the species of *Polymeridium*

- 1 Ascospores transversely septate. . . . . 2  
 Ascospores submuriform to muriform . . . . . 47
- 2(1) Ascospores regularly 3-septate . . . . . 3  
 Ascospores irregularly (3–)4–17-septate . . . . . 28
- 3(2) Thallus UV+ yellow, with lichexanthone . . . . . 4  
 Thallus UV–, without substances or rarely with medullary pigments or pigmented pruina on ascomata . . . . . 14
- 4(3) Hamathecium interspersed . . . . . 5  
 Hamathecium clear . . . . . 7
- 5(4) Ascospores 24–33 × 6–10 µm (this synopsis; Fig. 48G) . . . . .  
 . . . . . **Polymeridium subvirescens**  
 Ascospores 17–23 × 5–8 µm . . . . . 6
- 6(5) Ascospores 17–20 × 5–7 µm (this synopsis; Fig. 48H) . . . . .  
 . . . . . **Polymeridium pyrenuloides**  
 Ascospores 20–23 × 6–8 µm (this synopsis; Fig. 48I) . . . . .  
 . . . . . **Polymeridium albidovarians**
- 7(4) Ostioles eccentric, separate or fused; ascospores 24–33 µm long . . . . . 8  
 Ostioles apical; ascospores variable . . . . . 9
- 8(7) Ostioles fused (this synopsis; Fig. 48J) . . . . . **Polymeridium pyrenastroides**  
 Ostioles separate (this synopsis) . . . . . **Polymeridium stramineoatrum**
- 9(7) Ascospores IKI+ violet, 16–23 × 5–7 µm (this synopsis; Fig. 48K & L) . . . . .  
 . . . . . **Polymeridium amyloideum**  
 Ascospores IKI–, with variable size . . . . . 10
- 10(9) Ascospores 13–20 × 4–6 µm . . . . . 11  
 Ascospores 19–33 × 6–11 µm . . . . . 12
- 11(10) Ascospores 13–17 µm long (this synopsis; Fig. 49A) . . . . .  
 . . . . . **Polymeridium albopruinosum**  
 Ascospores 16–20 µm long (this synopsis; Fig. 49B) **Polymeridium bengoanum**
- 12(10) Ascomata mostly covered by thallus, with black ostioles bordered by white ring; ascospores relatively broad, 17–25 × 7–11 µm, *c.* 2.5 times as long as broad (this synopsis; Fig. 49C) . . . . . **Polymeridium xanthoreagens**  
 Ascomata pure black; ascospores narrower, 20–33 × 6–10 µm, about 3 times as long as broad . . . . . 13



- 13(12) Ascospores 20–23 × 6–8 μm (this synopsis; Fig. 49D) . . . . .  
 . . . . . **Polymeridium albidoreagens**  
 Ascospores 25–33 × 7–10 μm (this synopsis; Fig. 49E) . . . . .  
 . . . . . **Polymeridium catapastum**
- 14(3) Hamathecium inspersed; ostioles apical . . . . . 15  
 Hamathecium clear; ostioles variable . . . . . 20
- 15(14) Ascospores 24–34 μm long; ascomata laterally covered by thallus . . . . . 16  
 Ascospores 12–24 μm long; ascomata variable . . . . . 17
- 16(15) Ascospores with rough wall, 26–34 μm long; blackish ostiolar area broad (this  
 synopsis; Fig. 49F) . . . . . **Polymeridium glaucostrum**  
 Ascospores smooth, 24–30 μm long; blackish ostiolar area narrow (this synopsis;  
 Fig. 49G) . . . . . **Polymeridium suffusum**
- 17(15) Ascospores 12–20 × 3–6 μm . . . . . 18  
 Ascospores 20–24 × 5–10 μm . . . . . 19
- 18(17) Ascospores 12–16 μm long (this synopsis; Fig. 49H) . . . . . **Polymeridium contendens**  
 Ascospores 16–20 μm long (this synopsis; Fig. 49I) . . . . . **Polymeridium inspersum**
- 19(17) Ascomata with ostioles bordered by white ring; ascospores relatively broad, 20–  
 24 × 7–10 μm, *c.* 2.5–3 times as long as broad (this synopsis; Fig. 49J) . . . . .  
 . . . . . **Polymeridium tribulationis**  
 Ascomata pure black; ascospores narrower, 20–23 × 5–7 μm, *c.* 3–4 times as long as  
 broad (this synopsis) . . . . . **Polymeridium siamense**
- 20(14) Ascomata with internal or external, yellow-orange or red pigment . . . . . 21  
 Ascomata without pigments . . . . . 22
- 21(20) Ascomata with internal, yellow-orange, K+ purple pigment; ascospores 30–34 ×  
 9–10 μm (this synopsis; Fig. 49K) . . . . . **Polymeridium endocrocinum**  
 Ascomata with external, red, K+ red pruina; ascospores 17–19 × 4–5 μm (Aptroot  
*et al.* 2016a; Fig. 49L) . . . . . **Polymeridium rhodopruinosum**
- 22(20) Ostioles lateral . . . . . 23  
 Ostioles apical . . . . . 24
- 23(22) Ascomata grouped with fused ostioles; ascospores 26–30 × 8–10 μm (this synopsis;  
 Fig. 50A) . . . . . **Polymeridium biloculare**  
 Ascomata solitary with separate ostioles; ascospores 30–35 × 12–13 μm (this  
 synopsis; Fig. 50B) . . . . . **Polymeridium simulans**
- 24(22) Ascospores 24–33 μm long (this synopsis; Fig. 50C) . . . . .  
 . . . . . **Polymeridium catapastoides**  
 Ascospores 11–27 μm long . . . . . 25
- 25(24) Ascospores 11–16 × 3–6 μm (this synopsis; Fig. 50D) . . . . .  
 . . . . . **Polymeridium microsporium**  
 Ascospores (15–)16–27 × 5–11 μm . . . . . 26



- 39(38) Ostioles lateral; ascospores 3–6-septate, 22–26 × 7–9 µm (this synopsis) . . . . .  
 . . . . . **Polymeridium refertum**  
 Ostioles apical; ascospores variable . . . . . 40
- 40(39) Ascospores 4–7-septate . . . . . 41  
 Ascospores 7–12-septate . . . . . 42
- 41(40) Ascospores with rough wall, 7-septate, 30–33 × 9–10 µm (this synopsis; Fig. 51H) . . .  
 . . . . . **Polymeridium newirthii**  
 Ascospores smooth, (4–)5(–7)-septate, 18–28 × 4–7 µm (this synopsis; Fig. 51I–K)  
 . . . . . **Polymeridium quinqueseptatum**
- 42(40) Ascospores 7–11-septate, 25–36 × 5–9 µm (this synopsis; Fig. 51L) . . . . .  
 . . . . . **Polymeridium pleiomerellum**  
 Ascospores 8–12-septate, 40–50 × 9–11 µm (this synopsis; Fig. 52A) . . . . .  
 . . . . . **Polymeridium costaricense**
- 43(37) Ostioles lateral . . . . . 44  
 Ostioles apical . . . . . 45
- 44(43) Ascospores 7–9-septate, 40–50 × 8–9 µm (this synopsis; Fig. 52B & C) . . . . .  
 . . . . . **Polymeridium neblinae**  
 Ascospores 9–13-septate, (35–)50–75 × 12–16 µm (this synopsis; Fig. 52D) . . . . .  
 . . . . . **Polymeridium pleurothecium**
- 45(43) Ascospores 13–17-septate, 85–150 × 20–30 µm (this synopsis; Fig. 52E) . . . . .  
 . . . . . **Polymeridium bambusicola**  
 Ascospores 4–11-septate, 21–39 × 5–9 µm . . . . . 46
- 46(45) Ascospores (4–)5(–7)-septate, 21–30 × 5–9 µm (this synopsis) . . . . .  
 . . . . . **Polymeridium jordanii**  
 Ascospores 7–11-septate, (24–)28–39 × 6–9 µm (this synopsis; Fig. 52F–I) . . . . .  
 . . . . . **Polymeridium albocinereum**
- 47(1) Ostioles eccentric, fused; thallus corticate, UV+ yellow; ascospores 15–16 × 6–  
 8 µm; hamathecium clear (this synopsis) . . . . . **Polymeridium ocellatum**  
 Ostioles apical, separate; thallus ecorticate, UV–; ascospores 18–45 × 6–13 µm;  
 hamathecium variable . . . . . 48  
 If ostioles eccentric and ascospores at least 25 × 12 µm, see *Dictyomeridium*
- 48(47) Hamathecium inspersed, ascospores 18–20 × 6.0–7.5 µm (this synopsis; Fig. 52J) .  
 . . . . . **Polymeridium submuriforme**  
 Hamathecium clear, ascospores 25–45 × 9–13 µm . . . . . 49
- 49(48) Ascospores 30–45 × 9–11 µm, submuriform, 3–4 times as long as broad (this  
 synopsis; Fig. 52K) . . . . . **Polymeridium cinereonigrans**  
 Ascospores 25–29 × 11–13 µm, muriform, 2.0–2.5 times as long as broad (this  
 synopsis; Fig. 52L) . . . . . **Polymeridium julelloides**



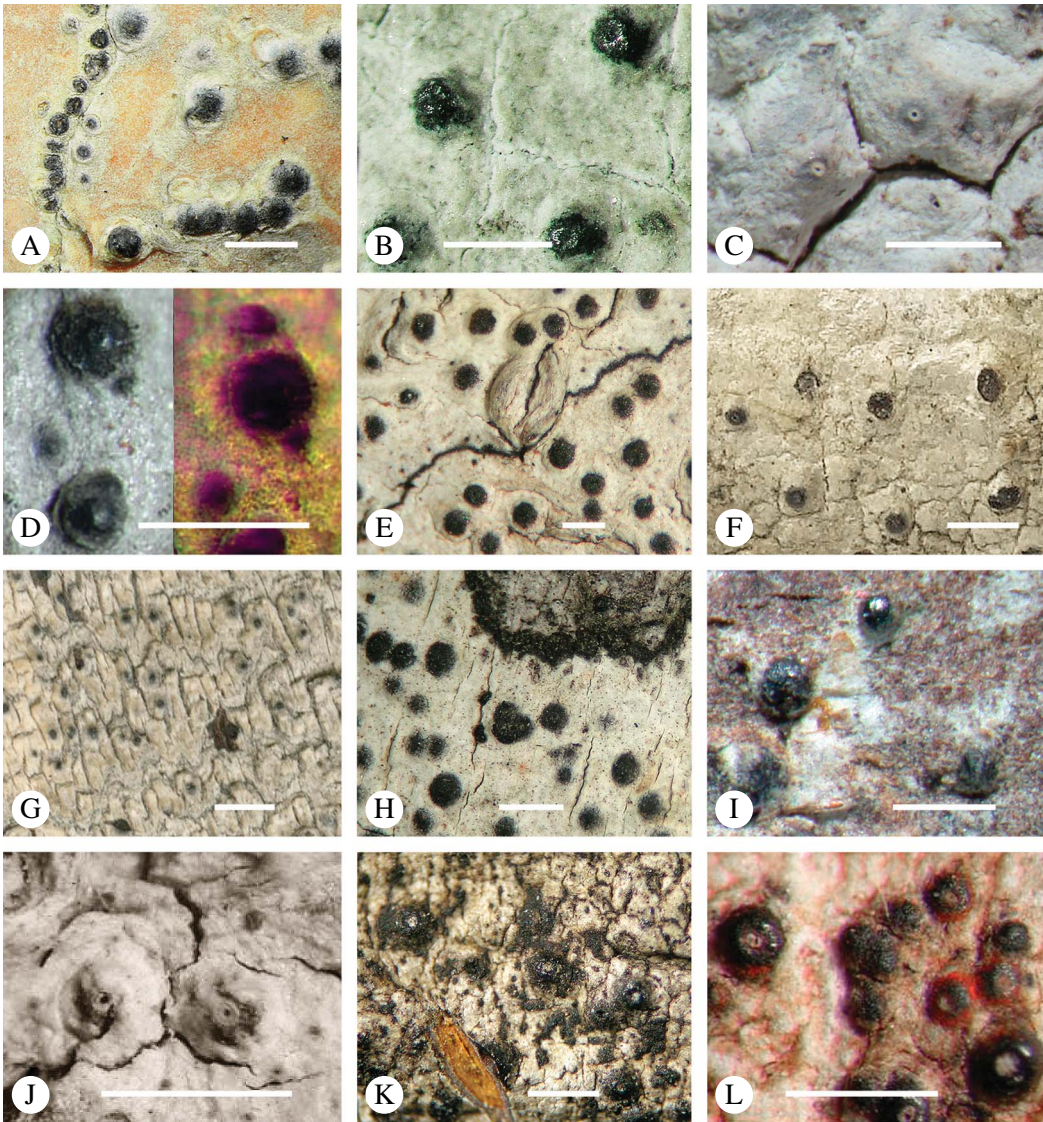


FIG. 49. Habitus of *Polymeridium* species. A, *P. albopruinosum* (India, isotype); B, *P. bengoanum* (Angola, holotype); C, *P. xanthoreagens* (Australia, isotype); D, *P. albidoreagens* (Brazil, isotype; right portion under UV light); E, *P. catapastum* (Bahamas, Britton 6650); F, *P. glaucoatrum* (Philippines, isotype); G, *P. suffusum* (New Zealand, isolecotype); H, *P. contendens* (Brazil, Brako 6107D); I, *P. inspersum* (Australia, isotype); J, *P. tribulationis* (Australia, isotype); K, *P. endocrocinum* (Brazil, holotype); L, *P. rhodopruinosum* (Puerto Rico, holotype). Scales = 1 mm.

***Polymeridium albidoreagens*  
Aptroot *et al.***

Municipal, 100m, 2012, Cáceres & Aptroot 15194  
(ISE—holotype; ABL—isotype).

In Aptroot & Cáceres, *Nova Hedwigia* 98: 7 (2014); type:  
Brazil, Rondônia, Porto Velho, Parque Natural

(Fig. 49D)



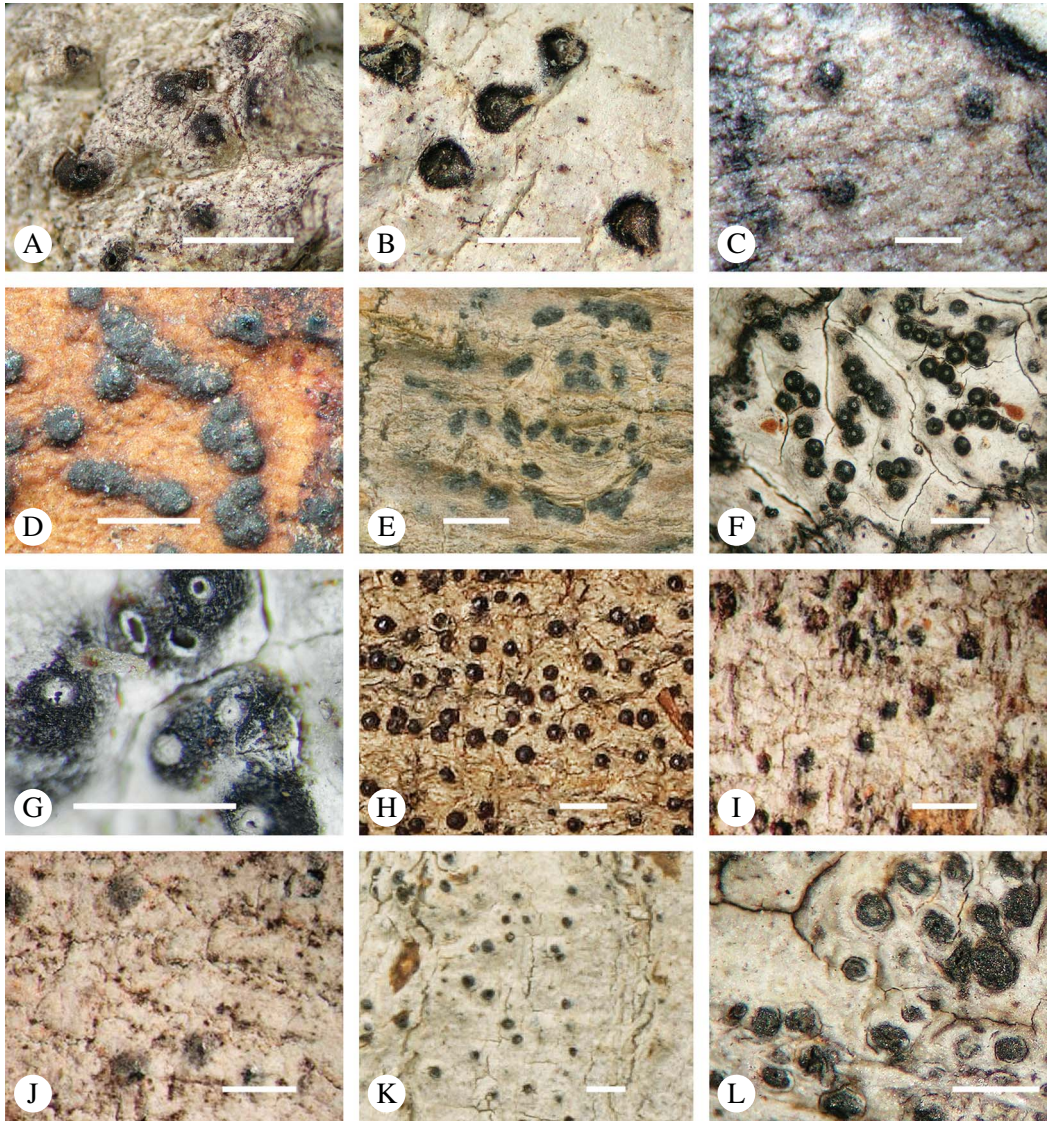


FIG. 50. Habitus of *Polymeridium* species. A, *P. biloculare* (Brazil, isotype); B, *P. simulans* (Brazil, holotype); C, *P. catapastoides* (Australia, holotype); D, *P. microsporium* (India, isotype); E & F, *P. subcinereum* (E, USA, Texas, lectotype; F, Dominican Republic, Harris 19593); G, *P. sulphurescens* (Australia, Streimann 29632); H, *P. albidum* (Brazil, holotype); I, *P. endoflavens* (Brazil, isotype); J, *P. longiflavens* (Brazil, isotype); K & L, *P. chioneum* (K, Cuba, holotype of *Verrucaria pleiomerooides*; L, Brazil, Buck 2980A). Scales = 1 mm.

*Thallus* ecorticate, whitish grey, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, exposed and black. *Hamathecium* clear. *Ascospores* 8 per

ascus, 3-septate, fusiform,  $20\text{--}23 \times 6\text{--}8 \mu\text{m}$ , hyaline, IKI–, wall smooth.

*Chemistry*. Thallus UV+ yellow, K–. TLC: lichexanthone.



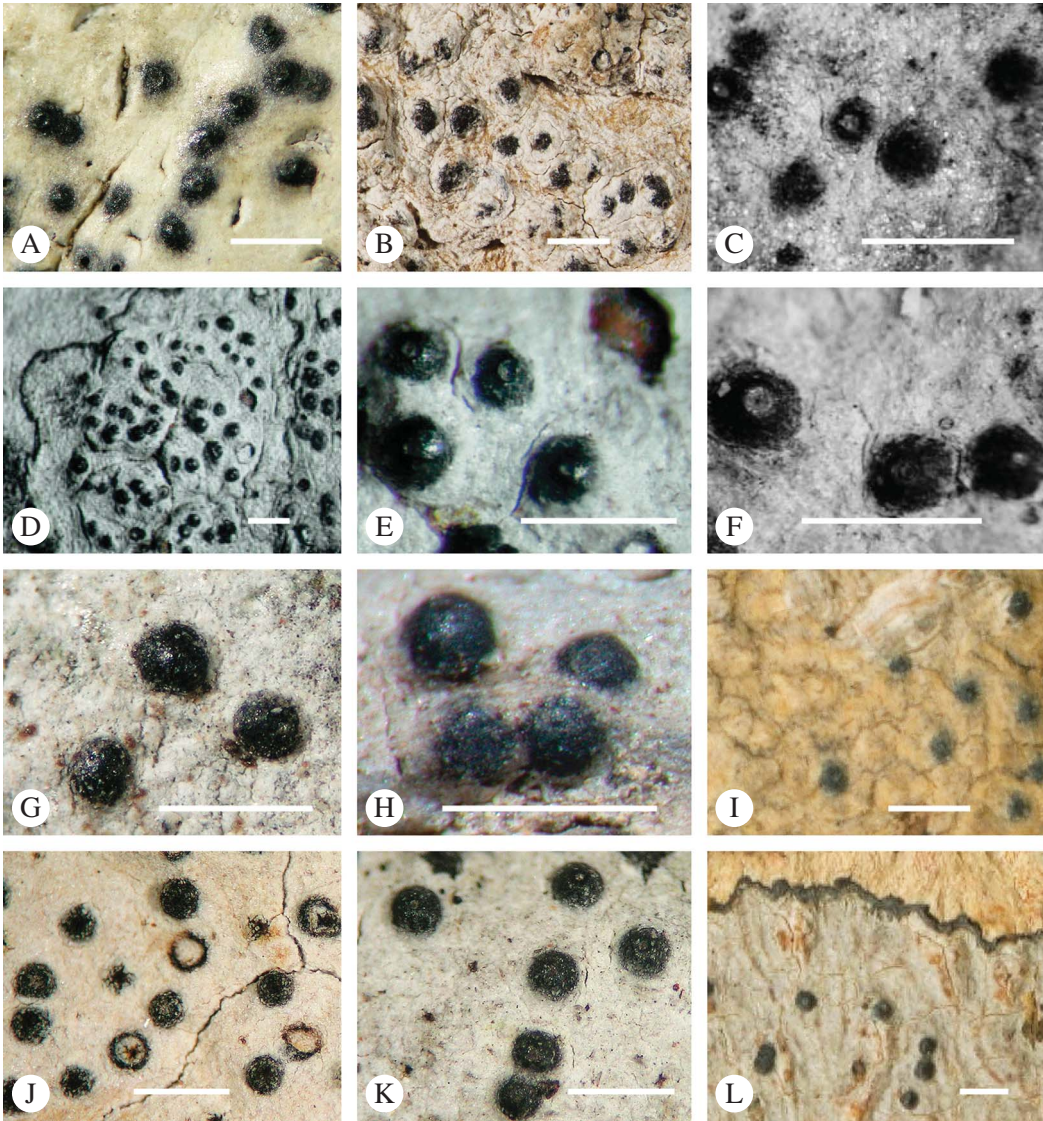


FIG. 51. Habitus of *Polymeridium* species. A, *P. dithecium* (Venezuela, holotype); B, *P. xanthoexcentricum* (Bolivia, holotype); C, *P. multiforme* (Guyana, isotype); D & E, *P. corticatum* (Brazil, holotype); F, *P. alboflavescens* (Venezuela, holotype); G, *P. flavothecium* (Dominican Republic, holotype); H, *P. newirthii* (Venezuela, isotype); I–K, *P. quinqueseptatum* (I, USA, South Carolina, isotype; J, Venezuela, López-Figueiras 19405; K, Brazil, Brako 6107); L, *P. pleiomerellum* (Cuba, holotype). Scales = 1 mm.

