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Standard Paper

Taxonomic innovations in *Megasporaceae* (lichenized *Ascomycota, Pertusariales*): *Antidea,* a new genus for *Aspicilia brucei*; two new species of *Aspicilia,* and new combinations in *Aspilidea* and *Lobothallia*

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Abstract

We present a robust, five-locus phylogeny of the *Megasporaceae* and, based on this, propose several taxonomic innovations. The new genus *Antidea* is erected for *Aspicilia brucei*, which occupies a position near the base of the phylogeny, and the new species *Aspicilia indeterminata* and *A. suavis* are described from Montana. We also show that all North American (and some European) records of *Aspilidea myrinii* are misidentifications with many representing a second species in the genus, differing from *A. myrinii* by having elevated apothecia and narrower ascospores and for which we make the new combination *Aspilidea subadunans.* Finally, we make the new combinations *Lobothallia determinata* and *L. peltastictoides,* and report the lichenicolous fungus *Sagediopsis aspiciliae* (on *A. subadunans*) as new to North America.

Keywords: generic delineation; lichenicolous fungus; Montana; North America; phylogeny; *Sagedia mastrucata*; *Sagediopsis*

(Accepted 17 July 2024)

Introduction

Megasporaceae was introduced by Lumbsch *et al.* (1994) for the single genus *Megaspora* (Clauzade & Cl. Roux) Hafellner & V. Wirth. Previously, Hafellner (1984) had included *Megaspora* in *Hymeneliaceae* Körb. (*Lecanorales* Nannf.), which at that time included *Aspicilia* s. lat., but Lumbsch *et al.* (1994) transferred the family to *Pertusariales* M. Choisy ex D. Hawksw. & O. E. Erikss. More recently, in a five-locus study of *Lecanoromycetes*, Miadlikowska *et al.* (2006) uncovered a strongly supported sister relationship between *Aspicilia* A. Massal. and *Ochrolechia* A. Massal. and included *Aspicilia* in *Pertusariaceae* Körb. Schmitt *et al.* (2006) further divided *Pertusariaceae* and grouped *Aspicilia* and *Lobothallia* (Clauzade & Cl. Roux) Hafellner with *Megaspora* in an expanded *Megasporaceae*.

Nordin *et al.* (2010) performed a two-locus (nuLSU, mtSSU) analysis focused on *Megasporaceae* and, although this had weak support for *Aspicilia* and was poorly resolved, they resurrected the genera *Sagedia* Ach. and *Circinaria* Link for two groups of species formerly included in *Aspicilia* while also excluding *Aspilidea* Hafellner from the family. In a revision of the vagrant 'manna group' members of *Circinaria*, Sohrabi *et al.* (2013*a*) recovered a topology that supported the generic delimitations in Nordin *et al.* (2010). Sohrabi *et al.* (2013*b*) later introduced the genus *Teuvoa* Sohrabi & S. D. Leav. for three species previously included in *Lobothallia*. Miadlikowska *et al.* (2014) suggested that *Sagedia* should be included within *Aspicilia*, and the expanded genus (*Aspicilia* + *Sagedia*) along with *Circinaria, Lobothallia* and *Aspilidea* (with low support), included in a highly supported *Megasporaceae* sister to *Ochrolechiaceae* R. C. Harris ex Lumbsch & I. Schmitt within *Pertusariales*. Subsequently, *Oxneriaria* S. Y. Kondr. & Lőkös was introduced for a large group of mostly Arctic species previously included in *Aspicilia* as sister to the *Aspicilia* s. str./*Sagedia* clade (Moniri *et al.* 2017). This permitted *Sagedia* to be recognized as a distinct genus. Zakeri *et al.* (2017) resurrected the genus *Aspiciliella* M. Choisy for a group of species sibling to *Circinaria*/*Megaspora*. A different approach was taken by McCune & Di Meglio (2021) who investigated the *Aspicilia reptans* group in NW North America using a two-locus phylogeny (ITS, nuLSU) and revealed a topology in which most of these recently recognized genera, although monophyletic, were either unsupported or nested within other genera. Consequently, they recognized only *Aspiciliella* and *Megaspora* among the recently segregated genera, leaving all other species in *Aspicilia* s. lat. Finally, Paukov *et al.* (unpublished data) have proposed the new genus