*Distribution.* Neotropical (reported from Brazil) (Fig. 48I)

### ***Polymeridium albidovarians* Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* 98: 7 (2014); type: Indonesia, Java, Kawi-complex, Tjemarakandang, 2700 m, 1937, *Groenhart* 5755 (L—holotype; ABL—isotype).

*Thallus* ecorticate, yellowish white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, exposed and



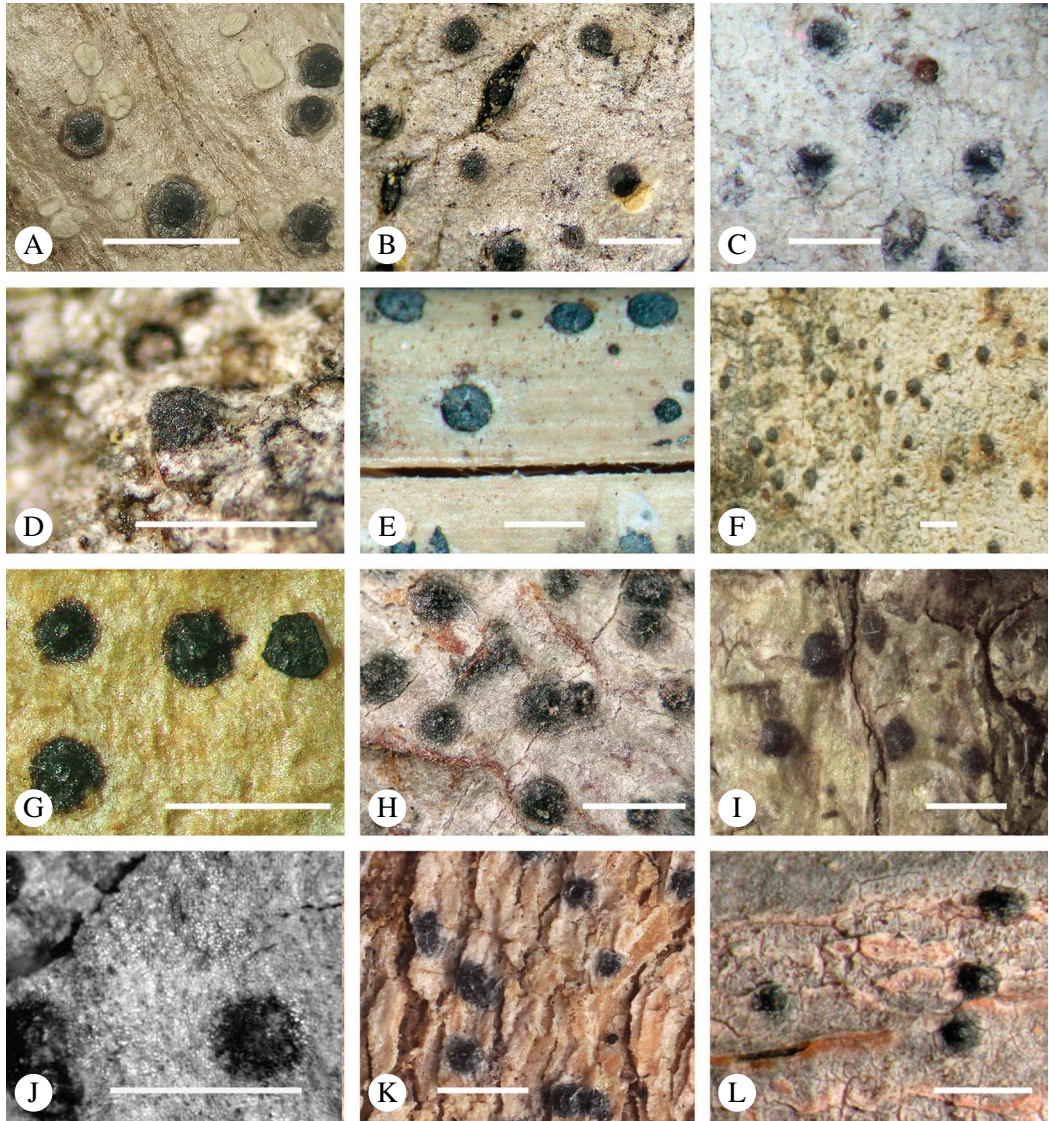


FIG. 52. Habitus of *Polymeridium* species. A, *P. costaricense* (Costa Rica, isotype); B & C, *P. neblinae* (Venezuela, holotype); D, *P. pleurothecium* (Guyana, holotype); E, *P. bambusicola* (Argentina, isotype); F–I, *P. albocinereum* (F, Brazil, isoelectotype; G, Philippines, holotype of *Pseudopyrenula pentameria*; H, Jamaica, *Imshaug* 13515; I, USA, Florida, *Lay* 143); J, *P. submuriforme* (Philippines, holotype); K, *P. cinereonigricans* (Brazil, isotype); L, *P. julleoides* (Brazil, isotype). Scales = 1 mm.

black. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 3-septate, fusiform, 20–23 × 6–8 μm, hyaline, IKI–, wall smooth.

*Chemistry*. Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution*. Pantropical (reported from Brazil and Indonesia)

***Polymeridium albidum* (Müll. Arg.)  
R. C. Harris**

*Acta Amazon. (Suppl.)* 14: 69 ('1984') [1986].—*Arthopyrenia albida* Müll. Arg., *Flora* 67: 664 (1884);

type: Brazil, Bahia, Caetit , *Martius* s. n. (G!—holotype).

(Fig. 50H)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., prominent, conical to wart-shaped, exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 20–23 × 6–8 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (previously reported from USA, Venezuela, Colombia, Brazil, Bolivia, Mozambique, Malaysia, Sarawak, Papua New Guinea and Australia). Incorrectly reported from Thailand.

*New country record. Solomon Islands:* Santa Isabel Island: 1965, Hill 11123 (BM).

### **Polymeridium albocinereum (Kremp.) R. C. Harris**

*Bol. Mus. Paraense Emilio Goeldi, Ser. Bot.* 7: 625 ('1991') [1993].—*Verrucaria albocinerea* Kremp., *Flora* 59: 524 (1876).—*Arthopyrenia albocinerea* (Kremp.) M ll. Arg., *Flora* 66: 318 (1883); type: Brazil, Rio de Janeiro, Glaziou 5025 (M—lectotype, Harris, *Bol. Mus. Paraense Emilio Goeldi, Ser. Bot.* 7: 625 ('1991') [1993], not seen; G!—isolectotype).

*Pseudopyrenula pentameria* Vain., *Ann. Soc. Zool. Bot. Fenn. Vanamo* 1(3): 55 (1921); type: Philippines, Robinson 9623 (TUR-Vain 30818!—holotype).

(Fig. 52F–I)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., prominent, hemispherical, exposed and grey-black. *Hamathecium* clear. *Ascospores* 8 per ascus, 7–11-septate, fusiform, (24–)28–39 × 6–9 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–; TLC: no substances detected.

*Distribution.* Pantropical (previously reported from Colombia, Brazil, Tanzania and Thailand).

*New country record. Madagascar:* Tulear: Betioky, 1984, Aptroot & Hensen 12595 (ABL).

### **Polymeridium alboflavescens Aptroot**

In Aptroot & C ceres, *Nova Hedwigia* 98: 8 (2014); type: Venezuela, Est. Amazonas, Alto Orinoco, 15 km W of Esmeralda, 110 m, 1997, Hafellner & Komposch 991-6-4 (GZU!—holotype)

(Fig. 51F)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., erumpent to prominent, exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 7–11-septate, fusiform, 28–39 × 6–9 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropical (Venezuela and Brazil).

### **Polymeridium albopruinosum (Makhija & Patw.) Aptroot**

In Aptroot & C ceres, *Nova Hedwigia* 98: 8 (2014).—*Trypethelium albopruinosum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 193 (1993); type: India, Andaman islands, Middle Andaman, Dhanimali, Patwardhan & Nagarkar AMH 85.2342 (ABL, BM!—isotypes).

(Fig. 49A)

*Thallus* ecorticate, yellowish white, smooth to uneven, often in patches around ascomata.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., erumpent, exposed and grey-black. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 13–17 × 4–7 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Pantropical (reported from Brazil, Tanzania and India).

**Polymeridium amyloideum**  
**R. C. Harris**

*Bol. Mus. Paraense Emílio Goeldi, Ser. Bot.* 7: 626 ('1991') [1993]; type: Brazil, Pará, Serra do Cochimbo, *Brako* 6107 (NY!—isotype).

(Fig. 48K & L)

*Thallus* ecorticate, white, smooth to uneven. *Ascomata* with lateral, fused ostioles, fused ascomata dispersed, 0.3–0.5 mm diam., erumpent, lens-shaped to applanately hemispherical, exposed and black but ostiolar area often pale. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 16–23 × 5–7 µm, hyaline, IKI+ violet (septa), wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropical (reported from Brazil).

**Polymeridium bambusicola** Aptroot  
& L. I. Ferraro

*Bonplandia* 10: 140 (2000); type: Argentina, Corrientes, Dep. Mercedes, Macrosistema Iberá, Estancia Rincón del Diablo, *Arbo et al.* 8269a (ABL!—isotype).

*Thallus* absent, not lichenized.

*Ascomata* with apical ostioles, solitary, 0.5–0.8 mm diam., erumpent, exposed and grey-black. *Hamathecium* clear. *Ascospores* 8 per ascus, 13–17-septate, oblong, 85–150 × 20–30 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Argentina).

*Discussion.* The absence of lichenization and the extremely large ascospores compared to other species of *Polymeridium* suggest that this might not actually be a genuine

*Polymeridium* but instead belong in a non-lichenized genus in Dothideomycetes.

**Polymeridium bengoanum** (Vain.)  
**Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* 98: 11 (2014).—*Pseudopyrenula bengoana* Vain., in Hiern, *Cat. Afr. Pl.* 2(2): 457 (1901); type: Angola, Quifandango, *Welwitsch* 437 (TUR-Vain 30820!—holotype; BM—!isotype).

(Fig. 49B)

*Thallus* ecorticate, white, smooth to uneven. *Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 16–19 × 4.5–6.0 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Pantropical (reported from USA, Venezuela, Angola, Mozambique, South Africa and Australia).

**Polymeridium biloculare** R. C. Harris

*Acta Amazon. (Suppl.)* 14: 70 ('1984') [1986]; type: Brazil, Roraima, Manaus-Boa Vista Road, *Buck* s. n. (NY!—isotype).

(Fig. 50A)

*Thallus* ecorticate, white, smooth to uneven. *Ascomata* with lateral, fused ostioles, usually two aggregated, 0.3–0.5 mm diam., erumpent, pear-shaped, upper part exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 26–30 × 8–10 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Brazil).

**Polymeridium catapastoides** Aptroot

In Aptroot & Cáceres, *Nova Hedwigia* 98: 12 (2014); type: Australia, Queensland, Cape Tribulation, N of



Daintree, 1983, *Hale* 64184 (US!—holotype; ABL!—isotype).

(Fig. 50C)

*Thallus* ecorticate, yellowish white, smooth to uneven.

*Ascomata* with mostly apical, rarely somewhat eccentric ostioles, solitary, 0.3–0.5 mm diam., erumpent, hemispherical, exposed and black. *Hamathecium* clear. *Ascospores* 4–8 per ascus, 3-septate, fusiform, 24–32 × 6–11 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from Indonesia, Papua New Guinea and Australia).

### **Polymeridium catapastum (Nyl.)**

**R. C. Harris**

*Acta Amazon. (Suppl.)* 14: 70 ('1984') [1986].—*Verrucaria catapasta* Nyl., *Acta Soc. Sci. Fenn.* 7: 488 (1863).—*Arthopyrenia catapasta* (Nyl.) Müll. Arg., *Flora* 66: 318 (1883); type: Colombia, Bogotá, *Lindig* 2869 (H-Nyl 7236!—lectotype, designated here; BM, BR—isolectotypes).

*Pyrenastrum album* var. *verrucarioides* Eschw., in *Martius, Flora Bras.* 1: 147 (1833).—*Arthopyrenia tumida* Müll. Arg., *Flora* 67: 669 (1884); type: Brazil, Bahia, *Martius* s. n. (G—lectotype, Harris, *Acta Amazon. (Suppl.)* 14: 70 ('1984') [1986], not seen).

(Fig. 49E)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm, erumpent, exposed and black but ostiolar area sometimes whitish. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 25–33 × 7–10 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Possibly pantropical (previously reported from the USA, Bahamas, Cayman Islands, Cuba, El Salvador, Guyana, Colombia, Venezuela and Brazil).

*New country record. Madagascar:* *Fianarantsoa:* Ambositra, Ambalamanakara, 1984, *Aptroot & Hensen* 12822 (ABL).

### **Polymeridium chioneum (Mont.)**

**R. C. Harris**

*Lichenogr. Thomsoniana:* 141 (1998).—*Verrucaria chionea* Mont., *Ann. Sci. Nat. Bot., sér. 2* 19: 58 (1843).—*Pyrenula chionea* (Mont.) Trevis., *Spighe e Paglie:* 17 (1853).—*Pseudopyrenula chionea* (Mont.) Zahlbr., *Catal. Lich. Univ.* 1: 355 (1922); type: French Guiana, *Leprieur* 613 (PC-Mont—lectotype, Harris, *Lichenogr. Thomsoniana:* 141, 1998, not seen).

*Polymeridium pleiomerooides* (Müll. Arg.) R. C. Harris, *Acta Amazon. (Suppl.)* 14: 70 ('1984') [1986].—*Arthopyrenia pleiomerooides* Müll. Arg., *Bot. Jahrb. Syst.* 6: 407 (1885); type: Cuba, *Wright* s. n. (G!—holotype; Müller, *Verr. Cub.* 76).

(Fig. 50K & L)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., erumpent, exposed and black. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 8–12-septate, oblong, 40–50 × 9–11 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropical (reported from Cuba, French Guiana, Guyana, Venezuela and Brazil).

### **Polymeridium cinereonigricans**

**(Vain.) R. C. Harris**

*Bol. Mus. Paraense Emilio Goeldi, Ser. Bot.* 7: 631 ('1991') [1993].—*Thelenella cinereonigricans* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 216 (1890).—*Clathroporina cinereonigricans* (Vain.) Zahlbr., *Catal. Lich. Univ.* 1: 416 (1922); type: Brazil, Minas Gerais, Caraça, *Vainio* s. n. (TUR-Vain 31357—holotype, not seen; BM!—isotype; *Vainio, Lich. Bras.* 657).

(Fig. 52K)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., erumpent, lens-shaped, with upper portion exposed and grey-black.

*Hamathecium* clear. *Ascospores* 8 per ascus, 8–11-septate, oblong-fusiform, 30–45 × 9–11 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Brazil) and Hawai'i.

**Polymeridium contendens (Nyl.)  
R. C. Harris**

In Tucker & Harris, *Bryologist* **83**: 12 (1980).—*Verrucaria contendens* Nyl., *Acta Soc. Sci. Fenn.* **7**: 492 (1863).—*Arthopyrenia contendens* (Nyl.) Müll. Arg., *Flora* **66**: 317 (1883); type: Colombia, San Antonio, Lindig 2877 (H-Nyl 7331!—holotype; BM!, BR—iso-types).

*Arthopyrenia atroalba* Vain., *Acta Soc. Fauna Fl. Fenn.* **7**(2): 234 (1890); type: Brazil, Minas Gerais, Lafayette, Vainio s. n. (TUR-Vain 32132—holotype, not seen; BM!—isotype; Vainio, *Lich. Bras.* 334).

(Fig. 49H)

*Thallus* ecorticate, white, smooth to uneven. *Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, lens-shaped, exposed and black. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 3-septate, oblong-fusiform, 12–16 × 4–6 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from USA, Costa Rica, Colombia, Venezuela, Guyana and Brazil). Incorrectly reported from Australia, Papua New Guinea and Tanzania.

**Polymeridium corticatum  
A.A. Menezes et al.**

In Aptroot et al., *Lichenologist* **45**: 546 (2013); type: Brazil, Ceará, Chapada do Araripe, 2012, Menezes s. n. (ISE 15888!—holotype).

(Fig. 51D & E)

*Thallus* corticate, cream-white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, conical, exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 9–13-septate, oblong, 32–36 × 6–7 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropical (reported from Brazil).

**Polymeridium costaricense Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* **98**: 14 (2014); type: Costa Rica, Guanacaste, Palo Verde National Park, trail to Rio Tempisque, 2003, Will-Wolf 12512d (INB!—holotype; WIS!—isotype).

(Fig. 52A)

*Thallus* ecorticate, white, smooth to uneven. *Ascomata* with apical ostioles, solitary, 0.4–0.6 mm diam., erumpent, exposed and black. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 8–12-septate, oblong-fusiform, 40–50 × 9–11 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Costa Rica and Brazil).

**Polymeridium dithecium R. C. Harris**

*Bol. Mus. Paraense Emílio Goeldi, Ser. Bot.* **7**: 632 ('1991') [1993]; type: Venezuela, Amazonas, Río Casiquiare, Kubitzki s. n. (NY!—holotype).

(Fig. 51A)

*Thallus* ecorticate, white, smooth to uneven. *Ascomata* with lateral, fused ostioles, usually two aggregated, 0.3–0.5 mm diam., erumpent, lens-shaped, upper part exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 7–9-septate, fusiform, 28–35 × 6–8 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropical (reported from Venezuela and Brazil).

**Polymeridium endocrocinum**  
**R. C. Harris**

*Bol. Mus. Paraense Emilio Goeldi, Ser. Bot. 7: 633* ('1991') [1993]; type: Brazil, Amazonas, Serra Aracá plateau, Samuels 521 (NY!—holotype).

(Fig. 49K)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., erumpent, hemispherical, exposed and black but with pale ostiolar area, internally with yellow-orange, K+ purple pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 30–34 × 9–10 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–; ascomata internally K+ purple, with yellow-orange anthraquinone.

*Distribution.* Neotropical (reported from Brazil).

**Polymeridium flavothecium**  
**R. C. Harris**

*Bol. Mus. Paraense Emilio Goeldi, Ser. Bot. 7: 633* ('1991') [1993]; type: Dominican Republic, Dist. Nacional, Sierra Prieta, 18 km NW of Villa Melia, Harris 20160 (NY!—holotype).

(Fig. 51G)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with lateral, separate ostioles, solitary, 0.3–0.4 mm diam., prominent, wart-shaped to conical, exposed and black. *Hamathecium* interspersed with yellow, K+ red granules below. *Ascospores* 8 per ascus, 8–12-septate, oblong-fusiform, 40–55 × 9–11 µm, hyaline, IKI–, wall smooth, often breaking into part spores.

*Chemistry.* Thallus UV–, K–; hamathecium K+ red, with yellow anthraquinone.

*Distribution.* Neotropical (reported from Costa Rica and the Dominican Republic).

**Polymeridium glaucostrum (Vain.)**  
**R. C. Harris**

*Bol. Mus. Paraense Emilio Goeldi, Ser. Bot. 7: 634* ('1991') [1993].—*Arthopyrenia glaucoatra* Vain., *Ann. Acad. Sci. Fenn. Ser. A 19*(15): 12 (1923); type: Philippines, Luzon, Benguet, Pauai, McGregor 8553 (TUR-Vain 32107!—holotype; BM!, F!, NY!, US!—isotypes).

(Fig. 49F)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., erumpent, laterally covered by thallus but apically exposed and black. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 3-septate, fusiform, 26–34 × 6–9 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from Sri Lanka and the Philippines).

**Polymeridium intersum Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* 98: 16 (2014); type: Australia, Queensland, Kuranda, Jumrum Creek track, 1988, *Aptroot & Aptroot* 22755 (CANB!—holotype; ABL!—isotype).

(Fig. 49I)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, exposed and black. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 3-septate, fusiform, 16–20 × 3–5 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Brazil, Philippines and Australia).

**Polymeridium jordanii (C. W. Dodge)**  
**Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* 98: 18 (2014).—*Pseudopyrenula jordanii* C. W. Dodge, *Nova Hedwigia, Beih. 12: 11* (1964); type: Sierra Leone, Colony, Sugar Loaf Mountain, Deighton M44440 (BM!—isotype).



(Fig. 52E)

*Thallus* ecorticate, white, smooth to uneven. *Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 4–7-septate, fusiform, 21–30 × 5–9 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from the USA, Puerto Rico, Brazil, Mozambique, Sierra Leone, Yemen, Aldabra, Hong Kong, the Philippines and Indonesia).

### **Polymeridium julelloides**

**E. L. Lima et al.**

In Aptroot et al., *Lichenologist* 45: 548 (2013); type: Brazil, Pernambuco, Buíque, Vale do Catimbau National Park, 900 m, 2011, *Lima* 145 (ISE!—holotype).

(Fig. 52L)

*Thallus* ecorticate, pale pinkish brown, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., erumpent to prominent, conical, exposed and black, with brownish ostiole. *Hamathecium* clear. *Ascospores* 8 per ascus, small muriform, ellipsoid to slightly clavate, 25–29 × 11–13 µm, hyaline, IKI–, wall smooth but generally constricted at some septa, septa often partly oblique.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Brazil).

### **Polymeridium microsporium** (Makhija & Patw.) Aptroot

In Aptroot & Cáceres, *Nova Hedwigia* 98: 18 (2014).—*Trypethelium microsporium* Makhija & Patw., *Ĵ. Hattori Bot. Lab.* 73: 201 (1993); type: India, Andaman Islands, Middle Andaman, Yeratta, *Sethy & Nagarkar* AMH 85.2210 (ABL!, BM!—isotypes).

(Fig. 50D)

*Thallus* ecorticate, white, smooth to uneven. *Ascomata* with apical ostioles, solitary, 0.2–0.3 mm diam., erumpent, exposed and black. *Hamathecium* inspersioned. *Ascospores* 8 per ascus, 3-septate, fusiform, 11–16 × 3–6 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Brazil, India, Papua New Guinea, Hawai'i and Fiji).

### **Polymeridium multiforme** Aptroot

In Aptroot & Cáceres, *Nova Hedwigia* 98: 18 (2014); type: Guyana, Rupununi Distr., trail at base of Mt. Makarapan, 1988, *Maas et al.* 7586c (B!—holotype; ABL!—isotype).

(Fig. 51C)

*Thallus* ecorticate, whitish grey, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.3 mm diam., erumpent, exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, (4–)5(–7)-septate, fusiform, 19–26 × 5–7 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropical (reported from Venezuela, Guyana and Brazil).

### **Polymeridium multiseptatum** Aptroot et al.

In Aptroot & Cáceres, *Nova Hedwigia* 98: 19 (2014); type: Brazil, Ceará, Chapada do Araraípe, 2012, *Menezes* 782 (ISE 15943!—holotype).

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, exposed and black. *Hamathecium* inspersioned. *Ascospores* 8 per ascus, 4–7-septate, fusiform, 18–28 × 5–7 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K-. TLC: lichexanthone.

*Distribution.* Pantropical (reported from Brazil and Angola).

### **Polymeridium neblinae R. C. Harris**

*Bol. Mus. Paraense Emilio Goeldi, Ser. Bot.* 7: 635 ('1991') [1993]; type: Venezuela, Amazonas, Cerro de la Neblina, Buck 10788 (NY!—holotype).

(Fig. 52B)

*Thallus* ecorticate, white-grey, smooth to uneven.

*Ascomata* with lateral, separate ostioles, solitary, 0.3–0.5 mm diam., erumpent, mostly exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 7–9-septate, fusiform, 40–50 × 8–9 µm, hyaline, IKI-, wall smooth.

*Chemistry.* Thallus UV-, K-. TLC: no substances detected.

*Distribution.* Neotropical (previously reported only from Venezuela).

*New country record. Brazil:* Sergipe: Santa Luzia do Itanh, Mata do Junco, 2011, Cáceres 8809 (ISE, ABL).

### **Polymeridium neuwirthii Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* 98: 20 (2014); type: Venezuela, Puerto Ajacucho, at Orinoco, 2005, *Neuwirth* 8409 (B!—holotype; ABL, hb. Neuwirth!—isotypes).

(Fig. 51H)

*Thallus* ecorticate, pinkish grey, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, exposed and black. *Hamathecium* interspersed with very large droplets. *Ascospores* 8 per ascus, 7-septate, fusiform, 30–33 × 9–10 µm, hyaline, IKI-, wall smooth.

*Chemistry.* Thallus UV-, K-. TLC: no substances detected.

*Distribution.* Neotropical (reported from Venezuela).

### **Polymeridium ocellatum (Müll. Arg.) Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* 98: 20 (2014).—*Polyblastia ocellata* Müll. Arg., *Flora* 65: 402 (1882).—*Verrucaria ocellata* Leight., *Trans. Linn. Soc. London* 35: 458 (1866) *non* Hoffm. (1790).—*Polyblastiopsis ocellata* (Müll. Arg.) Zahlbr., *Cat. Lich. Univ.* 1: 351 (1922).—*Exiliseptum ocellatum* (Müll. Arg.) R. C. Harris, *Acta Amazon. (Suppl.)* 14: 66 ('1984') [1986]; type: Brazil, Amazonas, São Gabriel, Spruce 244 (BM!—isotype).

*Thallus* ecorticate, greenish grey, smooth to uneven.

*Ascomata* with lateral, fused ostioles, a few aggregated, 0.2–0.3 mm diam., immersed, only uppermost part exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, submuriform, fusiform, with constrictions at septa, 15–16 × 6–8 µm, hyaline, IKI-, wall smooth.

*Chemistry.* Thallus UV+ yellow, K-. TLC: lichexanthone.

*Distribution.* Neotropical (reported from Brazil).

### **Polymeridium pleiomerellum (Müll. Arg.) R. C. Harris**

In Egan, *Bryologist* 90: 164 (1987).—*Arthopyrenia pleiomerella* Müll. Arg., *Bot. Jahrb. Syst.* 6: 406 (1885); type: Cuba, Wright s.vn. (G!—holotype; Müller, *Verr. Cub.* 107a).

(Fig. 51L)

*Thallus* ecorticate, white-grey, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., erumpent, exposed and grey-black. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 7–11-septate, fusiform, 25–36 × 5–9 µm, hyaline, IKI-, wall smooth.

*Chemistry.* Thallus UV-, K-. TLC: no substances detected.

*Distribution.* Probably pantropical (previously reported from the USA, Mexico,

Jamaica, Puerto Rico, Cuba, Brazil and Papua New Guinea).

*New country record. New Caledonia:* Yaté, 1950, *Baumann-Bodenheim* 6431 (hb. John).

### **Polymeridium pleurothecium**

**R. C. Harris**

*Bol. Mus. Paraense Emilio Goeldi, Ser. Bot.* 7: 636 ('1991') [1993]; type: Guyana, Mt Ayanganna, Potaro, *Samuels* 5085 (NY!—holotype).

(Fig. 52C)

*Thallus* ecorticate, white-grey, smooth to uneven.

*Ascomata* with lateral, separate ostioles, solitary, 0.3–0.6 mm diam., prominent, wart-shaped, exposed and grey-black. *Hamathecium* clear. *Ascospores* 8 per ascus, 9–13-septate, fusiform, (35–)50–70 × 12–15 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Costa Rica, Venezuela, Guyana, Papua New Guinea and Australia).

### **Polymeridium pyrenastroides** Aptroot

In Aptroot & Cáceres, *Nova Hedwigia* 98: 22 (2014); type: Venezuela, Est. Amazonas, Alto Orinoco, 15 km W of Esmeralda, W bank of Surumoni, 110 m, 1997, *Hafellner & Komposch* 209–6–41 (GZU!—holotype).

(Fig. 48J)

*Thallus* ecorticate, whitish grey, smooth to uneven.

*Ascomata* with lateral, fused ostioles, a few aggregated, 0.4–0.6 mm diam., erumpent, pear-shaped and appearing triangular from above, upper part exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 28–32 × 9–11 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropical (reported from Venezuela).

### **Polymeridium pyrenuloides** (Müll. Arg.) Aptroot

In Aptroot & Cáceres, *Nova Hedwigia* 98: 22 (2014).—*Arthopyrenia pyrenuloides* Müll. Arg., *Mém. Soc. Phys. Genève* 30(3): 27 (1888).—*Arthopyrenia verrucarioides* Zahlbr., *Catal. Lich. Univ.* 1: 312 (1921) nom. superfl.; type: South America, "in cortice cinchonarum" (G!—lectotype, Harris, *Bol. Mus. Paraense Emilio Goeldi, Ser. Bot.* 7: 639 ('1991') [1993]).

*Arthopyrenia paulensis* Zahlbr., *Akad. Wiss. Wien, math.-naturwiss. Kl. Denkschr.* 83: 89 (1909); type: Brazil, São Paulo, S. Cruz, Bella Vista, *Wettstein & Schiffner* s. n. (W—holotype, not seen).

(Fig. 48H)

*Thallus* ecorticate, white, smooth to uneven. *Ascomata* with apical ostioles, solitary, 0.2–0.3 mm diam., prominent, hemispherical to wart-shaped, exposed and black. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 3-septate, fusiform, 17–20 × 5–7 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Probably pantropical (reported from Brazil and Australia).

### **Polymeridium quinqueseptatum** (Nyl.) R. C. Harris

In Tucker & Harris, *Bryologist* 83: 12 (1980).—*Verrucaria quinqueseptata* Nyl., *Mém. Soc. Acad. Maine-et-Loire* 4: 58 (1858).—*Arthopyrenia quinqueseptata* (Nyl.) Müll. Arg., *Flora* 68: 326 (1885); type: USA, South Carolina, *Ravenel* s. n. (BM!—isotype).

*Verrucaria pustulosa* Stirt., *Proc. Roy. Philos. Soc. Glasgow* 13: 191 (1881); type: India, Assam, Tezapore, *Watt* s. n. (BM!—isotype).

*Arthopyrenia comparatula* Müll. Arg., *Bot. Jahrb. Syst.* 6: 406 (1885); type: Cuba, *Wright* s. n. (G!—lectotype, designated here; Müller, *Verr. Cub.* 152).

*Pseudopyrenula polyphragmia* Vain., *Bol. Soc. Broteriana sér. 2* 6: 178 (1930); type: Mozambique, Palma, *Pires de Lima* 303 (TUR-Vain 34713—lectotype, Harris, *Bol. Mus. Paraense Emilio Goeldi, Ser. Bot.* 7: 639 ('1991') [1993], not seen).

(Fig. 51I–K)



*Thallus* ecorticate, white-grey, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., erumpent to prominent, hemispherical, exposed and black. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 4–7-septate, fusiform, 18–28 × 5–7 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from the USA, Costa Rica, Cuba, Jamaica, Netherlands Antilles, Venezuela, Brazil, Angola, Mozambique, Seychelles, India, Thailand, Philippines and Australia).

### **Polymeridium refertum (Stirt.) Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* **98**: 23 (2014).—*Trypethelium refertum* Stirt., *Proc. Roy. Phil. Soc. Glasgow* **11**: 321 ('1878') [1879].—*Plagiotrema refertum* (Stirt.) Makhija & Patw., *J. Hattori Bot. Lab.* **73**: 209 (1993); type: India, Nilgiris, 1814, *Watt* s. n. (BM!—isolecotype, Makhija & Patwardhan, *J. Hattori Bot. Lab.* **73**: 209, 1993).

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with lateral, separate ostioles, solitary, 0.2–0.4 mm diam., erumpent to prominent, exposed and black. *Hamathecium* inspersed. *Ascospores* 8 per ascus, (3–)4(–6)-septate, fusiform, 22–26 × 7–9 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from India).

### **Polymeridium siamense (Vain.) Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* **98**: 24 (2014).—*Arthopyrenia siamensis* Vain., *Ann. Soc. Zool. Bot. Fenn. Vanamo* **1**(3): 55 (1921); type: Thailand, Doi Suthep, *Hosseus* s. n. (TUR-Vain 32114—holotype, not seen).

*Arthopyrenia obvelata* Vain., *Ann. Acad. Sci. Fenn.*, ser. *A* **19**(15): 11 (1923); type: Philippines, Luzon, Benguet

Prov., Pauai, *McGregor* 8606 (TUR-Vain 32108—holotype, not seen).

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., erumpent, exposed and black. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 3-septate, fusiform, 20–23 × 6–8 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (reported from Guyana, Brazil, Australia, Philippines and Thailand).

### **Polymeridium simulans R. C. Harris**

*Bol. Mus. Paraense Emilio Goeldi, Ser. Bot.* **7**: 641 ('1991') [1993]; type: Brazil, Amazonas, 5 km E of Borba, *Nelson* 1310 (NY!—holotype).

(Fig. 50B)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with lateral, separate ostioles, solitary, 0.4–0.6 mm diam., erumpent, pear-shaped, exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 30–35 × 12–13 µm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Venezuela, Guyana and Brazil).

### **Polymeridium stramineoatrum (Vain.) Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* **98**: 24 (2014).—*Arthopyrenia stramineoatra* Vain., *Acta Soc. Fauna Fl. Fenn.* **7**(2): 234 (1890); type: Brazil, Minas Gerais, Caraça, *Vainio* s. n. (TUR-Vain 32133—holotype, not seen; *Vainio*, *Lich. Bras.* 1566).

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with mostly lateral, separate ostioles, solitary, 0.3–0.4 mm diam., erumpent

to prominent, exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 24–30 × 7–10 µm, hyaline, IKI–, wall smooth.

**Chemistry.** Thallus UV+ yellow, K–. TLC: lichexanthone.

**Distribution.** Neotropical (reported from Venezuela and Brazil).

### **Polymeridium subcinereum (Nyl.)**

**R. C. Harris**

In Tucker & Harris, *Bryologist* **83**: 12 (1980).—*Verrucaria subcinerea* Nyl., *Mém. Soc. Acad. Maine-et-Loire* **4**: 37 (1858).—*Pyrenula subcinerea* (Nyl.) Tuck., *Gener. Lich.*: 273 (1872).—*Porina subcinerea* (Nyl.) Zahlbr., *Catal. Lich. Univ.* **1**: 405 (1922); type: USA, Texas, *Tuckerman* 85 (H-Nyl 1529!—lectotype, designated here).

*Arthopyrenia subimitans* Müll. Arg., *Bull. Soc. Roy. Bot. Belg.* **32**(1): 169 (1893); type: Costa Rica, Puntarenas, Boruca, *Tonduz* s. n. (G!—lectotype, designated here; BM, BR—isolectotypes; Pittier, *Pl. Costaric. Exs.* 6287).

*Pseudopyrenula follmannii* C. W. Dodge, *Nova Hedwigia* **12**: 308 (1966); type: Chile, Aconcagua Prov., Los Molles, *Follmann* 14852-D (FH-Dodge—holotype, not seen).

*Massarina operculicola* M. Morelet, *Bull. Soc. Sci. Nat. Archéol. Toulon & Var* **36**: 14 (1980); type: France, Entrecasteaux, *Morelet* 1276 (hb. Morelet, Champenoux [‘PFN’, ‘CNRF 898’, ‘INRA, Nancy’]—holotype).

(Fig. 50E & F)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary to sometimes confluent, 0.3–0.5 mm diam., erumpent, exposed and black. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 15–20 × 5–7 µm, hyaline, IKI–, wall smooth.

**Chemistry.** Thallus UV–, K–. TLC: no substances detected.

**Distribution.** Pantropical, extending into the subtropics (reported from the USA, Costa Rica, Dominican Republic, Colombia, Venezuela, Guyana, Brazil, Chile, France, Mozambique, Philippines, Papua New Guinea and Australia).

### **Polymeridium submuriforme**

**Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* **98**: 35 (2014); type: Philippines, Leyte, Prov. Leyte, between Camp Pandong Bato and Mt. Agipo, 2000, *Schumm & Schwarz* 774 (B!—holotype).

(Fig. 52J)

*Thallus* ecorticate, pinkish grey, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.6 mm diam., erumpent, wart-shaped to conical, exposed and black. *Hamathecium* inspersed. *Ascospores* 6–8 per ascus, submuriform, with partly oblique septa, fusiform, 18–20 × 6–8 µm, hyaline, IKI–, wall smooth.

**Chemistry.** Thallus UV–, K–. TLC: no substances detected.

**Distribution.** Eastern palaeotropical (reported from the Philippines).

### **Polymeridium subvirescens (Leight.)**

**Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* **98**: 25 (2014).—*Verrucaria subvirescens* Leight., *Trans. Linn. Soc. London* **25**: 488 (1866).—*Porina subvirescens* (Leight.) Zahlbr., *Cat. Lich. Univ.* **1**: 406 (1922); type: Brazil, Santarém, *Spruce* 358 (BM!—lectotype, Harris, *Acta Amazon. (Suppl.)* **14**: 70 (‘1984’) [1986]).

(Fig. 48G)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical and partly lateral, separate ostioles, solitary, 0.3–0.4 mm diam., erumpent to prominent, exposed and black. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 3-septate, fusiform, 24–33 × 6–10 µm, hyaline, IKI–, wall smooth.

**Chemistry.** Thallus UV+ yellow, K–. TLC: lichexanthone.

**Distribution.** Probably pantropical (reported from Brazil and Australia).

**Polymeridium suffusum (Knight)  
Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* **98**: 26 (2014).—*Verrucaria suffusa* Knight, *Trans. Proc. New Zealand Inst.* **15**: 356 (1882).—*Arthopyrenia suffusa* (Knight) Müll. Arg., *Bull. Soc. Roy. Bot. Belgique* **31**(2): 40 (1892); type: New Zealand, *Knight* s. n. (BM!—lectotype, designated here; H-Nyl 881!—isolectotype).

(Fig. 49G)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical or partly lateral, separate ostioles, solitary, 0.3–0.4 mm diam., erumpent, mostly covered by thallus but ostiolar area exposed and grey-black. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 3-septate, fusiform, 24–30 × 6–9 µm, hyaline, IKI–, wall smooth.

*Chemistry*. Thallus UV–, K–. TLC: no substances detected.

*Distribution*. Pantropical (reported from Costa Rica, Cuba, Puerto Rico, Brazil, Réunion, Sarawak and New Zealand).

**Polymeridium sulphurescens  
(Müll. Arg.) R. C. Harris**

*Lichenogr. Thomsoniana*: 147 (1998).—*Arthopyrenia sulphurescens* Müll. Arg., *Flora* **65**: 518 (1882).—*Pseudopyrenula sulphurescens* (Müll. Arg.) Müll. Arg., *Flora* **66**: 249 (1883); type: Australia, Queensland, Toowoomba, *Hartmann* s. n. (G!—holotype).

*Arthopyrenia oculata* Müll. Arg., *Rep. Australas. Assoc. Advancem. Sci.* **1895**: 451 (1895).—*Polymeridium oculatum* (Müll. Arg.) R. C. Harris, *Bol. Mus. Paraense Emílio Goeldi, Ser. Bot.* **7**: 635 ('1991') [1993]; type: Australia, Queensland, *Knight* 136 (G!—holotype).

*Arthopyrenia suboculata* Müll. Arg., *Bull. Herb. Boissier* **3**: 325 (1895); type: Australia, Queensland, *Knight* 199 (G!—holotype).

(Fig. 50G)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical or partly lateral, separate ostioles, solitary, 0.3–0.5 mm diam., erumpent, exposed and black but ostioles usually with a white rim. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 19–27 × 8–10 µm, hyaline, IKI–, wall smooth.

*Chemistry*. Thallus UV–, K–. TLC: no substances detected.

*Distribution*. Eastern palaeotropical (reported from Papua New Guinea and Australia), rarely also on rock.

**Polymeridium tribulationis Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* **98**: 26 (2014); type: Australia, Queensland, Cape Tribulation, 2 km off main road between Oil Palms and Coopers Creek, 1983, *Hale* 641717 (CANB!—holotype; ABL!, US!—isotypes).

(Fig. 49J)

*Thallus* ecorticate, yellowish white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., prominent to sessile, mostly covered by thallus and grey, except for black upper part, and ostioles usually with a white rim. *Hamathecium* interspersed. *Ascospores* 8 per ascus, 3-septate, fusiform, 20–24 × 7–10 µm, hyaline, IKI–, wall smooth.

*Chemistry*. Thallus UV–, K–. TLC: no substances detected.

*Distribution*. Possibly pantropical (previously known only from Australia), below reported from Brazil; the first species of the *P. sulphurescens*-group, characterized by sub-globose, rather sessile ascomata with a ring around the ostiole, found in the Neotropics.

*New country record*. **Brazil**: Ceará: Chapada do Araripe, Malhada Bonita, 2012, *Alves* 1526 (ISE, ABL).

**Polymeridium xanthoreagens Aptroot**

In Aptroot & Cáceres, *Nova Hedwigia* **98**: 27 (2014); type: Australia, Queensland, E of Mareeba, Davies Creek Road 17 km S of Kennedy Highway; 1983, *Hale* 64168 (CANB!—holotype; ABL!, US!—isotypes).

(Fig. 49C)

*Thallus* ecorticate, yellowish white, smooth to uneven.



*Ascomata* with apical and partly lateral, separate ostioles, solitary, 0.2–0.4 mm diam., erumpent, covered by thallus except grey-black ostiolar area with a white ring around the black ostiole. *Hamathecium* clear. *Ascospores* 8 per ascus, 3-septate, fusiform, 17–25 × 7–11 μm, hyaline, IKI–, wall smooth.

*Chemistry.* Thallus UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Eastern palaeotropical (Australia).

**Pseudopyrenula Müll. Arg.**

*Flora* 66: 247 (1883); type: *Pseudopyrenula diluta* (Fée) Müll. Arg. (lectotype; Clements & Shear, *The genera of fungi*: 288, 1931).

*Plagiotrema* Müll. Arg., *Bot. Jahrb. Syst.* 6: 387 (1885); type: *Plagiotrema cubanum* Müll. Arg. [= *Pseudopyrenula subnudata* Müll. Arg., previously cited as synonym of *Pseudopyrenula diluta* s. str. by Harris 1998, holotype].

*Thallus* ecorticate, more or less endoperidermal, white to pale yellowish or greyish, or absent in presumably non-lichenized species, smooth to uneven.

*Ascomata* solitary, exposed and black, not pseudostromatic, erumpent to prominent. *Ostioles* apical or rarely eccentric. *Hamathecium* colourless or sometimes yellow, usually interspersed with oil droplets. *Ascospores* 8 per ascus, irregularly biseriolate, symmetrically

3–5-septate, fusiform with subacute ends, not constricted at the septa when young, often surrounded by a thin gelatinous sheath, hyaline, IKI–, lumina diamond-shaped.

*Pycnidia* rather rare.

*Chemistry.* Thallus with or without lichexanthone; hamathecium and/or ascospore lumina occasionally with yellow anthraquinone.

*Discussion.* The genus *Pseudopyrenula* is a mostly tropical genus. So far, almost 100 species have been described within it, but a significant proportion of those are synonyms or have been transferred to other genera. *Pseudopyrenula* forms a monophyletic group that is characterized by a non-corticate or indistinct thallus (absent in apparently non-lichenized species) and hyaline, transversely septate, astrothelioid ascospores with diamond-shaped lumina, which separate this genus from superficially similar genera such as *Bogoriella*, *Constrictolumina*, *Dictyomeridium*, *Novomicrothelia*, and *Polymeridium*, while on the other hand it is the only genus combining an ecorticate thallus with astrothelioid ascospores. The presence of yellow oil in the ascospore lumina and/or the hamathecium is characteristics of many species in *Pseudopyrenula*. Presently, the genus encompasses less than 20 species.