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Atrostelia Paukov *et al.* (*ined.*) for a single species *A. magnifica* Davydov & Yakovchenko from the Republic of Tyva, Russia, which resolved as sister to *Aspiciliella* in their phylogenetic tree.

In recent years, *Aspicilia* s. lat. has been the subject of several regional studies. Thomson (1997) broadly surveyed the Arctic North American species, Owe-Larsson *et al.* (2007) described 19 new species as part of their treatment of the genus in SW North America, and Øvstedal *et al.* (2009) included 38 *Aspicilia* species in their account of the lichens of Svalbard. However, no comprehensive study of the group has been undertaken since Magnusson (1939). Here we present a robust five-locus phylogeny of *Megasporaceae*, erect a new genus for an early diverging species in the family, describe two new species of *Aspicilia* and make new combinations at the species level in *Aspilidea* and *Lobothallia*. We also report the lichenicolous fungus *Sagediopsis aspiciliae* (Zopf ex Sacc. & D. Sacc.) Nik. Hoffm. & Hafellner as new to North America.

Materials and Methods

Taxon sampling

The majority of the specimens used in this study were collected by the first author between 2007–2017, but further specimens were obtained from herbarium loans and the collecting efforts of other researchers. Analysis focused on specimens from the Northern Hemisphere, with efforts concentrated on the group in western North America and the northern Rocky Mountains, but specimens from eastern Canada and Scandinavia are also included (Supplementary Material S1 & S2, available online). Additional sequences were downloaded from GenBank (Supplementary Material S1).

Morphological study

Hand-cut sections of apothecia and pycnidia were mounted in water and tested by the addition of 10% KOH (K) and 50% HNO_3 (N). The presence of norstictic and stictic acids was inferred from positive reactions under the microscope with 10% KOH and para-phenylenediamine (Pd), respectively, and confirmed with thin-layer chromatography in solvent systems A and C (Orange *et al.* 2001). Ascospore measurements and ratios are given as: (lowest recorded–)normal range(–highest recorded), except for *Aspilidea* spp. and *Sagediopsis aspiciliae*, which are given as (lowest recorded–) $\bar{x} \pm$ standard deviation (–highest recorded); n = number of measurements.

DNA isolation and sequencing

Tissue samples for total DNA were extracted from 10–15 healthy apothecia and surrounding tissue. Two 3 mm steel beads were added to the sample tubes and frozen at −80 °C for 1 h. Samples were then mounted on the TissueLyser II (Qiagen, Germany) and ground in 30 s intervals for 1–2 min at 30/hz. DNA was extracted using the Qiagen DNeasy Plant Mini Kit (Qiagen, Germany) following the manufacturer's instructions, except for the following modifications: in the first step, samples were incubated in lysis buffer for 1 h and vortexed every 10 min; in the final step, the samples were eluted in 50 µl AE buffer twice. DNA quantity was tested on an Implen Nanodrop (Implen, München, Germany). Standard PCR amplifications were conducted in 25 µl reaction volumes using Ready-To-Go PCR Beads (GE Healthcare, UK) or Gotaq Green Master Mix (Promega) following manufacturers' recommendations. All primers used in this study appear in Table 1. Amplifications were carried out in an Eppendorf Mastercycler Pro thermal cycler (Eppendorf North America, New York, USA) and performed using the protocols in Table 2. PCR products were cleaned using the Qiagen PCR Purification Kit (Qiagen, Germany) or Agencourt AMPure XP beads (Beckman Coulter, Inc., Brea, California, USA), following manufacturers' instructions, and were visualized on 1% agarose gel stained with ethidium bromide. Sequencing reactions were performed by Eurofins Genomics (Louisville, Kentucky, USA).