**Key to the species of *Pseudopyrenula***

- 1 Thallus UV+ yellow, with lichexanthone . . . . . 2
- Thallus UV– . . . . . 6
- 2(1) Hamathecium clear; ascospores 30–45 × 8–11 μm (this synopsis) . . . . . **Pseudopyrenula cryptotheca**
- Hamathecium interspersed with hyaline or yellow oil droplets; ascospores under 37 μm long . . . . . 3
- 3(2) Hamathecium interspersed with yellow oil droplets . . . . . 4
- Hamathecium interspersed with hyaline oil droplets . . . . . 5
- 4(3) Ascospores 21–28 × 6–9 μm (Aptroot & Cáceres 2016; Fig. 53A & B) . . . . . **Pseudopyrenula flavoreagens**
- Ascospores 26–36 × 7–10 μm (Flakus *et al.* 2016; Fig. 53C) . . . . . **Pseudopyrenula flavosuperans**

- 5(3) Ascospores 21–25 × 6–9 μm (Aptroot *et al.* 2016a) . . . . . **Pseudopyrenula guianensis**  
 Ascospores 30–35 × 9–11 μm (this synopsis; Fig. 53D) . . . . . **Pseudopyrenula superans**
- 6(1) Ascospores 5-septate, 16–21 × 6–7 μm (Aptroot *et al.* 2016a) . . . . . **Pseudopyrenula hexamera**  
 Ascospores 3-septate . . . . . 7
- 7(6) Thallus corticate; ascospores 21–25 × 6–9 μm (Aptroot *et al.* 2016a; Fig. 53G) . . . . . **Pseudopyrenula thallina**  
 Thallus not corticate. . . . . 8
- 8(7) Hamathecium interspersed with hyaline or yellow oil droplets . . . . . 9  
 Hamathecium clear (but ascospores may contain yellow oil). . . . . 18
- 9(8) Hamathecium interspersed with yellow oil droplets . . . . . 10  
 Hamathecium interspersed with hyaline oil droplets (but ascospores may contain yellow oil). . . . . 13
- 10(9) Ascospores 37–44 × 10–12 μm (this synopsis; Fig. 53H) . . . . . **Pseudopyrenula endoxantha**  
 Ascospores under 35 × 10 μm . . . . . 11
- 11(10) Ascospores 25–30 × 7.5–8.5 μm (A. Aptroot & P. Diederich, unpublished data) . . . . . **Pseudopyrenula media**  
 Ascospores 18–25 × 6–9 μm . . . . . 12
- 12(11) Ascospores 21–25 × 6–9 μm; hamathecium K+ deep yellow to reddish (this synopsis; Fig. 53I–K) . . . . . **Pseudopyrenula subgregaria**  
 Ascospores 18–22 × 6–8 μm; hamathecium K+ weakly purplish (this synopsis) . . . . . **Pseudopyrenula endoxanthoides**
- 13(9) Ascoma wall with yellow, K+ red pigment; ascospores 21–32 × 7–10 μm (this synopsis; Fig. 53L) . . . . . **Pseudopyrenula cerei**  
 Ascoma wall without yellow pigment . . . . . 14
- 14(13) Thallus saxicolous; ascospores 35–45 × 11–13 μm (this synopsis; Fig. 54A) . . . . . **Pseudopyrenula saxicola**  
 Thallus corticolous; ascospores under 38 μm long . . . . . 15
- 15(14) Ascospores 33–37 × 10–12 μm (this synopsis; Fig. 54B) . . . . . **Pseudopyrenula dubia**  
 Ascospores under 33 μm long . . . . . 16
- 16(15) Ascospores (24–)26–32 × 7–10 μm (this synopsis; Fig. 54C–E) . . . . . **Pseudopyrenula diluta**  
 Ascospores 21–25 × 6–9 μm . . . . . 17
- 17(16) Ostioles eccentric (this synopsis; Fig. 54F) . . . . . **Pseudopyrenula cubana**  
 Ostioles apical (this synopsis; Fig. 54G–L) . . . . . **Pseudopyrenula subnudata**

- 18(8) Thallus without algae, brownish, of bark colour . . . . . 19  
 Thallus with algae, whitish . . . . . 21
- 19(18) Ascospores 45–55 × 12–15 µm (this synopsis) . . . . . **Pseudopyrenula staphyleae**  
 Ascospores under 40 µm long . . . . . 20
- 20(19) Ascospores 25–29 × 7–9 µm (this synopsis; Fig. 53E) . . . . . **Pseudopyrenula papuana**  
 Ascospores 30–39 × 6–8 µm (this synopsis) . . . . . **Pseudopyrenula serusiauxii**
- 21(18) Ascospores 26–32 × 7–10 µm (Aptroot *et al.* 2016a; Fig. 53F) . . . . .  
 . . . . . **Pseudopyrenula americana**  
 Ascospores 30–35 × 9–11 µm (this synopsis; Fig. 53D) . . . . .  
 . . . . . **Pseudopyrenula superans**

### **Pseudopyrenula cerei Vain.**

*Acta Soc. Fauna Fl. Fenn.* 7(2): 212 (1890); type: Brazil, Rio de Janeiro, Cerei, *Vainio* s. n. (TUR-Vain 30815!—holotype; Vainio, *Lich. Bras.* 21).

(Fig. 53L)

*Thallus* ecorticate, white, smooth to uneven.  
*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., prominent to almost sessile, hemispherical to subglobose, exposed and black, with yellow pigment in wall. *Hamathecium* inspersed, hyaline. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 21–32 × 7–10 µm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus and ascomata UV–, K–; ascomata internally K+ deep yellow, with yellow pigment.

*Distribution.* Neotropical (reported from Brazil).

### **Pseudopyrenula cryptotheca Komposch et al.**

*Lichenologist* 34: 229 (2002); type: Venezuela, Estado Amazonas, Alto Orinoco c. 15 km W of La Esmeralda, plot of tower crane on the W riverbank of Surumoni, *Hafellner & Komposch* 3085 (GZU!—isotype).

(Fig. 53A)

*Thallus* ecorticate, white to yellowish, apparently not lichenized, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., immersed-erumpent, covered by thallus. *Hamathecium* clear, hyaline. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 30–45 × 8–11 µm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus and ascomata UV+ yellow, K–. TLC: lichexanthone.

*Distribution.* Neotropical (reported from Venezuela).

### **Pseudopyrenula cubana (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816791

*Plagiotrema cubanum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 387 (1885); type: Cuba, *Wright* s. n. (G!—lectotype, designated here; L!—isoelectotype; Müller, *Verr. Cub.* 62).

(Fig. 54F)

*Thallus* ecorticate, whitish to pale brownish, smooth to uneven.

*Ascomata* with eccentric ostioles, solitary, 0.3–0.5 mm diam., erumpent, pear-shaped, exposed and black. *Hamathecium* inspersed, hyaline. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 21–25 × 6–9 µm, hyaline but sometimes lumina filled with yellow oil, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.



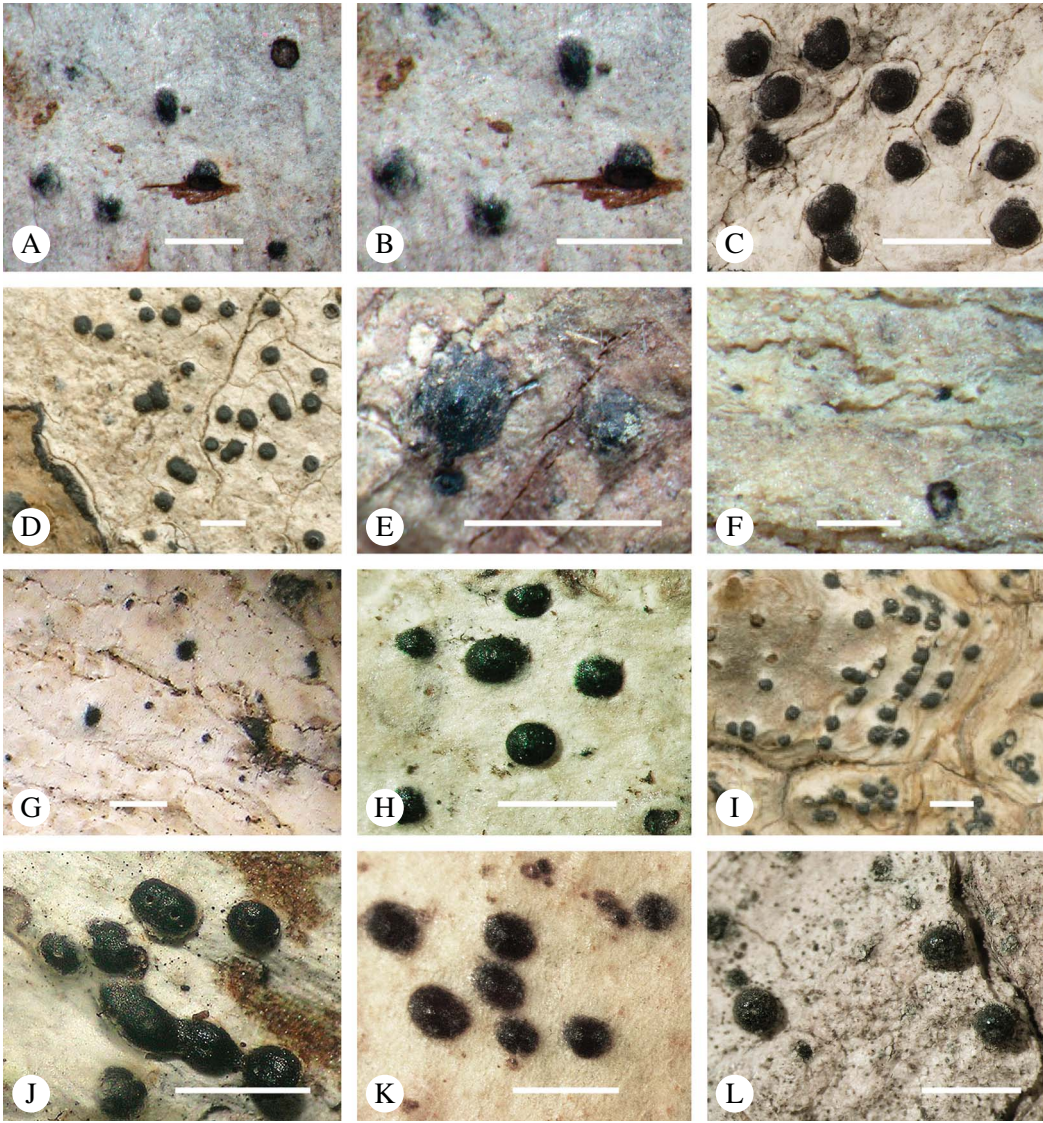


FIG. 53. Habitus of *Pseudopyrenula* species. A & B, *P. flavoreagens* (Brazil, isotype); C, *P. flavosuperans* (Bolivia, holotype); D, *P. superans* (Cuba, holotype); E, *P. papuana* (Papua New Guinea, isotype); F, *P. serusiauxii* (Papua New Guinea, isotype); G, *P. thallina* (Costa Rica, holotype); H, *P. endoxantha* (Dominica, holotype); I–K, *P. subgregaria* (I, Cuba, holotype; J, Costa Rica, Lücking s. n.; K, USA, Florida, Nelsen s. n.); L, *P. cerei* (Brazil, holotype). Scales = 1 mm.

*Distribution.* Neotropical (reported from Cuba).

***Pseudopyrenula diluta* (Fée) Müll. Arg.**

*Flora* 66: 249 (1883).—*Verrucaria diluta* Fée, *Essai Crypt. Écorc. Suppl.*: 85 (1837).—*Pyrenula diluta* (Fée) Tuck.,

*Proceed. Americ. Acad. Arts Sci.* 7: 234 (1868); type: South America, s.col. (G!—lectotype, Harris, *Lichenogr. Thomsoniana*: 137, 1998).

*Verrucaria diremta* Nyl., *Ann. Soc. Sci. Fenn.* 7: 492 (1863).—*Pseudopyrenula diremta* (Nyl.) Müll. Arg., *Flora* 66: 249 (1883); type: Colombia, Villeta, Lindg 2827 (H-Nyl 1039!—holotype; BM, BR—iso-types).



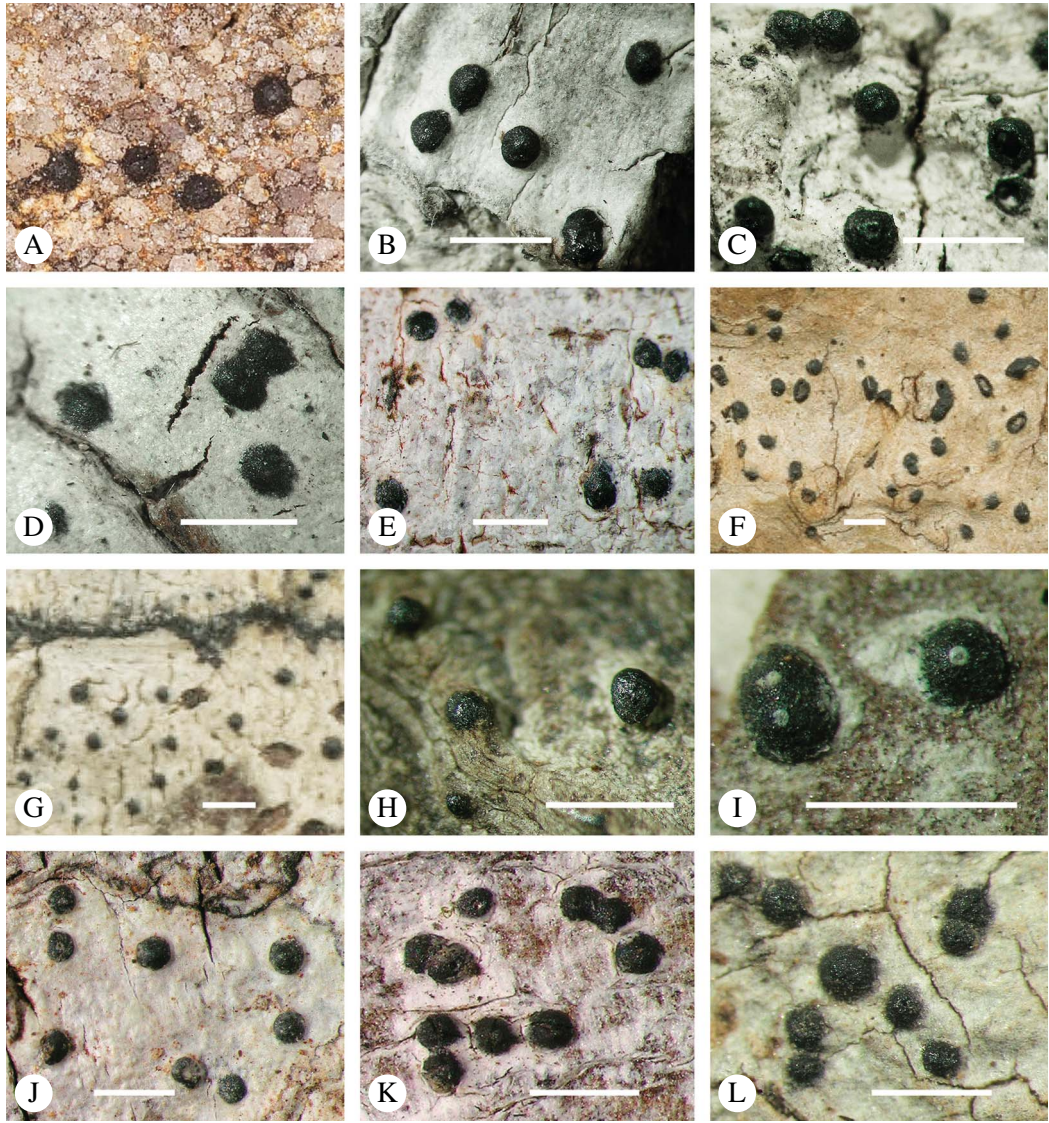


FIG. 54. Habitus of *Pseudopyrenula* species. A, *P. saxicola* (Brazil, lectotype); B, *P. dubia* (Guadeloupe, holotype); C–E, *P. diluta* (C, Brazil, holotype of *P. atroalba*; D, Brazil, holotype of *P. sitiana*; E, Fiji, Lumbsch 19825i); F, *P. cubana* (Cuba, lectotype); G–L, *P. subnudata* (G, Brazil, holotype; H, Brazil, holotype of *P. araucariae*; I, Thailand, holotype of *P. diluta* var. *degenerans*; J, Fiji, Lumbsch 19815t; K, Fiji, Lumbsch 19845g; L, Brazil, Cáceres 893). Scales = 1 mm.

*Pseudopyrenula albonitens* Müll. Arg., *Flora* **66**: 271 (1883); type: Brazil, Apiahy, *Puiggari* 497 (G!—holotype).

*Pseudopyrenula atroalba* Vain., *Acta Soc. Fauna Fl. Fenn.* **7**(2): 211 (1890); type: Brazil, Minas Gerais, Caraça, *Vainio* s. n. (TUR-Vain 30816!—holotype; BM!—isotype; *Vainio, Lich. Bras.* 1402).

*Pseudopyrenula sitiana* Vain., *Acta Soc. Fauna Fl. Fenn.* **7**(2): 213 (1890); type: Brazil, Sitio, *Vainio* s. n. (TUR-Vain 30814!—holotype; BM!—isotype; *Vainio, Lich. Bras.* 1089).

*Pseudopyrenula erumpens* Müll. Arg., *Bull. Soc. Roy. Bot. Belg.* **32**(1): 170 (1893); type: Costa Rica, Puntarenas,

Boruca, *Tondus* s. n. (G!—holotype; BR—iso-type; Pittier, *Pl. Costaric. Exs.* 6300).

*Pseudopyrenula oahuensis* H. Magn., *Ark. Bot. ser.* 2 3(10): 234 (1955); type: Hawai'i, Oahu, *Andersson* s. n. (UPS—holotype, not seen).

(Fig. 54C–E)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., prominent, hemispherical, exposed and black. *Hamathecium* inspersed, hyaline (reports of yellow hamathecium can be attributed to yellow ascospore lumina). *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 24–32 × 7–10 μm, hyaline but often partly with yellow oil in the lumina, IKI–, not ornamented.

*Chemistry.* Thallus and *ascomata* UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical, extending into temperate regions (previously reported from Honduras, Costa Rica, Cuba, Hispaniola, Jamaica, Puerto Rico, Nevis, St Lucia, Guadeloupe, Dominica, Martinique, Tobago, Colombia, Venezuela, Guyana, French Guiana, Galapagos, Brazil, Paraguay, Azores, Cape Verdes, St Helena, Cameroon, Guinea, Ivory Coast, Tanzania, Seychelles, India, Sri Lanka, Thailand, Sarawak, Japan, Marquesas, New Caledonia, Hawai'i and Australia).

*New country records.* **Netherlands Antilles:** *Saba:* Mt. Scenery, 2007, *Sipman* 54819 (B).—**Papua New Guinea:** *Eastern Highlands:* Mount Gahavisuka Provincial Park, 2300–2450 m, 1992, *Aptroot* 32430 (ABL).—**Malaysia:** *Sabah:* Kota Belud, Mount Kinabalu, 2800 m, 1989, *Sipman & Tan* 31290 (B).

### ***Pseudopyrenula dubia* Vain.**

*Ann. Acad. Sci. Fenn., ser. A* 6: 354 (1915); type: Guadeloupe, Savane-aux-Ananas, *Duss* 1496 (TUR-Vain 30831!—holotype; BM!—isotype).

(Fig. 54B)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., prominent, hemispherical, exposed and black. *Hamathecium* inspersed,

hyaline. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 33–37 × 10–12 μm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus UV+ yellow, K–, with lichexanthone; *ascomata* UV– yellow, K–.

*Distribution.* Neotropical (previously reported from Guadeloupe).

*Discussion.* Although synonymized with *Pseudopyrenula diluta* by Harris (1995), the species is reinstated here, because the *ascospores* are substantially larger than in the latter species.

*New country record.* **Venezuela:** *Bolivar:* Cerro Guaiquinima, 1200 m, 1990, *Sipman* 26840 (B).

### ***Pseudopyrenula endoxantha* Vain.**

*J. Bot.* 34: 292 (1896); type: Dominica, Morne Anglais, *Elliott* s. n. (TUR-Vain 30821!—holotype; BM!—isotype).

(Fig. 53H)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.4–0.6 mm diam., prominent, hemispherical, exposed and black. *Hamathecium* inspersed, yellow. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 37–44 × 10–12 μm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus and *ascomata* UV–, K–; *hamathecium*, K+ reddish, with yellow anthraquinone.

*Distribution.* Neotropical (previously reported from Dominica).

*New country record.* **Costa Rica:** *Guanacaste:* Volcán Tenorio National Park, 15 km NNW of Tilarán, 950–1000 m, 2004, *Aptroot* 60602 (ABL, INB).

### ***Pseudopyrenula endoxanthoides* Vain.**

*Hedwigia* 46: 180 (1907); type: Thailand, Koh Chang, *Schmidt* 16 (TUR-Vain 30829—holotype, not seen).

*Thallus* ecorticate, white, smooth to uneven.



*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., prominent, hemispherical, exposed and black. *Hamathecium* yellow interspersed. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 18–22 × 6–8 µm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus and ascomata UV–, K–; hamathecium K+ weakly purplish, with yellow pigment.

*Distribution.* Eastern palaeotropical (reported from Thailand).

*Discussion.* This taxon is reinstated here from synonymy with *Pseudopyrenula subgregaria*, due to subtle anatomical differences supported by molecular data (Lücking *et al.* 2016a). Thus, *P. subgregaria* has slightly larger ascospores and the hamathecium reacts K+ deep yellow to reddish, not weakly purplish, indicating the presence of different pigments.

### ***Pseudopyrenula papuana* Aptroot**

In Aptroot *et al.*, *Biblioth. Lichenol.* **64**: 148 (1997); type: Papua New Guinea, Madang, near Bogia, between Bunapas and Bunapas Mission, *Aptroot* 30326 (B!—holotype).

(Fig. 53E)

*Thallus* ecorticate, brownish, apparently not lichenized, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.8–1.6 mm diam., erumpent, lens-shaped, exposed and black. *Hamathecium* clear, hyaline. *Ascospores* 5–8 per ascus, 3-septate, fusiform-ellipsoid, 25–29 × 7–9 µm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from Papua New Guinea).

### ***Pseudopyrenula saxicola* Malme**

*Ark. Bot.* **22A**(6): 8 (1928); type: Brazil, Minas Gerais, São João d'el Rey, *Malme* 239 (S!—lectotype, Harris, *Lichenogr. Thomsoniana*: 139, 1998).

(Fig. 54A)

*Thallus* saxicolous, ecorticate, pale brownish, uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., erumpent to prominent, hemispherical, exposed and black. *Hamathecium* interspersed (rarely indistinctly so), hyaline. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 35–45 × 11–13 µm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (reported from Brazil).

### ***Pseudopyrenula serusiauxii* Aptroot**

*Tropical Bryology* **14**: 29 (1998); type: Papua New Guinea, Madang Province, Balek Wildlife Sanctuary, c. 15 km S of Madang along road to Lae, *Aptroot* 36864 (B!—holotype).

(Fig. 53F)

*Thallus* ecorticate, brownish (bark colour), not lichenized.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., erumpent to prominent, hemispherical with flattened top, exposed and black. *Hamathecium* clear, hyaline. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 30–39 × 6–8 µm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Eastern palaeotropical (reported from Papua New Guinea).

### ***Pseudopyrenula staphyleae* (Petr.) Aptroot**

*Nova Hedwigia* **66**: 156 (1998).—*Massarina staphyleae* Petrak, *Sydowia* **6**: 7 (1952); type: USA, Florida, Wekiwa Spa, *Shear* P787 p.p. (W 06032!—holotype).

*Thallus* ecorticate, brownish (bark colour), not lichenized.

*Ascomata* with apical ostioles, solitary, 0.3–0.5 mm diam., erumpent to prominent, hemispherical, exposed and black. *Hamathecium* clear, hyaline. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 45–55 × 12–15 µm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* North American (USA).

### ***Pseudopyrenula subgregaria* Müll. Arg.**

*Bot. Jahrb. Syst.* 6: 408 (1885); type: Cuba, *Wright* s. n. (G!—holotype; L!—isotype; Müller, *Verr. Cub.* 80).

Fig. 53I–K

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.3–0.4 mm diam., prominent, hemispherical, exposed and black. *Hamathecium* yellow interspersed. *Ascospores* 8 per ascus, 3-septate, fusiform-ellipsoid, 21–25 × 6–9 µm, hyaline, IKI–, not ornamented.

*Chemistry.* Thallus and ascomata UV–, K–; hamathecium, K+ deep yellow to reddish, with yellow anthraquinone.

*Distribution.* Pantropical (previously reported from the USA, Costa Rica, Cuba, Sri Lanka and Australia).

*Discussion.* Specimens with comparatively small ascospores and yellow hamathecium interspersed (which constitutes a rare, constant character, not to be confused with yellow oil inside the ascospores, which seems to be an inconstant character in this group) are now recognized as a species separate from *Pyrenula subnudata*, with *P. subgregaria* being the oldest available name; the yellow-interspersed taxon is less widespread than *P. subnudata*. Unfortunately, the name *P. subgregaria* has been used mostly in the sense of *P. subnudata* s. lat. (including both hyaline and yellow-interspersed specimens),

so that most reports in the literature cannot be evaluated; they are tentatively listed under *P. subnudata* below.

*New country records.* **El Salvador:** Ahuachapan, San Francisco Menendez, 1993, *Sipman et al.* 37961 (B).—**Panamá:** Veraguas: Bahía Honda, 2001, *Cabrera & Etayo* 18518 (ABL, hb. Etayo).—**French Guiana:** Saül, 1986, *Montfoort & Ek* 8 (B).—**Guyana:** Upper Takutu: Rupununi Savannah, Karanambo Ranch, 1992, *Sipman* 57268 (B).—**Brazil:** Minas Gerais: Serra do Caraça, Parque Natural do Caraça, 1270 m, 1997, *Aptroot* 41518, 41519, 41425, 41474 (ABL, SP).—**China:** Yunnan: Xishuangbanna, Menglun, 2002, *Aptroot* 57111 (ABL).—**India:** West Bengal: Sundarban Biosphere Reserve, *Jagadeesh Ram* 749 (ABL, BSA).—**Indonesia:** Irian Jaya: Padjah Ampat Archipelago, P. Misool, Lilinta, *Zaneveld*, 1949 (ABL, L).—**Java:** Serang, 1937, *Groenhart* 592 (ABL, L).

### ***Pseudopyrenula subnudata* Müll. Arg.**

*Flora* 66: 272 (1883); type: Brazil, Apiahy, *Puiggari* 138b p.p. (G!—holotype).

*Pseudopyrenula flavicans* Müll. Arg., *Bot. Jahrb. Syst.* 6: 408 (1885); type: Cuba, *Wright* s. n. (G!—lectotype, designated here; BM!—isolectotype; Müller, *Lich. Cub.*, Ser. II: 650).

*Pseudopyrenula elliptica* Müll. Arg., *Bot. Jahrb. Syst.* 6: 409 (1885); type: Cuba, *Wright* s. n. (G!—holotype).

*Pseudopyrenula araucariae* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 212 (1890); type: Brazil, Minas Gerais, Caraça, *Vainio* s. n. (TUR-Vain 30775!—holotype; *Vainio*, *Lich. Bras.* 1461).

*Arthopyrenia minutissima* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 234 (1890); type: Brazil, Minas Gerais, Lafayette, *Vainio* s. n. (TUR-Vain 32106—holotype, not seen; BM!—isotypes; *Vainio*, *Lich. Bras.* 323).

*Pseudopyrenula diluta* var. *degenerans* Vain., in *Schmidt*, *Bot. Tidsskr.* 29: 148 (1909); type: Thailand, Koh Chang, *Schmidt* 10 (TUR-Vain 30823!—holotype).

*Pseudopyrenula confluens* G. Merr. ex Hedrick, *Mycologia* 22: 247 (1930); type: Puerto Rico, Aibonito, *Fink* 1856 (MICH!—holotype).

*Pyrenula hagmannii* Redinger, *Hedwigia* 73: 56 (1933); type: Brazil, Amazonas, *Ginzberger* s. n. (W!—holotype).

*Pseudopyrenula limitata* Szatala, *Ann. Mus. Nat. Hungar. n.s.* 7: 17 (1956); type: Papua New Guinea, *Biró* s. n. (BP!—holotype).

(Fig. 54G–L)

*Thallus* ecorticate, white, smooth to uneven.

*Ascomata* with apical ostioles, solitary, 0.2–0.4 mm diam., prominent, hemispherical, exposed and black. *Hamathecium* interspersed, hyaline. *Ascospores* 8 per ascus, 3-septate,

fusiform-ellipsoid, 21–25 × 6–9 μm, hyaline but sometimes lumina with yellow oil, IKI–, not ornamented.

**Chemistry.** Thallus and ascomata UV–, K–. TLC: no substances detected.

**Distribution.** Pantropical (previously reported from the USA, Guatemala, Honduras, Costa Rica, Cuba, Cayman Islands, Hispaniola, Jamaica, Puerto Rico, St Eustatius, Nevis, Dominica, Trinidad, Colombia, Venezuela, Guyana, Surinam, French Guiana, Ecuador, Galapagos, Brazil, Bolivia, Cameroon, Sierra Leone, Zaire, Tanzania, Seychelles, India, Sri Lanka, Thailand, Malaysia, Sarawak, Philippines, Hong Kong, Taiwan, Hawai'i, Papua New Guinea and Australia).

**Discussion.** This species and *Pseudopyrenula diluta* have recently been reduced to varietal status (Harris 1998), but they are maintained as distinct species here based on preliminary phylogenetic data (Nelsen *et al.* 2014; Lücking *et al.* 2016a) and because no intermediates occur and their distributions differ, with *P. diluta* extending further into temperate regions (e.g. Azores and Japan). Furthermore, specimens with yellow hamathecium inspersion are now recognized as an additional, separate species, *P. subgregaria*. Unfortunately, these names have been used mostly in a broad sense, including specimens with and without hamathecium inspersion. Therefore, the distribution given above is tentative, although there is no doubt that *P. subnudata* s. str. is the most common species of the genus.

**New country records.** **China:** Yunnan: Xishuangbanna, Menglun, 2002, Aptroot 5732 (ABL).—**Indonesia:** Java: Ngantang, 1937, Groenhart 4125 (ABL, L); Cibodas, Mt. Gede, 1950, Nurta & Madrodji s. n. (ABL, L).—**New Caledonia:** Oui Pouen, 1950, Baumann-Bodenheim 7600 (hb. John).

### ***Pseudopyrenula superans* Müll. Arg.**

*Bot. Jahrb. Syst.* 6: 408 (1885); type: Cuba., Wright s. n. (G!—holotype; Müller, *Verr. Cub.* 71).

(Fig. 53D)

**Thallus** ecorticate, white, smooth to uneven.

**Ascomata** with apical ostioles, solitary, 0.3–0.4 mm diam., prominent, hemispherical, exposed and black. **Hamathecium** inspersion, hyaline. **Ascospores** 8 per ascus, 3-septate, fusiform-ellipsoid, 30–35 × 9–11 μm, hyaline, IKI–, not ornamented.

**Chemistry.** Thallus and ascomata UV–, K–. TLC: no substances detected.

**Distribution.** Neotropical (reported from Cuba and Jamaica).

### ***Trypethelium* Spreng.**

*Anleit. Kemtn. Gew.* 3: 350 (1804); type: *Trypethelium eluteriae* Spreng. (holotype).

*Holstiella* P. Henn., in Engler, *Die Pflanzenwelt Ostafrikas* C: 33 (1895); type: *Holstiella usambarensis* P. Henn. [= *Trypethelium eluteriae* Spreng.]

**Thallus** green to grey or yellowish to brownish, smooth to uneven or becoming somewhat bullate, corticate. **Ascomata** black, globose, immersed in prominent to sessile pseudostromata or rarely erumpent from the thallus, often at least the sides covered by the thallus. **Hamathecium** colourless, clear or inspersion with oil droplets. **Ascospores** 8 per ascus, IKI–, irregularly biserial, colourless, fusiform with subacute ends, transversely septate, not constricted at the septa, when young surrounded by a gelatinous sheath, lumina rectangular when mature.

**Conidiomata** rather rare.

**Chemistry.** Thallus and/or pseudostromata often with lichexanthone (or 1,8-dihydroxy-3,6-dimethoxyxanthone) or anthraquinones.

**Discussion.** *Trypethelium* as defined here is a strictly tropical genus. Well over 300 taxa have been described or recombined under this name, but a significant proportion of these are synonyms of other species or now accepted in other genera, mostly *Astrothelium*. Phylogenetic studies of the family *Trypetheliaceae* (Nelsen *et al.* 2014; Lücking *et al.* 2016a) have shown that the



type species, *T. eluteriae* Spreng., does not cluster with the majority of the species that were until recently classified under this name, including the common species known as *T. nitidiusculum*, *T. ochroleucum* and *T. tropicum*, which are now included in *Astrothelium* and *Nigrovothelium*, respectively. As already suggested by Harris (1995), *Trypethelium* s. str. forms a small, monophyletic group of taxa; this group is characterized by more or less distinctly pseudostromatic ascospores usually filled or covered with anthraquinone crystals, but the most distinctive feature are the hyaline, multiseptate, transversely septate ascospores with thin septa and more or less rectangular lumina when mature. This ascospore type appears to be rare within the family, otherwise found only in the genera *Bathelium*, *Polymeridium*, and *Viridothelium*, whereas most other derived members of the *Trypetheliaceae* have astrothelioid ascospores with diamond-shaped

lumina. While *Polymeridium* is distinguished from *Trypethelium* by the ecorticate, whitish thallus and solitary, exposed ascospores, species of *Bathelium* have fully exposed, brown-black pseudostromata with usually few ascospores, a morphology not found in the known species of *Trypethelium*. The distinction between *Trypethelium* and *Viridothelium* is less straightforward; where *Trypethelium* typically has prominent to sessile pseudostromata and in *Viridothelium* the ascospores are usually immersed-erumpent and solitary, the type species of the latter, *V. virens*, has pseudostromatic, erumpent ascospores very similar to those of *Trypethelium inaequale* (see below). Yet, both are placed within their corresponding genera based on molecular data. In its now restricted sense, the genus *Trypethelium* encompasses 15 species. Its closest relative is the muriform-spored genus *Marcelaria* (Aptroot *et al.* 2013a; Nelsen *et al.* 2014; Lücking *et al.* 2016a).

### Key to the species of *Trypethelium*

- |      |   |                                      |
|------|---|--------------------------------------|
| 1    | Thallus UV+ yellow, with lichexanthone . . . . .  | 2                                    |
|      | Thallus UV- . . . . .   | 5                                    |
| 2(1) | Pseudostromata covered with orange pigment; hamathecium clear; ascospores 45–65 × 9–12 µm, 8–14-septate (Flakus <i>et al.</i> 2016; Fig. 55A) . . . . .         |                                      |
|      | . . . . . <b><i>Trypethelium xanthoplatystomum</i></b>  |                                      |
|      | Pseudostromata lacking external pigment; hamathecium inspersed or not; ascospores 60–110 × 10–15 µm, 11–21-septate . . . . .                                    | 3                                    |
| 3(2) | Hamathecium clear; pseudostromata internally with yellow pigment granules (Lücking <i>et al.</i> 2016b) . . . . .   | <b><i>Trypethelium tolimense</i></b> |
|      | Hamathecium inspersed; pseudostromata internally with orange pigment granules or lacking pigment . . . . .  | 4                                    |
| 4(3) | Pseudostromata internally with orange pigment granules, erumpent; ascospores 60–110 × 12–15 µm, 11–21-septate (Aptroot <i>et al.</i> 2016b; Fig. 55B) . . . . . |                                      |
|      | . . . . . <b><i>Trypethelium luteolucidum</i></b>   |                                      |
|      | Pseudostromata lacking pigment, prominent; ascospores (65–)83–97 × 11–15 µm, 13–19-septate (this synopsis; Fig. 55C & D) . . . . .                              | <b><i>Trypethelium regnellii</i></b> |
| 5(1) | Pseudostromata inside and/or outside with yellow or orange pigments (sometimes thin and not readily visible) . . . . .  | 6                                    |
|      | Pseudostromata lacking pigments . . . . .   | 11                                   |

- 6(5) Ostiolar areas very broad, disc-shaped or fused in lobate fashion; pigments usually sparse . . . . . 7  
 Ostiolar areas narrow, visible as small dots; pigments conspicuous . . . . . 9
- 7(6) Ostiolar areas disc-shaped, uniformly brown-black, marginally with small, black papillae arranged in circular fashion (this synopsis; Fig. 55E–G) . . . . . **Trypethelium krempelhuberi**  
 Ostiolar areas fused in lobate fashion, contrasting with a bordering whitish rim, without marginal papillae . . . . . 8
- 8(7) Ostiolar area centrally with dark red pigment in addition to orange pigment bordering the ostiolar lobes; ostioles sometimes eccentric and fused; ascospores 65–100 µm long (Flakus *et al.* 2016; Fig. 55H & I) . . . **Trypethelium astroideum**  
 Ostiolar area only with bordering orange pigment; ostioles always apical; ascospores 55–75 µm long (this synopsis; Fig. 55J–L) . . . . . **Trypethelium platystomum**
- 9(6) Pseudostromata immersed to erumpent; ascospores 37–42 µm long, 7–9-septate (Aptroot *et al.* 2016a; Fig. 56A) . . . . . **Trypethelium infraeluteriae**  
 Pseudostromata prominent to sessile; ascospores (37–)42–85 µm long, 9–17-septate . . . . . 10
- 10(9) Pseudostromata inside and/or outside with yellow pigment; ascospores 37–52 × 8–11 µm, 9–13-septate (this synopsis; Fig. 56B–L) . . . . **Trypethelium eluteriae**  
 Pseudostromata inside and/or outside with orange-yellow pigment; ascospores 60–85 × 11–12 µm, 13–16-septate (this synopsis; Fig. 57A–E) . . . . . **Trypethelium subeluteriae**
- 11(5) Pseudostromata immersed-erumpent, with ascomata clearly distinguished and individually protruding, brown-black . . . . . 12  
 Pseudostromata erumpent to prominent, with ascomata completely immersed in the pseudostromata and not individually protruding, with whitish ostiolar spot or ostiolar area surrounded by irregular whitish to cream-coloured rim or pseudostromata entirely whitish . . . . . 13
- 12(11) Thallus verrucose-rugose; individual ascomata with flattened top; ascospores 45–55 × 6–8 µm, 12–17-septate (this synopsis; Fig. 57F) . . . . . **Trypethelium plicatorimosum**  
 Thallus smooth to uneven; individual ascomata with convex top; ascospores 21–40 × 9–15 µm, 5–11-septate (this synopsis; Fig. 57G & H) . . . . . **Trypethelium inaequale**  
 If ascospores larger and comparatively narrower (38–80 × 7–15 µm, over 5 times as long as broad compared to 2–3 times as long as broad in the above species), see also *Viridothelium virens* and *V. cinereoglaucescens* (this synopsis)
- 13(11) Pseudostromata erumpent to prominent, entirely white or cream-coloured; hamathecium clear . . . . . 14  
 Pseudostromata prominent to sessile, grey to black with contrasting, white ostiolar spots; hamathecium interspersed . . . . . 15

- 14(13) Pseudostromata entirely white, with small, dark ostiolar spots; ascospores 30–60  $\mu\text{m}$  long, 5–9(–13)-septate (this synopsis; Fig. 57I–K) . . . . . **Trypethelium epileucodes**  
 Pseudostromata cream-coloured, with larger, often angular-lobate ostiolar spots; ascospores 58–78  $\mu\text{m}$  long, 9–15-septate (this synopsis; Fig. 58A–D) . . . . . **Trypethelium foveolatum**
- 15(13) Pseudostromata sessile with constricted base, upper part black, sharply contrasting with white ostiolar spots; ascospores 80–110  $\times$  14–18  $\mu\text{m}$ , 13–19-septate (this synopsis; Fig. 58E–I) . . . . . **Trypethelium sphaerocephalum**  
 Pseudostromata prominent without constricted base, grey (black with thin whitish cover), diffusely contrasting with white ostiolar spots; ascospores 60–70  $\times$  10–14  $\mu\text{m}$ , 11–15-septate (this synopsis; Fig. 58J–L) . . . **Trypethelium ornatum**

### Trypethelium eluteriae Spreng.

*Anleitung zur Kenntnis der Gewächse* 3: 351 (1804).—*Pseudopyrenula eluteriae* (Spreng.) Vain., *Ann. Acad. Sci. Fenn., ser. A* 6(7): 353 (1921); type: Indonesia, *Sprengel* s. n. (L!—holotype).

*Trypethelium sprengelii* Ach., *Lichenogr. Univ.*: 306 (1810).—*Pseudopyrenula eluteriae* var. *sprengelii* (Ach.) Vain., *Bol. Soc. Broteriana ser. 2* 6: 177 (1930).—*Trypethelium eluteriae* var. *sprengelii* (Ach.) Zahlbr., *Catal. Lich. Univ.* 10: 102 (1938); type: Surinam, *Schwartz* s. n. (H-ACH 875!—holotype; BM!—isotype).

*Trypethelium perrotetii* Fée, *Ann. Sci. Nat., Bot.* 23: 432 (1831); type: Senegal, s. col. (G—holotype, not seen).

*Trypethelium anacardii* Fée, *Ann. Sci. Nat., Bot.* 23: 430 (1831).—*Trypethelium sprengelii* var. *anacardii* (Fée) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 141 (1857).—*Trypethelium eluteriae* var. *expallidum* Müll. Arg., *Mém. Soc. Phys. Hist. Nat. Genève* 30(3): 16 (1888).—*Trypethelium eluteriae* var. *anacardii* (Fée) Zahlbr., *Catal. Lich. Univ.* 1: 491 (1922).—*Pseudopyrenula eluteriae* var. *anacardii* (Fée) Vain., *Bol. Soc. Broteriana ser. 2* 6: 177 (1930); type: Guadeloupe, *Bertero* s. n. (G!—lectotype, Harris, *Lichenogr. Thomsoniana*: 142, 1998).

*Trypethelium sprengelii* var. *nigricans* Fée, *Ann. Sci. Nat., Bot.* 23: 430 (1831).—*Trypethelium eluteriae* var. *nigricans* (Fée) Trevis., *Flora* 44: 20 (1861): type: s.dat. (G—holotype, not seen).

*Astrothelium varium* Eschw., in *Martius, Flora Bras.* 1: 161 (1833); type: Brazil, *Martius* s. n. (M!—lectotype, Harris, *Acta Amazon. (Suppl.)* 14: 73 ('1984') [1986]).

*Astrothelium varium* var. *citrinum* Eschw., in *Martius, Flora Bras.* 1: 162 (1833).—*Trypethelium sprengelii* var. *citrinum* (Eschw.) Müll. Arg., *Flora* 67: 671 (1884).—*Trypethelium eluteriae* var. *citrinum* (Eschw.) Müll. Arg., *Bot. Jahrb. Syst.* 6: 393 (1885); type: Brazil, *Martius* s. n. (M!—lectotype, Harris, *Acta Amazon. (Suppl.)* 14: 73 ('1984') [1986]).

*Trypethelium areolatum* Mont., in *Hooker, London J. Bot.* 4: 5 (1845); type: Philippines, s. col. (BM—holotype, not seen).

*Trypethelium luteum* Taylor, *Lond. J. Bot.* 6: 157 (1847); type: India, Madras, *Wight* s. n. (BM!—isotype).

*Verrucaria trypetheliiformis* Mont., *Ann. Sci. Nat., Bot., sér. 3* 16: 67 (1851).—*Trypethelium montagnei* Trevis., *Flora* 44: 20 (1861); type: French Guiana, *Leprieur* s. n. (PC-Mont—holotype, not seen).

*Trypethelium crocosarca* Cooke, in *Berkeley & Broome, Grevillea* 20(95): 83 (1873); type: Sri Lanka, *Thwaites* 131 (BM—holotype, not seen).

*Trypethelium assimile* Stirt., *Proc. Roy. Philos. Soc. Glasgow* 13: 193 (1881); type: India, Assam, *Watt* s. n. (BM!—isotype).

*Trypethelium insigne* Müll. Arg., *Flora* 68: 256 (1885); type: South America, "cinchoncola" (G!—lectotype, designated here).

*Trypethelium eluteriae* var. *truncatum* Müll. Arg., *Bot. Jahrb. Syst.* 6: 393 (1885); type: Cuba, *Wright* s. n. (G!—lectotype, designated here; Müller, *Verr. Cub., Ser. II*: 585 p.p.).

*Trypethelium eluteriae* var. *endochlorum* Müll. Arg., *Flora* 68: 255 (1885); type: South America, "quassiacola et cort. Bonplandiae" (G-G00295257!—lectotype, designated here).

*Pseudopyrenula eluteriae* ssp. *subsulphurea* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2): 205 (1890).—*Trypethelium eluteriae* var. *subsulphureum* (Vain.) Riddle, in *Britton & Millspaugh, Bahama Flora*: 530 (1920).—*Trypethelium subsulphureum* (Vain.) Zahlbr., *Catal. Lich. Univ.* 1: 500 (1922); type: Brazil, Rio de Janeiro, *Sepitiba, Vainio* 413 (TUR-Vain 30744!—holotype; BM!, M!—isotype).

*Trypethelium pringlei* Eckfeldt, *Bull. Torrey Bot. Club* 21: 395 (1894); type: Mexico, San Luis Potosi, Las Palmas, *Pringle* 226 (NY!, US!—isotype).

*Trypethelium scitulens* Eckfeldt, *Bull. Torrey Bot. Club* 21: 395 (1894); type: Mexico, San Luis Potosi, Las Palmas, *Pringle* 200 (NY!, US!—isotype).

*Holstiella usambarensis* P. Henn., in *Engler, Die Pflanzenwelt Ostafrikas* C: 33 (1895); type: Tanzania, Dodo, *Holst* s. n. (FH-Höhnell!—lectotype, Aptroot, *Nova Hedwigia* 66: 156, 1998).

*Trypethelium medians* Harm., *Bull. Soc. Sci. Nancy sér. 3* 12: 142 (1911); type: New Caledonia ["Australia"], *Pionnier* s. n. (DUKE!—holotype).

*Trypethelium leprosum* Zahlbr., *Ann. Mycol.* 30: 499 (1932); type: China, Fukien, Kulang, *Chung* 371 & 376 (W—syntypes; FH—isosyntypes, not seen).

(Fig. 56B–L)

*Thallus* corticate, olive-green to yellowish, smooth to uneven.