Sequence alignment. Sequences were quality checked and sequence ends were manually trimmed in Aliview (Larsson 2014). Each sequence was checked against the NCBI nucleotide database (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to verify that the desired organism had been sequenced. Alignments were visually checked in AliView and minor misalignments were manually adjusted.

Phylogenetic analyses. Maximum likelihood trees for each locus (not shown) were constructed in raxmlGUI 2.0 (Stamatakis 2014; Edler *et al.* 2021), and the bootstrap support values compared for each clade. Using a 70% bootstrap value threshold, clades were compared and conflict was assumed to be significant where a monophyletic group was supported with bootstrap values ≥ 70% within one locus and the same group of taxa was supported ≥ 70% as non-monophyletic within another locus (Mason-Gamer & Kellogg 1996). Since no strongly supported conflicts were uncovered among the five loci, downstream relationships and analyses were performed on the concatenated dataset. Analyses were run using raxmlGUI 2.0 to reconstruct a maximum likelihood (ML) concatenated five-locus tree. We used *Lepra albescens* as the root and ran 1000 thorough maximum likelihood bootstraps with the substitution model set to GTRGAMMA.

Table 1. Primers used in this study

Primer name	Primer sequence (5'-3')	Reference
ITS1F	CTTGGTCATTTAGAGGAAGTAA	Gardes & Bruns 1993
ITS4	TCCTCCGCTTATTGATATGC	White *et al.* 1990
LrlecF	CCTCAGTAACGGCGAG	Schneider *et al.* 2015
LR7	TACTACCACCAAGATCT	Vilgalys unpublished
mtSSU1	AGCAGTGAGGAATATTGGTC	Zoller *et al.* 1999
mtSSU3R	ATGTGGCACGTCTATAGCCC	Zoller *et al.* 1999
MCM7for	CGTCACTACAAAACAATTCACC	This study
MCM7rev	CGCCCATCTCTTTTGTGAC	This study
MCM7for_long	TGGAGTATGGCACGCAG	This study
MCM7rev_long	GATTTGCAGCAGCAAGTAT	This study
fRPB2-5F	GAYGAYMGWGATCAYTTYGG	Liu *et al.* 1999
fRPB2-7cR	CCCATRGCTTGYTTRCCCAT	Liu *et al.* 1999

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Table 2. PCR protocols used in this study

Marker	Initial denaturation	35 cycles of	Final extension
nuITS	2 min at 94 °C	94 °C for 1 min, 54 °C for 1 min, 72 °C for 45 s	72 °C for 7 min
nuLSU	4 min at 95 °C	94 °C for 1 min, 54 °C for 1 min, 72 °C for 45 s	72 °C for 5 min
mtSSU	4 min at 95 °C	94 °C for 1 min, 54 °C for 1 min, 72 °C for 45 s	72 °C for 5 min
Mcm7	4 min at 95 °C	95 °C for 30 s, 50 °C for 40 s, 72 °C for 1 min	72 °C for 5 min
RPB2	4 min at 95 °C	95 °C for 30 s, 52 °C for 40 s, 72 °C for 1 min	72 °C for 5 min

Results

We obtained sequence data from 98 specimens, representing *c.* 52 taxa, for a total of 337 new sequences (Supplementary Material S1, available online). In total, 77 nuITS, 73 nuLSU, 75 mtSSU, 76 *Mcm7* and 36 *RPB2* sequences were recovered. The final concatenated alignment contained 172 sequences and 5676 positions.