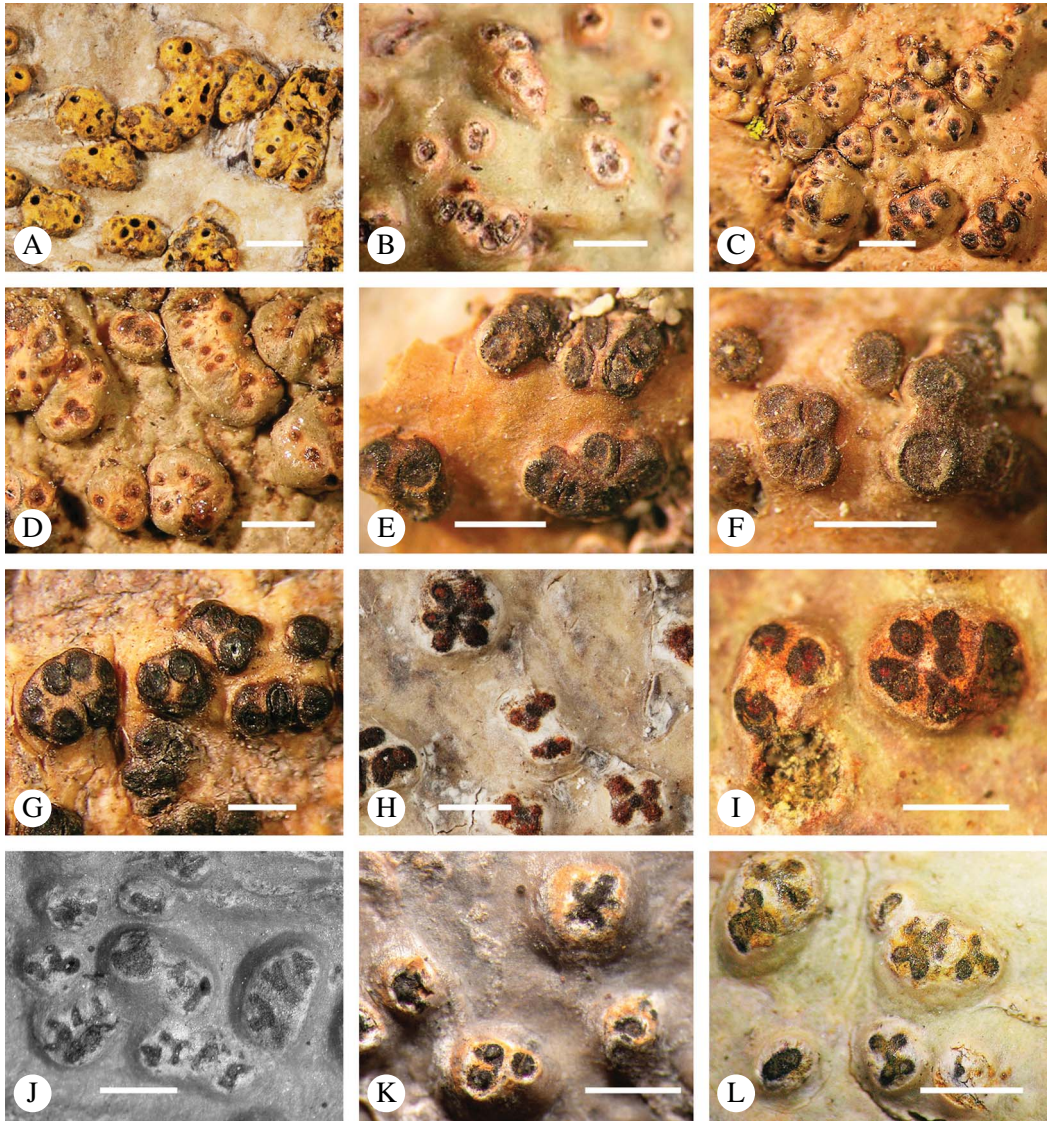


FIG. 55. Habitus of *Trypethelium* species. A, *T. xanthoplatystomum* (Bolivia, holotype); B, *T. luteolucidum* (Brazil, holotype); C & D, *T. regnellii* (Paraguay, holotype); E–G, *T. krempelhuberi* (E & F, Vietnam, holotype; G, Brazil, lectotype of *T. platystomum* var. *denudatum*); H & I, *T. astroideum* (H, Bolivia, holotype; I, Peru, *Nelsen* s. n.); J–L, *T. platystomum* (J, French Guiana, isotype; K, Brazil, *Cáceres & Aptroot* 11485; L, Colombia, *Moncada* 3267). Scales = 1 mm.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata containing numerous ascomata, 1–2 mm diam., prominent to almost sessile, brownish to dark brown but usually covered by yellow pigment except for dark ostioles; internally usually with yellow pigment.

*Hamathecium* clear. *Ascospores* 8 per ascus, 9–13-septate, fusiform,  $37\text{--}52 \times 8\text{--}11 \mu\text{m}$ , hyaline, IKI–.

*Chemistry*. Thallus UV–, K–; pseudostromata UV+ red, K+ purple, with yellow anthraquinone.



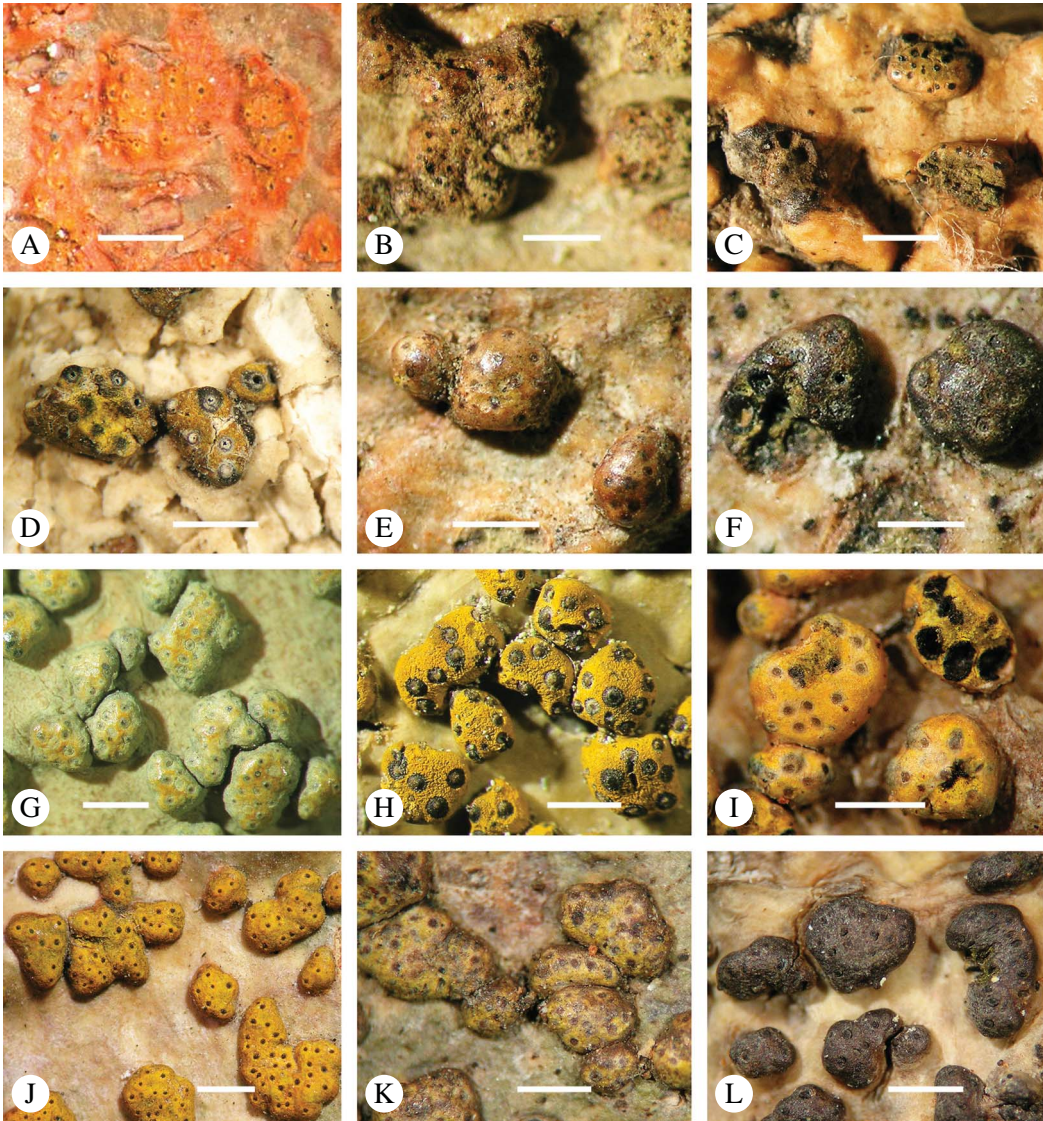


FIG. 56. Habitus of *Trypethelium* species. A, *T. infraeluteriae* (Vietnam, holotype); B–L, *T. eluteriae* (B, Indonesia, holotype; C, ‘South America’, lectotype of *T. insigne*; D, Mexico, isotype of *T. pringlei*; E & F, Surinam, holotype of *T. sprengelii*; G, Brazil, holotype of *Pseudopyrenula eluteriae* ssp. *subsulphurea*; H, Brazil, Cáceres 134; I, Bahamas, Brace 5049; J, Colombia, *Moncada* 3399; K, Dominican Republic, *Harris* 26423; L, Dominican Republic, *Harris* 26708). Scales = 1 mm.

*Distribution.* Pantropical (previously reported from the USA, Mexico, Guatemala, El Salvador, Costa Rica, Guadeloupe, Cuba, Colombia, Venezuela, Surinam, French Guiana, Galapagos, Brazil, Paraguay, Gambia, Tanzania, Seychelles, China, Hong Kong, India, Sri Lanka, Thailand,

Cambodia, Vietnam, Indonesia, Papua New Guinea, Philippines, Taiwan, Japan, New Caledonia and Australia).

*Discussion.* *Trypethelium eluteriae* as circumscribed here most certainly remains a collective taxon. Typically, the pseudostromata are



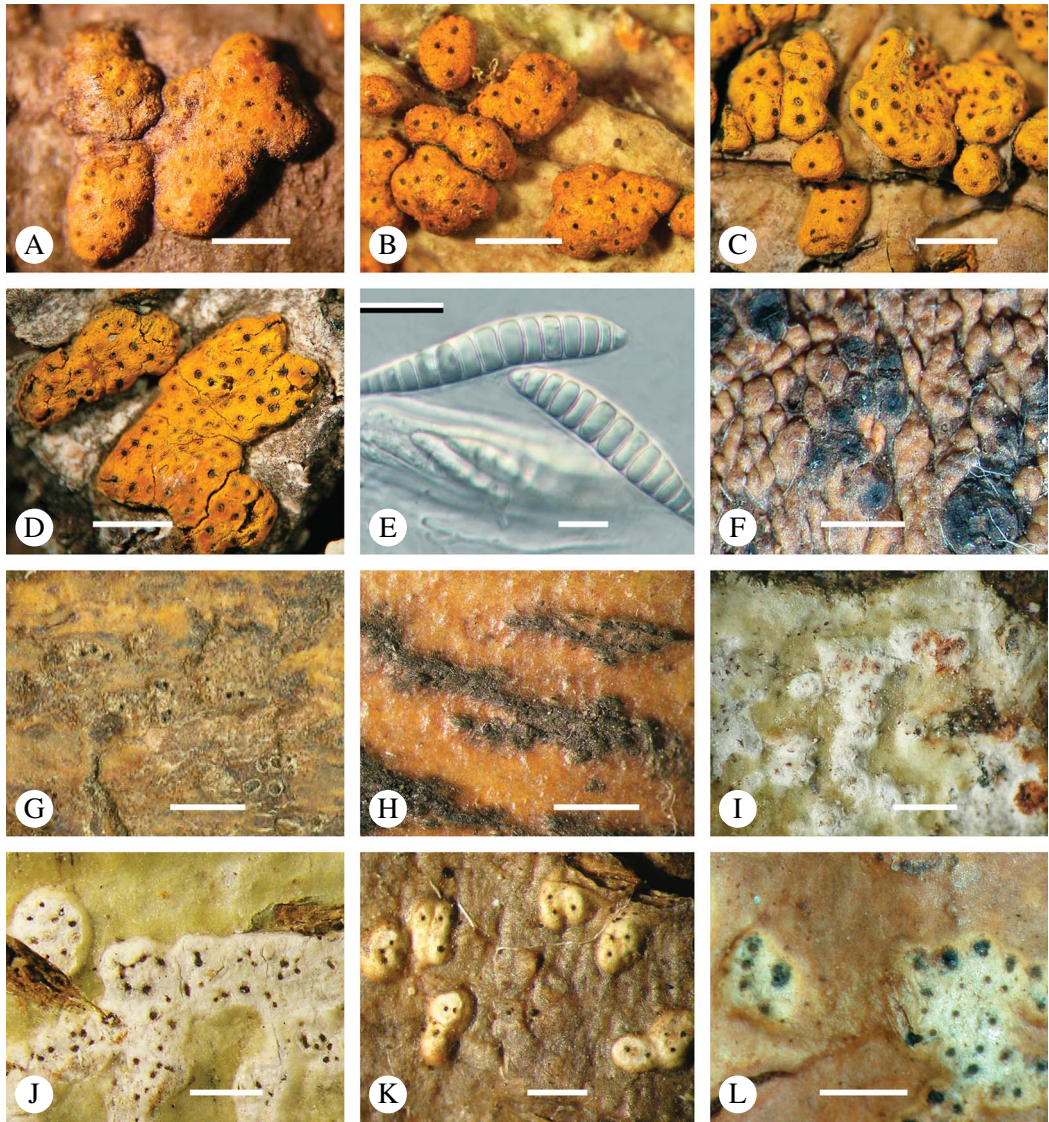


FIG. 57. Habitus and ascospores of *Trypethelium* species. A–E, *T. subeluteriae* (A, Brazil, lectotype of *T. eluteriae* var. *polystomum*; B, USA, Florida, *Nelsen* s. n.; C & D, Venezuela, *López-Figueiras* 21191; E, Costa Rica, *Lücking* 17611, ascospores); F, *T. plicatorimosum* (India, isotype); G & H, *T. inaequale* (G, Peru, holotype; H, India, isolectotype of *T. inamoenum*); I–L, *T. epileucodes* (I & J, Malaysia, Labuan, lectotype; K, Australia, lectotype of *T. virginicum*; L, India, isotype of *T. andamanicum*). Scales: A–D, F–L = 1 mm; E = 10  $\mu$ m.

covered by a yellow pigment, but specimens particularly from the Caribbean deviate by their dark brown pseudostromata completely lacking an external pigment but having the pigment inside the pseudostromata instead. Phylogenetic data support their separation as a

taxon basal to *T. eluteriae* s. str. (Lücking *et al.* 2016a), and *T. sprengelii* would then be the oldest available name, as tentatively suggested by Lücking *et al.* (2016a). Other collections, for example from Africa, have light brown pseudostromata lacking an external pigment.



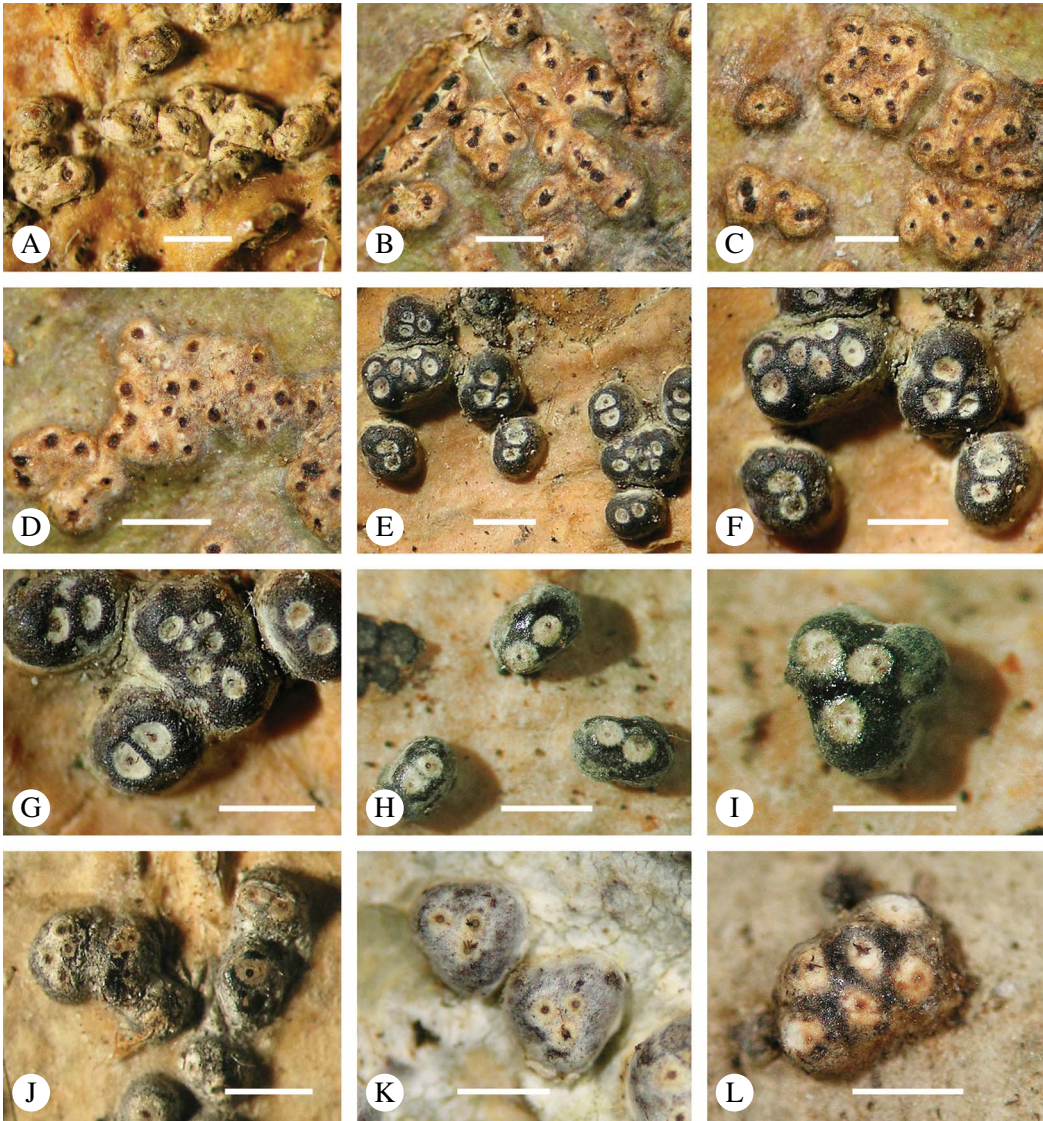


FIG. 58. Habitus of *Trypethelium* species. A–D, *T. foveolatum* (A, Brazil, lectotype; B–D, Puerto Rico, Harris 24390); E–I, *T. sphaerocephalum* (E–G, São Tomé and Príncipe, holotype of *T. platystomum* f. *leucostomum*; H & I, Angola, lectotype); J–L, *T. ornatum* (J, Cuba, lectotype; K, Brazil, Oliveira 351; L, Venezuela, López-Figueiras 16540e). Scales = 1 mm.

The situation is complicated by the fact that the external pigment in old collections is often abraded.

*New country records.* **Nicaragua:** *Rivas:* Playa El Coco, 2001, Breuss 19271 (LD).—**Puerto Rico:** *Mayaguez:* Bosque Estatal de Susua, 1989, Aptroot & Aptroot 25894, 25879, 25900, 25905 (ABL).—**Dominican Republic:** *La*

*Romana:* 13 km NE of La Romana, Harris 20282 (ABL, NY).—**Guyana:** *Upper Takutu:* Rupununi, Dadanawa Ranch, 1992, Sipman 57390 (B).—**Madagascar:** *Tulear:* Ifaty, 1984, Aptroot & Hensen 12616 (ABL).—**Bangladesh:** *Dhaka Division:* Bhawal National Park, 2001, Hopman s. n. (ABL).—**Singapore:** University campus, 2000, Sipman 45531 (B).—**Vanuatu:** *Efate:* Iririki Island, 1998, Sreimann & Ala 61992 (B, CBG).

**Trypethelium epileucodes Nyl.**

*Lich. Japon.*: 116 (1890); type: Malaysia, Labuan, *Almqvist* s. n. (H-Nyl 272!)—lectotype, Makhija & Patwardhan, *Int. J. Mycol. Lichenol.* 5: 241, 1992; S!—isolectotype).

*Bathelium sundaicum* Müll. Arg., *Nuovo Giorn. Botan. Ital.* 23: 277 (1891).—*Laurera sundaica* (Müll. Arg.) Zahlbr., *Catal. Lich. Univ.* 1: 507 (1922); type: Singapore, *Beccari* s. n. (G!—holotype).

*Trypethelium virginicum* Müll. Arg., *Rep. Australas. Assoc. Advancem. Sci.* 1895: 461 (1895); type: Australia, Queensland, *Knight* 351 (G!—lectotype, designated here).

*Trypethelium subnitidiusculum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 207 (1993); type: India, Karnataka, Coorg, Talcauvery, *Patwardhan & Prabha* AMH 74.3368 (ABL—istotype).

*Trypethelium andamanicum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 193 (1993); type: India, Andaman Islands, South Andaman, Baratang, 1985, *Nagarkar & Sethy* AMH 85.471 (ABL!—istotype).

(Fig. 57I–K)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata containing few to numerous ascomata, 0.5–1.5 mm broad, erumpent, whitish with dark ostioles. *Hamathecium* clear. *Ascospores* 8 per ascus, 5–9(–13)-septate, fusiform, 30–60 × (5–)8–13 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Palaeotropical (previously reported from India, Sri Lanka, Taiwan, Thailand, Hong Kong, Singapore, Indonesia, Papua New Guinea and Australia).

*New country records.* **Malaysia:** *Johor:* Gunung Pulai Forest Reserve, 2000, *Sipman et al.* 46414 (B).—**Philippines:** *Sorsogon:* Luzon, Irosin, 1916, *Elmer* 15761 (ABL, B).—**Solomon Islands:** *Santa Isabel Island:* 1965, *Hill* 9918 (BM).

**Trypethelium foveolatum Müll. Arg.**

*Flora* 68: 255 (1885).—*Trypethelium papillosum* Kremp., *Flora* 59: 527 (1876), *nom. illeg., non Ach.*; type: Brazil, Rio de Janeiro, *Glaziou* 5071 (G!—lectotype, designated here; M!—isolectotype).

(Fig. 58A–D)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata usually containing few ascomata, 0.7–1.5(–2.0) mm diam., prominent, laterally covered by thallus but upper part cream-coloured, with relatively broad, dark, often confluent ostiolar spots. *Hamathecium* clear. *Ascospores* 8 per ascus, 9–15-septate, fusiform, 58–78 × 10–13 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Brazil).

**Trypethelium inaequale Fée**

*Ann. Sci. Nat., Bot.* 23: 439 (1831).—*Trypethelium sprengelii* f. *inaequale* (Fée) Nyl., *Mém. Soc. Acad. Maine-et-Loire* 4: 77 (1858).—*Trypethelium eluteriae* var. *inaequale* (Fée) Müll. Arg., *Bot. Jahrb. Syst.* 6: 393 (1885); type: Peru (G!—holotype).

*Trypethelium inamoenum* Müll. Arg., *J. Linn. Soc. London, Bot.* 29: 230 (1892); type: India, Manipur, *Watt* 98 (G!—lectotype, Makhija & Patwardhan, *J. Hattori Bot. Lab.* 73: 199, 1993, not seen; BM!—isolectotype).

(Fig. 57G & H)

*Thallus* corticate, olive-green to yellowish or brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, diffusely to distinctly pseudostromatic; pseudostromata with numerous ascomata, 0.5–1.0 mm broad, immersed to erumpent, often linear, with individual ascomata largely exposed and blackish brown. *Hamathecium* clear. *Ascospores* 8 per ascus, 5–11-septate, fusiform, 21–45 × 9–15 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Pantropical (previously reported from Peru and India).

*Discussion.* The collections from the Neotropics and the eastern Palaeotropics agree well with each other in morphology and ascospore type. The species is virtually indistinguishable from *Viridothelium virens* (see below), both in morphology and ascospore type, but collections of both taxa

collected within or close to the area of origin of either type fall phylogenetically within either *Trypethelium* (specimen from Thailand) or *Viridothelium* (specimen from the USA).

*New country records.* **Guyana:** Upper Mazaruni: Pakaraima mountains, Kamarang, 1985, *Sipman & Aptroot* 18259 (ABL, B).—**Thailand:** *Lücking* 24125 (B, F).—**Indonesia:** *Borneo:* Kalimantan, *Wolseley* 1288 p.p. (BM).

### ***Trypethelium krempelhuberi* Makhija & Patw.**

*Int. J. Mycol. Lichenol.* 5: 241 (1992) [as *krempelhuberi*]; type: Vietnam, Tu-phap, *Balansa* s. n. (S!—isotype).

*Trypethelium platystomum* var. *demudatum* Malme, *Ark. Bot.* 19(1): 27 (1924); type: Brazil, Matto Grosso, Cuyabá, *Malme* 2600 (S!—lectotype, designated here).

(Fig. 55E–G)

*Thallus* corticate, olive-green to brownish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata with few ascomata, 0.5–1.2 mm diam., erumpent to prominent, laterally covered by thallus but upper portion of individual ascomata exposed and blackish brown, conspicuously flattened, disc-shaped and margins of ‘discs’ with numerous small, black papillae arranged in circular fashion, around the ostioles thinly furnished with orange pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 13–15-septate, fusiform, 59–72 × 13–15 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata apically UV+ red, K+ purple, with thin, orange anthraquinone.

*Distribution.* Brazil and Vietnam.

### ***Trypethelium ornatum* Müll. Arg.**

*Bot. Jahrb. Syst.* 6: 393 (1885) non Hellb. (1896); type: Cuba, *Wright* s. n. (G!—holotype; Müller, *Verr. Cub.*, Ser. II: 557).

(Fig. 58J–L)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata with few ascomata, 0.7–1.5 mm diam., prominent, grey-black but usually covered by a thin whitish layer, with ostiolar areas forming broad, weakly contrasting, white spots. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 11–15-septate, fusiform, 60–70 × 10–14 µm, hyaline, IKI–.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Neotropical (Cuba, Venezuela and Brazil).

### ***Trypethelium platystomum* Mont.**

*Ann. Sci. Nat., Bot. Sér. 2* 19: 72 (1843); type: French Guiana, *Leprieur* (BR, L!—isotypes).

(Fig. 55J–L)

*Thallus* olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata with few ascomata, 0.8–1.5 mm diam., prominent, cream-coloured and usually paler than the thallus, but ostiolar spots dark and usually confluent in lobate pattern, surround by thin layer of orange pigment. *Hamathecium* clear. *Ascospores* 8 per ascus, 12–18-septate, fusiform, 55–75 × 8–15 µm, hyaline, IKI–.

*Chemistry.* Thallus UV–, K–; pseudostromata apically UV+ red, K+ purple, with orange anthraquinone.

*Distribution.* Pantropical (previously reported from Costa Rica, Guyana, French Guiana, Venezuela, Brazil, Paraguay, India, Sri Lanka and Thailand).

*New country records.* **Puerto Rico:** *Aguadilla:* Bosque Estatal de Guajataca, 1989, *Aptroot & Aptroot* 25746 (ABL).—**El Salvador:** Santa Ana, Metapan, Parque Nacional Montecristo, 1993, *Sipman et al.* 37370 (B).—**Colombia:** *Risaralda:* Puerto Caldas, 1985, *Wolf* 407 (B).—**DR Congo:** *Mongala Province:* Lisala, 2009, *Ertz* 14181 (BR).—**Gabon:** 2006, *Ertz* 9715 (BR).—**Sierra Leone:** *Southern Province:* Njala, 1954, *Deighton* 5843 (BM).—**China:** *Yunnan:* Xishuangbanna, Menglun,



2002, *Aptroot* 57272 (ABL).—**Singapore:** University campus, 2000, *Sipman* 45605 (B).—**Indonesia:** *Java:* Mt. Parangklakah, 1937, *Groenhart* 5830 (ABL, L); Malang, 1932, *Groenhart* 356 (ABL, L); Bogor, Djalan Bamtam, 1941, *Groenhart* 3142 (ABL, L).—**Australia:** *Queensland:* Cairns, near Centenary Lakes, 1988, *A. & M. Aptroot* 22229 (ABL).

### ***Trypethelium plicatorimosum* Makhija & Patw.**

*J. Hattori Bot. Lab.* 73: 205 (1993) [as '*plicato-rimosum*']; type: India, Maharashtra, Amboli, 1975, *Patwardhan & Prabhu* AMH 75.528 (ABL!—isotype).

*Trypethelium rubrocinctum* Makhija & Patw., *J. Hattori Bot. Lab.* 73: 206 (1993); type: India, Assam, Gauhati-Shilong road, near Burhatti, 1977, *Patwardhan & Nagarkar* AMH 77.704 (ABL!—isotype).

(Fig. 57F)

*Thallus* corticate, olive-green to yellowish, verrucose-rugulose.

*Ascomata* trypethelioid, with apical ostioles, diffusely pseudostromatic; pseudostromata with few ascomata, 0.5–1.0 mm broad, erumpent, basally covered by thallus but upper part exposed, brown-black, flattened and disc-shaped. *Hamathecium* clear. *Ascospores* 8 per ascus, 12–17-septate, fusiform, 45–55 × 6–8 μm, hyaline, IKI–.

**Chemistry.** Thallus and pseudostromata UV–, K–. TLC: no substances detected.

**Distribution.** Palaeotropical (previously reported only from India.).

*New country record.* **Zaire:** *Kivu:* Pinga, 1100 m, 1991, Müller s. n. (DR).

### ***Trypethelium regnellii* Malme**

*Ark. Bot.* 19(1): 25 (1924); type: Paraguay, Colonia Risso, *Malme* 1875 (S!—holotype).

*Trypethelium globolucidum* Aptroot *et al.*, *Lichenologist* 46: 100 (2014); type: Argentina, Prov. Misiones, Iguazú National Park, along railroad, 200 m, 2013, *Ferraro et al.* 10630 (CTES!—holotype; ABL!—isotype).

(Fig. 55C & D)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata with mostly few ascomata, 0.7–1.3 mm diam., erumpent to prominent, covered by thallus except brown ostiolar areas surrounded by cream-coloured to whitish rim; pseudostromata 1–3 mm diam., individual ascomata 0.4–0.8 mm diam. *Hamathecium* inspersed. *Ascospores* 8 per ascus, 13–19-septate, fusiform, (65–)83–97 × 11–15 μm, with slight constriction at the median septum, hyaline, IKI–.

**Chemistry.** Thallus UV–, K–; whitish parts of pseudostromata surrounding the ostioles UV+ yellow, K–. TLC: lichexanthone.

**Distribution.** Neotropical (Argentina, Paraguay and Brazil).

**Discussion.** The type specimens of *Trypethelium regnellii* and *T. globolucidum* look superficially different, but the numerous collections from Brazil show all intermediate stages.

### ***Trypethelium sphaerocephalum* (Vain.) Zahlbr.**

*Catal. Lich. Univ.* 1: 500 (1922).—*Pseudopyrenula sphaerocephala* Vain., in Hiern, *Cat. Afr. Pl.* 2(2): 456 (1901); type: Angola, Luanda, *Wekwitsch* 191 (TUR-Vain 30790!—holotype; BM!—isotype).

*Trypethelium platystomum* f. *leucostomum* Nyl., *Flora* 69: 178 (1886).—*Trypethelium anomalum* f. *leucostomum* (Nyl.) Zahlbr., *Catal. Lich. Univ.* 1: 487 (1922).—*Trypethelium leucostomum* (Nyl.) C. W. Dodge, *Ann. Missouri Bot. Gard.* 40: 292 (1953) non Kremp. (1875).—*Trypethelium platyleucostomum* Makhija & Patw., *Int. J. Mycol. Lichenol.* 5: 243 (1992); type: São Tomé and Príncipe, Bom Puccesso, Müller s. n. (H-Nyl 254!—holotype).

(Fig. 58E–I)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata with few ascomata, 0.6–1.3 mm diam., sessile, exposed and laterally grey-black, apically black, with ostiolar areas forming broad, strongly contrasting, white spots. *Hamathecium* inspersed. *Ascospores*

8 per ascus, 13–19-septate, fusiform, 80–115 × 14–18 µm, hyaline, IKI–.

**Chemistry.** Thallus and pseudostromata UV–, K–. TLC: no substances detected.

**Distribution.** African palaeotropical (Uganda, São Tomé and Príncipe).

**Discussion.** This species is rather similar to the neotropical *Trypethelium ornatum* but differs in the sessile pseudostromata with strongly contrasting ostiolar spots and the larger ascospores.

### **Trypethelium subeluteriae Makhija & Patw.**

*Int. J. Mycol. Lichenol.* 5: 245 (1992); type: Sri Lanka, Peradenya, *Thwaites* 184, “2” (BM—holotype).

*Trypethelium eluteriae* var. *polystomum* Malme, *Ark. Bot.* 19(1): 25 (1924) [incorrectly given as ‘*platystomum*’ in *Zahlbruckner’s Catalogus*]; type: Brazil, Matto Grosso, Buriti, 1894, *Malme* 16 vi 1894 (S!—lectotype, designated here).

*Trypethelium ceylonicum* Makhija & Patw., *Int. J. Mycol. Lichenol.* 5: 239 (1992); type: Sri Lanka, Peradenya, *Thwaites* 184, “3” (BM!—holotype).

(Fig. 57A–E)

**Thallus** olive-green to yellowish brown, smooth to uneven.

**Ascomata** trypethelioid, with apical ostioles, distinctly pseudostromatic; pseudostromata with numerous ascomata, 1–2 mm diam., prominent to sessile, brownish but covered by orange pigment except for dark ostioles. **Hamathecium** clear. **Ascospores** 8 per ascus, 11–19-septate, fusiform, 55–75 × 11–12 µm, hyaline, IKI–.

**Chemistry.** Thallus UV–, K–; pseudostromata UV+ red, K+ purple, with orange anthraquinone.

**Distribution.** Pantropical (USA, Costa Rica, Cuba, Puerto Rico, Venezuela, Guyana, French Guiana, Brazil, Paraguay, Bolivia, Argentina, South Africa, India, Sri Lanka, Malaysia, Philippines, New Caledonia, Papua New Guinea and Australia, often reported as ‘aff. *eluteriae*’).

### **Viridothelium Lücking et al.**

In Lücking et al., *Lichenologist* 48: 758 (2016); type: *Viridothelium virens* (Tuck. ex Michener) Lücking et al. (holotype).

**Thallus** corticate, often warted.

**Ascomata** simple or aggregated in pseudostromata, which can be hardly to clearly raised and are usually not of a different structure and colour to the thallus. **Ostioles** apical or eccentric, simple or fused. **Wall** hyphal (*textura intricata*), usually carbonized. **Hamathecium** clear or interspersed with oil droplets, filaments thin, anastomosing paraphysoids. **Ascospores** distoseptate, hyaline, transversely septate.

**Pycnidia** occasionally present.

**Chemistry.** No secondary substances known except anthraquinones in one species (*V. leptoseptatum*).

**Discussion.** The newly established genus *Viridothelium* is a phylogenetically distinctive clade (Lücking et al. 2016a), but combines features of the genera *Astrothelium* (general morphology) and *Trypethelium* (ascospores). Species can hence be readily assigned to *Viridothelium* if they have *Trypethelium*-type ascospores (i.e. with rather thin but numerous septa) but their ascomata are not distinctly pseudostromatic and raised, and the thallus is more or less greenish when fresh. The placement of several taxa, such as *V. leptoseptatum*, is tentative and requires molecular data. An interesting situation arises with *Trypethelium inaequale* (including its current synonym, *T. inamoenum*); this taxon is very similar to *Viridothelium virens* in most aspects but a sequenced specimen clusters within *Trypethelium*, whereas a morphologically similar specimen of *V. virens* from North America defines the *Viridothelium* clade (Lücking et al. 2016a). This rather striking example of homoplasy is comparable to what has been found in *Graphidaceae*, with phenotypically similar taxa belonging to often unrelated clades (Rivas Plata & Lumbsch 2011).

**Key to the species of *Viridothelium***  
(see also key to species of *Astrothelium*)

- 1 Ascospores muriform; thallus and ascomata strongly contrasting in colour, with thallus brownish and ascomata white with black ostiolar areas (Lücking *et al.* 2016b; Fig. 59A) . . . . . **Viridothelium tricolor**  
Ascospores transversely septate; thallus and ascomata not strongly contrasting in colour, more or less olive-green to yellowish brown with ascomata sometimes blackish . . . . . 2
- 2(1) Ostioles eccentric . . . . . 3  
Ostioles apical . . . . . 5
- 3(2) Ascospores 75–98 × 17–20 µm, 15–19-septate (Aptroot *et al.* 2016a; Fig. 59B) . . . . . **Viridothelium solomonense**  
Ascospores 90–152 × 22–33 µm . . . . . 4
- 4(3) Ascospores 99–152 × 26–33 µm, (9–)15–17-septate (this synopsis; Fig. 59C) . . . . . **Viridothelium megaspermum**  
Ascospores 90–100 × 22–26 µm, 15–21-septate (Lücking *et al.* 2016b; Fig. 59D) . . . . . **Viridothelium vonkonratii**
- 5(2) Thallus and ascomata thinly furnished with orange pigment; ascospores 3-septate (Aptroot *et al.* 2016b; Fig. 59E) . . . . . **Viridothelium leptoseptatum**  
Thallus and ascomata lacking pigment; ascospores (5–)7–17-septate . . . . . 6
- 6(5) Hamathecium interspersed; ascospores 60–75 × 12–17 µm, 12–14-septate (Aptroot *et al.* 2016a; Fig. 59F) . . . . . **Viridothelium inspersum**  
Hamathecium clear . . . . . 7
- 7(6) Ascospores 90–150 µm long . . . . . 8  
Ascospores 38–80 µm long . . . . . 9
- 8(7) Ascospores 90–105 × 12–16 µm, (9–)13–17-septate (this synopsis; Fig. 59G) . . . . . **Viridothelium indutum**  
Ascospores 100–150 × 18–23 µm, 17–25-septate (Aptroot *et al.* 2016a; Fig. Fig. 59H) . . . . . **Viridothelium kinabaluense**
- 9(7) Ascospores 38–52 × 7–10 µm (this synopsis; Fig. 59I–K) . . . . . **Viridothelium virens**  
Ascospores 50–80 × 8–15 µm (this synopsis; Fig. 59L) . . . . . **Viridothelium cinereoglaucescens**  
If ascospores smaller and relatively broader (21–40 × 9–15 µm, 2–3 times as long as broad compared to more than 5 times as long as broad in the above species), see also *Trypethelium inaequale* (this synopsis)

**Viridothelium cinereoglaucescens**  
(Vain.) Lücking, M. P. Nelsen  
& Aptroot comb. nov.

Mycobank No.: MB 817024

*Pseudopyrenula cinereoglaucescens* Vain., *Bot. Mag. Tokyo* 35: 76 (1912).—*Trypethelium cinereoglaucescens* (Vain.)

R. C. Harris, *Lichenogr. Thomsoniana*: 141 (1998); type: Japan, Kozuke, Yasuda 197 (TUR 30813!—holotype).

(Fig. 59L)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.



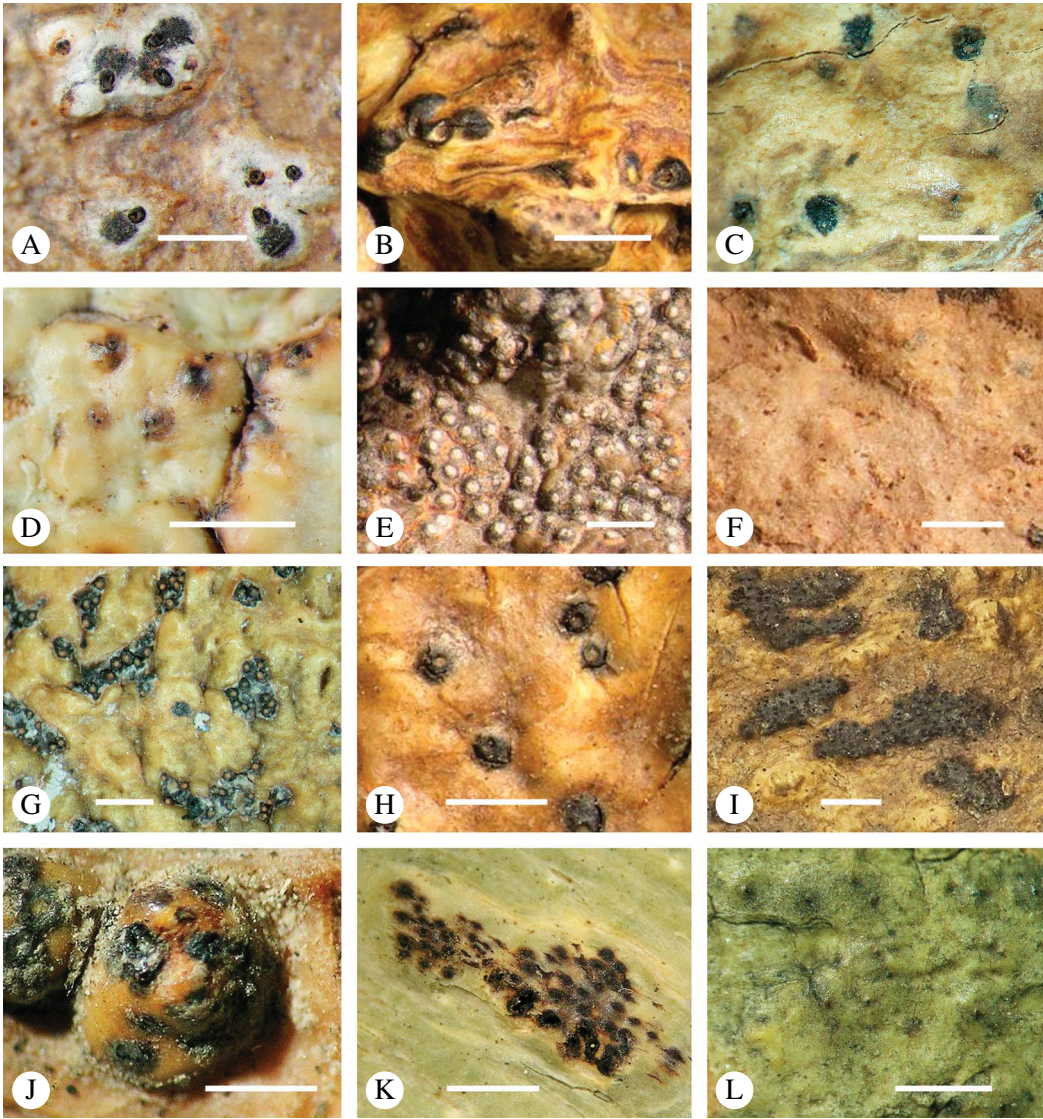


FIG. 59. Habitus of *Viridothelium* species. A, *V. tricolor* (Panama, holotype); B, *V. solomonense* (Solomon Islands, holotype); C, *V. megaspermum* (India, isotype); D, *V. vonkonratii* (Fiji, holotype); E, *V. leptoseptatum* (Brazil, holotype); F, *V. inspersum* (Papua New Guinea, holotype); G, *V. indutum* (Australia, Streimann 45933); H, *V. kinabaluense* (Malaysia, Sabah, holotype); I–K, *V. virens* (I, USA, Arkansas, isotype; J, USA, Louisiana, holotype of *Trypethelium exocanthum*; K, USA, New York, Harris 30395); L, *V. cinereoglauescens* (Japan, holotype). Scales = 1 mm.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.4–0.6 mm diam., immersed-erumpent, completely covered by thallus. *Hamathecium* clear. *Ascospores* 8 per ascus, (5–)7–11-septate, fusiform,

50–80 × 8–15 μm, with rather thin septa, hyaline, IKI+ weakly violet.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* Subtropical to temperate Asia (reported from India, Japan, South Korea).

**Viridothelium indutum (Stirt.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 817025

*Trypethelium indutum* Stirt., *Proc. Philosop. Soc. Glasgow* **13**: 193 (1881); type: India, Assam, Tejpore, *Watt* s. n. (BM!)—isolecotype, Makhija & Patwardhan, *J. Hattori Bot. Lab.* **73**: 199, 1993).

*Trypethelium deforme* Makhija & Patw., *Int. J. Mycol. Lichenol.* **5**: 240 (1992) *non* Fée [as *deformis*]; type: Singapore, Maingay 165 (BM!)—holotype).

(Fig. 59G)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, solitary to irregularly confluent, 0.2–0.4 mm diam., erumpent, laterally covered by thallus but upper part exposed, brown-black. *Hamathecium* clear. *Ascospores* 8 per ascus, (9–)13–17-septate, fusiform, 90–105 × 12–16 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–. TLC: no substances detected.

*Distribution.* Palaeotropical (previously reported from India, Singapore and Australia). Reports of *Trypethelium elmeri* from Australia in Aptroot (2009a) also belong here.

*New country records.* **Indonesia:** Sulawesi: Tondano, 1000 m, 1988, *Hensen* s. n. (ABL).—**Philippines:** Sorsogon: Bulusan Volcano National Park, 1994, *Diederich* 13131 (hb. Diederich).—**Papua New Guinea:** Central: Varirata National Park, 1987, *Aptroot* 19140, 19147, 1987 (ABL).

**Viridothelium megaspermum (Makhija & Patw.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 817027

*Pleurotrema megaspermum* Makhija & Patw., *Biovigyanam* **16**: 24 (1990), *non* *Trypethelium megaspermum* Mont. (1843).—*Trypethelium karnatakense* R. C. Harris, *More Florida Lichens*: 147 (1995); type: India, Karnataka, Agumbe, 1974, *Kulkarni* AMH 74.2991 (ABL!)—isotype).