Several conclusions can be drawn from the resulting phylogenetic tree (Fig. 1):

1) *Aspilidea* is basal to the *Megasporaceae*, with high support, and consists of two distinct taxa.
2) *Aspicilia brucei* Owe-Larss. & A. Nordin forms a well-supported clade between *Aspilidea* and the rest of the *Megasporaceae*.
3) The relationships among the genera (including *Sagedia*) are well supported except for *Megaspora* and *Oxneriaria*, the positions of which as siblings to *Circinaria* and *Aspicilia* respectively have poor support.
4) The infrageneric groups in *Aspicilia* and *Oxneriaria* have poor support.
5) Two undescribed species of *Aspicilia* are indicated.
6) As previously shown by Nordin *et al.* (2010), the presence of marginal lobes is confirmed not to be a genus-level character in *Megasporaceae,* and two species of *Aspicilia* without marginal lobes should be transferred to *Lobothallia*.
7) The sequenced collection of *Sagedia mastrucata* (Wahlenb.) A. Nordin *et al.* is not conspecific with previous sequenced collections of this species.

We deal with many of these below.

Taxonomy

A new genus for Aspicilia brucei

The species *Aspicilia brucei*, described from California (Owe-Larsson *et al.* 2007) and subsequently reported from France (Roux *et al.* 2011) and the Czech Republic (Vondrák *et al.* 2022), was known to be morphologically and chemically similar to *A. cinerea* (L.) Körb. (Owe-Larsson *et al.* 2007).

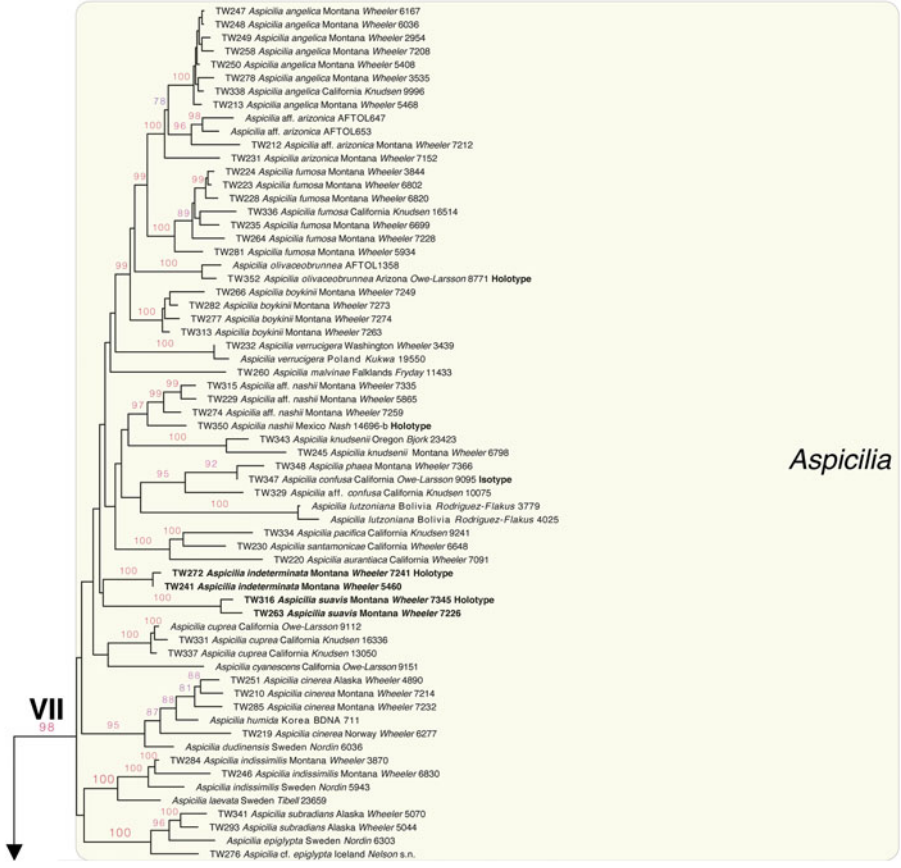

Figure 1. Five-locus (nuITS, nuLSU, mtSSU, *Mcm7* and *RPB2*) concatenated maximum likelihood tree. Bootstrap support values ≥ 60% are indicated above branches. New species, new combinations and sequenced types are in bold. Coloured polygons correspond to the 11 currently accepted genera. Roman numerals correspond to the seven supported monophyletic clades. In colour online.