(Fig. 59C)

*Thallus* corticate, olive-green to yellowish brown, smooth to uneven.

*Ascomata* trypethelioid, with mostly eccentric ostioles, solitary, 0.4–0.6 mm diam., deeply (*c.* 2 mm) immersed in the bark, covered by thallus except for black ostioles. *Hamathecium* clear. *Ascospores* 4 per ascus, (9–)15–17-septate, fusiform, 99–152 × 26–33 µm, hyaline, IKI–.

*Chemistry.* Thallus and ascomata UV–, K–; reported to be K+ orange, but no substances detected.

*Distribution.* Eastern palaeotropical (India).

*Discussion.* The hamathecium of this species was erroneously reported as heavily interspersed in the protologue, and the thallus as K+ orange (Makhija & Patwardhan 1990). The original epithet *megaspermum* can be used in the genus *Viridothelium*.

**Viridothelium virens (Tuck. ex Michener) Lücking et al.**

In Lücking et al., *Lichenologist* **48**: 759 (2016); *Trypethelium virens* Tuck. ex Michener, *W. Dard. Fl. Cest. ed. 3*: 453 (1853).—*Trypethelium eluteriae* var. *virens* (Tuck. ex Michener) Trevis., *Flora* **44**: 20 (1861); type: USA, Arkansas, Dardanelle, 1853, *Michener* s. n. (FH—holotype, not seen; M!—isotype).

*Trypethelium exocanthum* Tuck. in Nyl., *Ann. Sci. Nat., Bot., sér. 4* **20**: 258 (1863); type: USA, Louisiana, *Hale* s. n. (H-Nyl!—holotype).

*Trypethelium scorites* Tuck. in Nyl., *Ann. Sci. Nat., Bot., sér. 4* **20**: 259 (1863); type: USA, Mississippi, *s.col.* (H-Nyl—holotype, not seen).

*Verrucaria concatervata* Nyl., *J. Linn. Soc. London, Bot.* **20**: 68 (1883).—*Pseudopyrenula concatervata* (Nyl.) Vain., *Bot. Mag. Tokyo* **35**: 76 (1921).—*Trypethelium concatervatum* (Nyl.) Zahlbr., *Catal. Lich. Univ.* **1**: 489 (1922); type: Japan, Yokohama, *Maingay* s. n. (BM!—isotype).

(Fig. 59I–K)

*Thallus* corticate, olive-green to yellowish, smooth to uneven.

*Ascomata* trypethelioid, with apical ostioles, pseudostromatic; pseudostromata

0.6–1.5 mm diam., immersed-erumpent, with the upper parts of individual ascomata exposed and dark brown. *Hamathecium* clear. *Ascospores* 8 per ascus, 7–11-septate, fusiform, 38–52 × 7–10 µm, with rather thin septa, hyaline, IKI+ weakly violet.

*Chemistry.* Thallus and pseudostromata UV–, K–. TLC: no substances detected.

*Distribution.* North America and temperate East Asia (USA and Japan).

### Taxa newly excluded from the *Trypetheliaceae*

#### ***Phyllobathelium chlorogastricum* (Müll. Arg.) Aptroot & Lücking comb. nov.**

Mycobank No.: MB 816792

*Heufleria chlorogastrica* Müll. Arg., *Flora* **66**: 243 (1883).—*Cryptothelium chlorogastricum* (Müll. Arg.) Zahlbr., *Cat. Lich. Univ.* **1**: 521 (1922).—*Campylothelium chlorogastricum* (Müll. Arg.) Aptroot in Aptroot *et al.*, *Biblioth. Lichenol.* **98**: 52 (2008); type: Brazil, Apiahy, Puiggari 1079 (G!—holotype).

*Thelenella thaxteri* Vain., *Proc. Am. Acad. Arts Sci.* **58**: 144 (1923).—*Phyllobathelium thaxteri* (Vain.) Zahlbr., *Catalogus Lichenum Universalis* **8**: 142 (1931); type: Trinidad and Tobago, Trinidad, Port of Spain, La Seiva Valley, *Thaxter* 46 (TUR!—holotype).

*Thelenella thaxteri* var. *heterogena* Vain., *Proc. Am. Acad. Arts Sci.* **58**: 144 (1923); type: Trinidad and Tobago, Trinidad, Port of Spain, La Seiva Valley, *Thaxter* 66 (TUR!—holotype).

*Thelenella megapotamica* Malme, *Arkiv för Botanik* **22A**: 7 (1928).—*Phyllobathelium megapotamicum* (Malme) R. Sant., *Symb. Bot. Upsal.* **12**(1): 290 (1952); type: Brazil, Rio Grande do Sul, Silveira Martins, *Malme* 1190 (S!—lectotype *fide* Santesson 1952: 290; UPS!—isolectotype).

*Discussion.* The type material of *Heufleria chlorogastrica* is a typical representative of *Phyllobathelium* and the ascospore measurements (50–65 × 23–30 µm) fit those of *Thelenella thaxteri* well; hence this is an older name for the taxon long known as *Phyllobathelium thaxteri* (Lücking 2008).

***Laurera monospora* Breuss in Breuss & Brunnbauer, *Ann. Naturhist. Mus. Wien, Ser.***

***B* 99: 730 (1997); type: Sri Lanka, Sinharaje Forest, 1984, Brunnbauer s. n. (LI—istotype).**

*Discussion.* This is a new synonym of *Ocellularia massalongoi* (Mont.) Hale, with columella, K+ red thallus, unbranched paraphyses and ascospores *c.* 300 × 45 µm.

***Laurera subsphaerioides* Makhija & Patw., *Mycotaxon* **31**: 582 (1988); type: India, Andaman Islands, South Andaman, Wimberliganj, *Patwardhan et al.* AMH 85.168 (ABL, BM—istotypes).**

*Discussion.* The istotypes contain a sterile *Astrothelium* (Fig. 33D) and a fertile *Ocellularia* from which the ascospore and hamathecium characters in the protologue were derived. The *Astrothelium* might be an additional synonym of *A. subdiscretum*.

***Trypethelium deustum* G. Mey., *Syst. Veg., Ed. 16, 4*(1): 326 (1827); type: Brazil, Serra dos Orgaos (L—istotype).**

*Discussion.* A saprobic fungus, cf. *Botryosphaeria* sp.: stromatic, ascospores hyaline, simple, *c.* 15 × 7 µm.

***Trypethelium favulosum* Ach., *Mém. Soc. Imp. Nat. Moscou* **5**: 166 (1817).**

*Discussion.* The type is a mixture of *Pyrenula anomala* (Ach.) Vain. and *Glyphis cicatricosa* Ach.

***Trypethelium lageniferum* Ach., *Synops. Lich.*: 105 (1814).—*Plagiotrema lageniferum* (Ach.) Müll. Arg., *Flora* **68**: 251 (1885); type: (BM-Ach!—istotype).**

*Discussion.* The type consists of two specimens, one is *Pyrenula adacta* Fée (*P. marginatula* Müll. Arg.), for which this would be an older epithet, but the description of the spores probably originates from the second specimen, which is now sterile.

***Trypethelium melanothrix* Eschw. (1833).—*Phyllothelium melanothrix* (Eschw.) Trevis. (1861); type: Brazil (type lost).**



*Discussion.* Type and only species of *Phyllothelium* Trevis. (Trevisan 1861). This is a foliose lichen with rhizines below and lichenicolous fungi above, following the description by Trevisan.

***Trypethelium peltigerum*** G. Merr. (1910); type: Jamaica, on thallus of *Peltigera*, Cummings 11/111 1905, distributed in Merrill, *Lich. Exs.* 85 (L!—isotype).

*Discussion.* This is a new synonym of the lichenicolous fungus *Pyrenidium actinellum* Nyl. No hamathecium is present. Ascospores are brown, 3-septate, *c.* 25 × 10 µm, and constricted at the septa.

**Taxa described or placed in genera belonging in *Trypetheliaceae* but previously excluded from the family at the species level, and their current names**

- Astrothelium africanum* Zahlbr. (1931) = *Lithothelium obtectum* (Müll. Arg.) Aptroot (*Pyrenulaceae*).
- Astrothelium congregans* Eckf. (nom. inval.) = *Anthracotheceum australiense* (Müll. Arg.) Aptroot (*Pyrenulaceae*).
- Astrothelium cryptothelium* (Müll. Arg.) Nyl. (1892) = *Pyrenula cryptothelia* (Müll. Arg.) Aptroot & Etayo (*Pyrenulaceae*).
- Astrothelium epiphyllum* R. Sant. (1952) = *Trypetheliopsis epiphylla* (R. Sant.) Aptroot (*Monoblastiaceae*).
- Astrothelium fugax* Müll. Arg. (1895) = *Lithothelium fugax* (Müll. Arg.) Aptroot (*Pyrenulaceae*).
- Astrothelium interlatens* Nyl. (1868) = *Anthracotheceum* sp. (*Pyrenulaceae*).
- Astrothelium interlatens* var. *nudatum* Nyl. (1868) = *Anthracotheceum* sp. (*Pyrenulaceae*).
- Astrothelium isabellinum* Vain. (1891), non Eschw. = *Lithothelium obtectum* (Müll. Arg.) Aptroot (*Pyrenulaceae*).
- Astrothelium ochrocleistum* Nyl. (1888) = *Pyrenula prostrata* (Stirt.) D. J. Galloway (*Pyrenulaceae*).
- Astrothelium parmularia* Leight. (1871) = non-lichenized fungus *vide* Zahlbruckner (1922).
- Astrothelium prostratum* Stirt. (1873).—*Heufleridium prostratum* (Stirt.) Müll. Arg. (1883).—*Parmentaria prostrata* (Stirt.) Müll. Arg. (1894) = *Pyrenula prostrata* (Stirt.) D. J. Galloway (*Pyrenulaceae*).
- Astrothelium pyrenastraeum* Nyl. (1890) = *Pyrenula septicollaris* (Eschw.) R. C. Harris (*Pyrenulaceae*).
- Astrothelium pyrenastroides* (C. Knight) C. Knight (1875).—*Verrucaria pyrenastroides* C. Knight (1860).—*Parmentaria pyrenastroides* (C. Knight) Müll. Arg. (1894) = *Pyrenula pyrenastroides* (C. Knight) D. J. Galloway (*Pyrenulaceae*).
- Astrothelium septicollare* (Eschw.) Leight. (1866) = *Pyrenula septicollaris* (Eschw.) R. C. Harris (*Pyrenulaceae*).
- Astrothelium speciosum* Zahlbr. (1927, 1928) = typographic error (lapsus) for *Anthracotheceum speciosum* Zahlbr. (*Pyrenulaceae*).
- Astrothelium umbilicatum* Fr. (1825) Incorrectly synonymized (*vide* Aptroot 1991) with *Architrypethelium uberinum* by Zahlbruckner (1922).
- Bathelium epiphyllum* Müll. Arg. (1883) = *Phyllobathelium epiphyllum* (Müll. Arg.) Müll. Arg. (*Strigulaceae*).
- Bathelium madreporiforme* var. *obscurius* (C. Bab. ex Hook. f.) Müll. Arg. (1894) = non-lichenized fungus (*Xylariaceae* sp.).
- Bathelium megaspermum* var. *tasmanicum* Jatta (1911) = *Pyrenula ravenelii* (Tuck.) R. C. Harris (*Pyrenulaceae*).
- Bathelium pyrenuloides* (Mont.) Trevis. (1853) = *Pyrenula pyrenuloides* (Mont.) R. C. Harris (*Pyrenulaceae*).
- Bathelium velatum* Müll. Arg. (1882) = non-lichenized fungus *vide* Letrouit-Galinou (1957).
- Campylothelium defossium* Müll. Arg. (1891) = *Graphidaceae* or *Porinaceae* sp.
- Heufleria alpina* Auersw. = non-lichenized fungus (*Rhytismatales*).
- Laurera astroidella* (Vain.) Zahlbr. (1938) = non-lichenized fungus *vide* Letrouit-Galinou (1957).
- Laurera madreporiformis* var. *obscurior* (C. Bab. ex Hook. f.) Zahlbr. (1922) = non-lichenized fungus (*Xylariaceae* sp.).
- Laurera megasperma* var. *tasmanica* (Jatta) Zahlbr. (1922) = *Pyrenula ravenelii* (Tuck.) R. C. Harris (*Pyrenulaceae*).
- Laurera ochroleucodes* (Vain.) Zahlbr. (1938) = ?*Cryptothecia* sp. *vide* Letrouit-Galinou (1957) (*Arthoniaceae*).
- Laurera pauperrima* (Müll. Arg.) Zahlbr. (1922) = non-lichenized fungus *vide* Letrouit-Galinou (1957).
- Laurera velata* (Müll. Arg.) Zahlbr. (1922) = non-lichenized fungus *vide* Letrouit-Galinou (1957).
- Pseudopyrenula awajiensis* Vain. = *Pyrenula awajiensis* (Vain.) Kashiw. (*Pyrenulaceae*).
- Pseudopyrenula balia* (Kremp.) Müll. Arg. (1883) = *Pyrenula balia* (Kremp.) R. C. Harris (*Pyrenulaceae*).
- Pseudopyrenula conica* (Müll. Arg.) Müll. Arg. (1883) = non-lichenized fungus (*Saccardoella* sp.).
- Pseudopyrenula galactina* Shirley (1893) = *Pyrenula dermatodes* (Borrer) Schaer. (*Pyrenulaceae*).
- Pseudopyrenula illota* (Nyl.) Vain. (1909) = *Lithothelium illotum* (Nyl.) Aptroot (*Pyrenulaceae*).
- Pseudopyrenula majuscula* H. Magn. (1955) = *Pyrenula massariospora* (Starb.) R. C. Harris (*Pyrenulaceae*).
- Pseudopyrenula obvolvata* (Nyl.) Zahlbr. (1922) = *Pyrenula obvolvata* (Nyl.) R. C. Harris & Aptroot (*Pyrenulaceae*).
- Pseudopyrenula octomera* H. Magn. (1955) = non-lichenized fungus (*Saccardoella* sp.).
- Pseudopyrenula quintaria* Zahlbr. (1930) = non-lichenized fungus.
- Pseudopyrenula ramosii* Vain. (1921) = *Myriotrema* sp. (*Graphidaceae*).

- Pseudopyrenula subvelata* (Nyl.) Müll. Arg. (1883) = *Arthopyrenia subvelata* (Nyl.) R. C. Harris (*Arthopyreniaceae*).
- Trypethelium amulare* var. *subdepressum* Nyl. (1858) = *Pyrenula oleagina* Fée. (*Pyrenulaceae*).
- Trypethelium anomalum* Ach. (1814) = *Pyrenula anomala* (Ach.) Vain. (*Pyrenulaceae*).
- Trypethelium anomalum* var. *obscurescens* (Vain.) Zahlbr. (1938) = *Pyrenula anomala* (Ach.) Vain. (*Pyrenulaceae*).
- Trypethelium chiodectonoides* Fée (1824) = *Pertusaria jeeana* Zahlbr. (*Pertusariaceae*).
- Trypethelium cinnabarinum* C. Knight ex F. M. Bailey (1886) = *Pyrenula cruenta* (Mont.) Vain. (*Pyrenulaceae*).
- Trypethelium coccinatum* Stizenb. (1891) = cf. *Pyrenula cruenta* (Mont.) Vain. (*Pyrenulaceae*).
- Trypethelium conglobatum* Ach. (1814).—*Trypethelium eluteriae* var. *conglobatum* (Ach.) Zahlbr. (1922) = non-lichenized fungus on dead lichen.
- Trypethelium commivens* Stirt. (1873); non Nyl.; *Melanotheca commivens* Zahlbr. = *Pyrenula cruenta* (Mont.) Vain. (*Pyrenulaceae*).
- Trypethelium cruentatum* Nyl. (1876); nom. nud. = *Pyrenula cruenta* (Mont.) Vain. (*Pyrenulaceae*).
- Trypethelium cruentulum* Nyl. (1876) = *Pyrenula* aff. *cruenta* fide Zahlbruckner (1922) (*Pyrenulaceae*).
- Trypethelium cruentum* Mont. (1837) = *Pyrenula cruenta* (Mont.) Vain. (*Pyrenulaceae*).
- Trypethelium cruentum* var. *subdecolor* Nyl. = *Pyrenula cruenta* (Mont.) Vain., based on description in Galloway (1985) (*Pyrenulaceae*).
- Trypethelium erumpens* Stirt. (1875); non Fée.—*Melanotheca stirtioniana* Müll. Arg. (1894).—*Trypethelium stirtonianum* (Müll. Arg.) Hellb. (1896) = *Pyrenula* sp., based on description in Galloway (1985) (*Pyrenulaceae*).
- Trypethelium fuscum* Kremp. (1873).—*Melanotheca fusca* (Kremp.) Müll. Arg. (1888) = *Pyrenula* sp. non *Pyrenula fusca* fide Zahlbruckner (1922) (*Pyrenulaceae*).
- Trypethelium gregale* C. Knight (1886) = *Anthracothecium gregale* (C. Knight) Aptroot (*Pyrenulaceae*).
- Trypethelium hemisphaericum* Eschw. in Martius (1833) = *Porina hemisphaerica* (Eschw.) Müll. Arg. (*Porinaceae*).
- Trypethelium inarense* Vain. (1883) = *Polycoccum* sp. (*Polycoccaceae*).
- Trypethelium inconspicuum* C. F. W. Meissn. (1831).—*Melanotheca inconspicua* (C. F. W. Meissn.) Müll. Arg. (1885) = *Pyrenula* sp. fide Zahlbruckner (1922) (*Pyrenulaceae*).
- Trypethelium leucotrypum* Nyl. (1867) = *Pyrenula leucotrypa* (Nyl.) Upreti (*Pyrenulaceae*).
- Trypethelium madreporiforme* var. *obscurius* C. Bab. ex Hook. f. (1855) = non-lichenized fungus (*Xylariaceae* sp.).
- Trypethelium melanophthalmum* (Mont.) Nyl. (1857) = *Pyrenula melanophthalma* (Mont.) Trevis. (*Pyrenulaceae*).
- Trypethelium melanophthalmum* f. *arctecinctum* (Fée) Nyl. (1857) = *Pyrenula arctecincta* Fée (*Pyrenulaceae*).
- Trypethelium nanosporum* C. Knight (1886) = *Lithothelium nanosporum* (C. Knight) Aptroot (*Pyrenulaceae*).
- Trypethelium nigrutulum* Nyl. (1863) = *Pyrenula* sp. fide Zahlbruckner (1922) (*Pyrenulaceae*).
- Trypethelium nudum* Fée (1837) = *Pyrenula* sp. fide Zahlbruckner (1922) (*Pyrenulaceae*).
- Trypethelium oblitescens* Stirt. (1879).—*Pyrenastrum oblitescens* (Stirt.) Makhija & Patw. (1992) = probably *Pyrenula cruenta* (Mont.) Vain., based on descriptions (*Pyrenulaceae*).
- Trypethelium ocellatum* Zenker (1827) = *Pyrenula mamillana* (Ach.) Trevis. fide Zahlbruckner (1922) (*Pyrenulaceae*).
- Trypethelium ornatum* (Müll. Arg.) Hellb. (1896); non Müll. Arg.; *Melanotheca ornata* Müll. Arg. = *Pyrenula cruenta* (Mont.) Vain., based on description in Galloway (1985) (*Pyrenulaceae*).
- Trypethelium pallidum* C. Knight (1886) = *Anthracothecium prasinum* (Eschw.) R. C. Harris (*Pyrenulaceae*).
- Trypethelium papillatum* C. Knight (1886) = *Pyrenula quassicola* Fée (*Pyrenulaceae*).
- Trypethelium paradoxum* Ach. (1817) = *Sclerophyton seriale* (Ach.) Sparrius (*Roccellaceae*).
- Trypethelium pauperrimum* Müll. Arg. (1882) = non-lichenized fungus fide Letrouit-Galinou (1957).
- Trypethelium planum* C. Knight (1886) = *Pyrenula subvariolosa* (C. Knight) Aptroot (*Pyrenulaceae*).
- Trypethelium purpurascens* (Müll. Arg.) Stizenb. (1895).—*Melanotheca purpurascens* Müll. Arg. (1895) = *Pyrenula* sp., probably *P. cruenta* (Mont.) Vain. fide Zahlbruckner (1922) (*Pyrenulaceae*).
- Trypethelium pyrenuloides* Mont. (1843) = *Pyrenula pyrenuloides* (Mont.) R. C. Harris (*Pyrenulaceae*).
- Trypethelium rubescens* C. Knight (1889) = *Pyrenula cruenta* (Mont.) Vain. (*Pyrenulaceae*).
- Trypethelium rubrum* C. Knight (1884) = *Pyrenula cruenta* (Mont.) Vain. (*Pyrenulaceae*).
- Trypethelium schizostomum* Leight. (1869) = *Thelotrema schizostomoides* Zahlbr. fide Zahlbruckner (1924) (*Graphidaceae*).
- Trypethelium sclerotium* Fée (1824) = *Pertusaria sclerotium* (Fée) Müll. Arg. fide Zahlbruckner (1928) (*Pertusariaceae*).
- Trypethelium scoria* Fée (1824); nom. illeg. = *Pyrenula anomala* (Ach.) Vain. (*Pyrenulaceae*).
- Trypethelium sordidescens* Fée (1837) = *Leucodecton compunctum* A. Massal. (*Graphidaceae*).
- Trypethelium stirtonianum* (Müll. Arg.) Hellb. (1896).—*Trypethelium erumpens* Stirt. (1875) non Fée.—*Melanotheca stirtioniana* Müll. Arg. (1894) = *Pyrenula* sp., based on description in Galloway (1985) (*Pyrenulaceae*).
- Trypethelium subinruentum* Nyl. (1890) = *Pyrenula cruenta* (Mont.) Vain. (*Pyrenulaceae*).
- Trypethelium subplanum* C. Knight (1886) = *Anthracothecium gregale* (C. Knight) Aptroot (*Pyrenulaceae*).
- Trypethelium subumbilicatum* C. Knight (1886) = *Pyrenula subumbilicata* (C. Knight) Aptroot (*Pyrenulaceae*).
- Trypethelium tetrathalamium* Fée (1824) = *Pertusaria tetrathalamia* (Fée) Nyl. (*Pertusariaceae*).
- Trypethelium umbilicatum* C. Knight (1886) = *Pyrenula subvariolosa* (C. Knight) Aptroot (*Pyrenulaceae*).
- Trypethelium verrucarioides* Fée (1837).—*Chiodecton verrucarioides* (Fée) Müll. Arg. (1887) = *Enterographa verrucarioides* (Fée) Müll. Arg. (1885) (*Roccellaceae*).
- Trypethelium verrucosum* Fée (1824) = *Pertusaria* sp. fide Zahlbruckner (1928) (*Pertusariaceae*).

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