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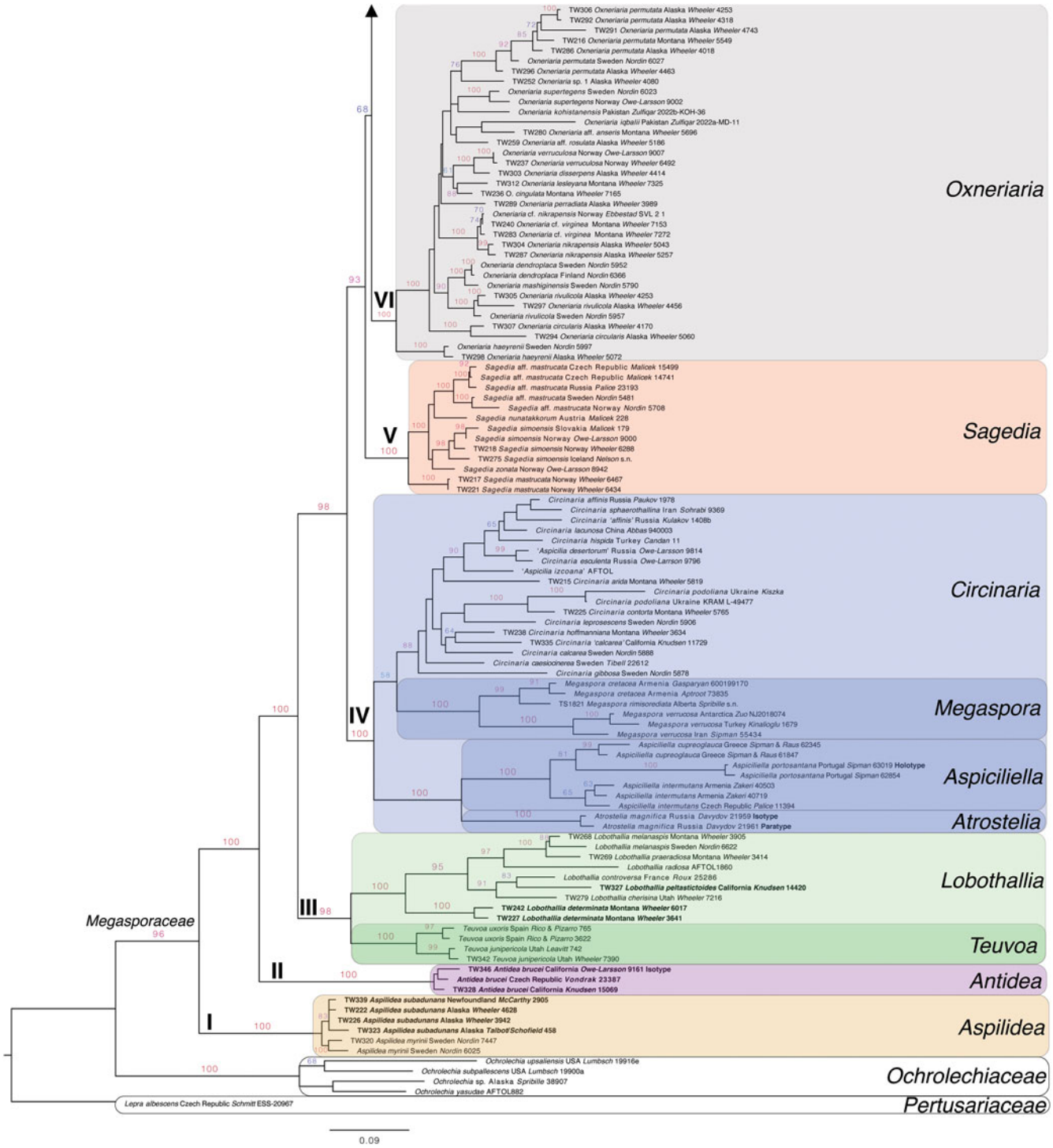

Figure 1. Continued.

However, it differed from that species by having smaller ascospores and shorter, bacilliform conidia. Molecular data from two specimens of *A. brucei*, both from California and including an isotype (*Owe-Larsson* 9161), were sequenced and analyzed along with sequences from a Czech Republic specimen downloaded from GenBank. *Aspicilia brucei* was recovered as a highly supported group near the base of *Megasporaceae*, and the new genus *Antidea* is described to accommodate this monotypic clade.

Antidea T. B. Wheeler gen. nov.

MycoBank No.: MB 822149

Similar to *Aspicilia* in general morphology and in producing norstictic acid but differing in the smaller ascospores and shorter, bacilliform to filiform conidia. Also differing in its molecular sequence data.

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Typus generis: *Antidea brucei* (Owe-Larss. & A. Nordin) T. B. Wheeler.

Etymology. *Antidea*, an early Latin meaning of 'to come before' and 'in the past', is a reference to the early diverging position of the genus in the *Megasporaceae*.

Notes. This monotypic genus is morphologically very similar to some forms of *A. cinerea*. However, the single species, *A. brucei*, differs in having smaller ascospores (9–13 × 5–8 µm vs (10–)12–18(–22) × 7–11(–14) µm in *A. cinerea*), shorter conidia (6–10 µm vs (10–)12–19(–22) µm in *A. cinerea*), and non-moniliform to submoniliform paraphyses (moniliform in *A. cinerea*).

Antidea brucei (Owe-Larss. & A. Nordin) T. B. Wheeler comb. nov.

MycoBank No.: MB 822154

Aspicilia brucei Owe-Larss. & A. Nordin, *Lichen Flora of the Greater Sonoran Desert Region* (Tempe) **3**, 73 (2007).

(Fig. 2)

A full description of this species is given by Owe-Larsson *et al.* (2007) and is not repeated here. See Fig. 2 for a visual comparison of *Antidea brucei* and *Aspicilia cinerea*.

Two new species of Aspicilia

Massalongo (1852) introduced the name *Aspicilia* for a disparate group of lichens with innate apothecia, including species currently placed in *Bellemerea* Hafellner & Cl. Roux, *Ionaspis* Th. Fr. and *Rhizocarpon* Ramond ex DC. Massalongo (1852) also introduced the new name *Aspicilia polygonia* (Vill.) A. Massal. based on *Lichen polygonius* Vill., which Choisy (1929) implied to be the lectotype of the genus. Since Clauzade & Roux (1984) could not locate any material of this species in Villars' herbarium, Laundon & Hawksworth (1988), in their proposal to conserve *Aspicilia*, selected the illustration of *L. polygonius* (Villars 1789) as the lectotype. Unfortunately, it is impossible to determine to which species this illustration refers, and so the Committee for Fungi amended Laundon & Hawksworth's proposal to include as the conserved type for *Aspicilia* a Schaerer exsiccate specimen (Exc. Lich. Helv. #127) in Verona (VER) that had been cited by Massalongo (1852) in the protologue of his new genus (Gams 1993). This specimen is referable to *Aspicilia cinerea* (L.) Körb. (basionym *Lichen cinereus* L.), which is the conserved type of the genus. Later, Jørgensen *et al.* (1994) selected the same exsiccate number as the neotype for *L. cinereus*, but selected the specimen in Uppsala (UPS), rather than the one in Verona, as the type of the species.

Although *Aspicilia* was initially accepted by contemporary authors (Koerber 1855; Mudd 1861), later authors almost always treated it as a section in *Lecanora* Ach. (Zahlbruckner 1928; Magnusson 1939, 1951), and it was not until the 1970s that *Aspicilia* was again widely accepted as a separate genus (Poelt 1974; Roux 1977; Clauzade & Roux 1984; Hafellner 1984).

Aspicilia s. str. was highly supported in our analysis, but the relationships within the genus were poorly resolved. We also identified two additional species in the genus that are described below.

Aspicilia indeterminata T. B. Wheeler sp. nov.

MycoBank No.: MB 853846

Similar to the *A. cinerea* group in its immersed apothecia, greyish thallus, olive green epihymenium, and production of norstictic acid, but differing in the larger ascospores, submoniliform paraphyses, pruinose apothecia, and lack of additional substances.

Type: USA, Montana, Beaverhead Co., Pioneer Mountains, Vipond Park, 45.730623°N, 112.863999°W, 2015 m, on quartzite talus, 23 June 2016, *Wheeler* 7241 (ASU).

(Fig. 3)

Hypothallus lacking. *Thallus* contiguous, areolate, dense, separated by deep cracks, non-determinate, 4–10 cm diam. *Areoles* greyish white to grey, epruinose to slightly white pruinose, angular, 0.2–1 mm diam., 0.1–0.5 mm thick. *Upper cortex* pseudoparenchymatous, 15–30 µm thick, cells to 4–6 µm diam. *Algal layer* continuous, undulating, 40–50 µm thick, algal cells chlorococcoid, mostly *c.* 10 µm diam. *Medulla* obscure, *c.* 200 µm tall.

Apothecia usually one per areole, lecanorine/aspicilioid, round, with a thin to thick margin the same colour as the thallus or slightly darker; *disc* sunken, concave, proper margin thin and slightly pruinose, mature disc black, weakly to densely white pruinose, 0.25–1.25 mm diam., eventually raised above the thallus. *Exciple* pseudoparenchymatous, cells 4–5 µm, dark grey to hyaline, up to 100 µm thick. *Epihymenium* 10–20 µm tall, olive green, K+ brown. *Paraphyses* submoniliform, top 2–3 cells rounded and expanded to 4 µm, occasionally branching and anastomosing, 2–3 µm thick. *Hymenium* 100–130 µm tall, I+ blue. *Asci* 8-spored, *c.* 90 × 25 µm, *Aspicilia*-type. *Ascospores* simple, hyaline, (15–)17–21(–22) × 10.5–13 µm, broadly ellipsoid. *Hypothecium* hyaline, 40–60 µm tall, with small oil droplets, algal layer not continuous below hypothecium.

Pycnidia c. 150 × 100 µm, rare, inconspicuous. *Conidia* straight, 14–15 × 1–1.5 µm.

Spot tests and chemistry. Spot tests: K+ red crystals in the type specimen, but K− in the additional specimens; however, norstictic acid was present in all specimens analyzed with TLC.

Etymology. Named for the indeterminate thalli, and confusion it created when initially discovered.

Ecology and distribution. Currently known only from Montana, where it has been collected from granitic boulders and quartzite talus in dry, forested montane sites, from 1500–2015 m altitude.

Notes. *Aspicilia indeterminata* is an indistinctive, thin to thick, greyish *Aspicilia* with sunken discs. In the type specimen the discs are weakly pruinose, in contrast to the densely pruinose discs of other specimens. It is close to *A. verrucigera* Hue in general morphology, conidia and spore size, but differs in lacking stictic acid and having an epihymenium that is distinctively green to olive green, as opposed to olive-brown. *Aspicilia cinerea* differs in having smaller ascospores, moniliform paraphyses, an olive-brown epihymenium and non-pruinose apothecial discs.

Additional specimens examined. **USA:** *Montana*: Lewis and Clark Co., Orofino Gulch Road, 46.542127°N, 112.097662°W,

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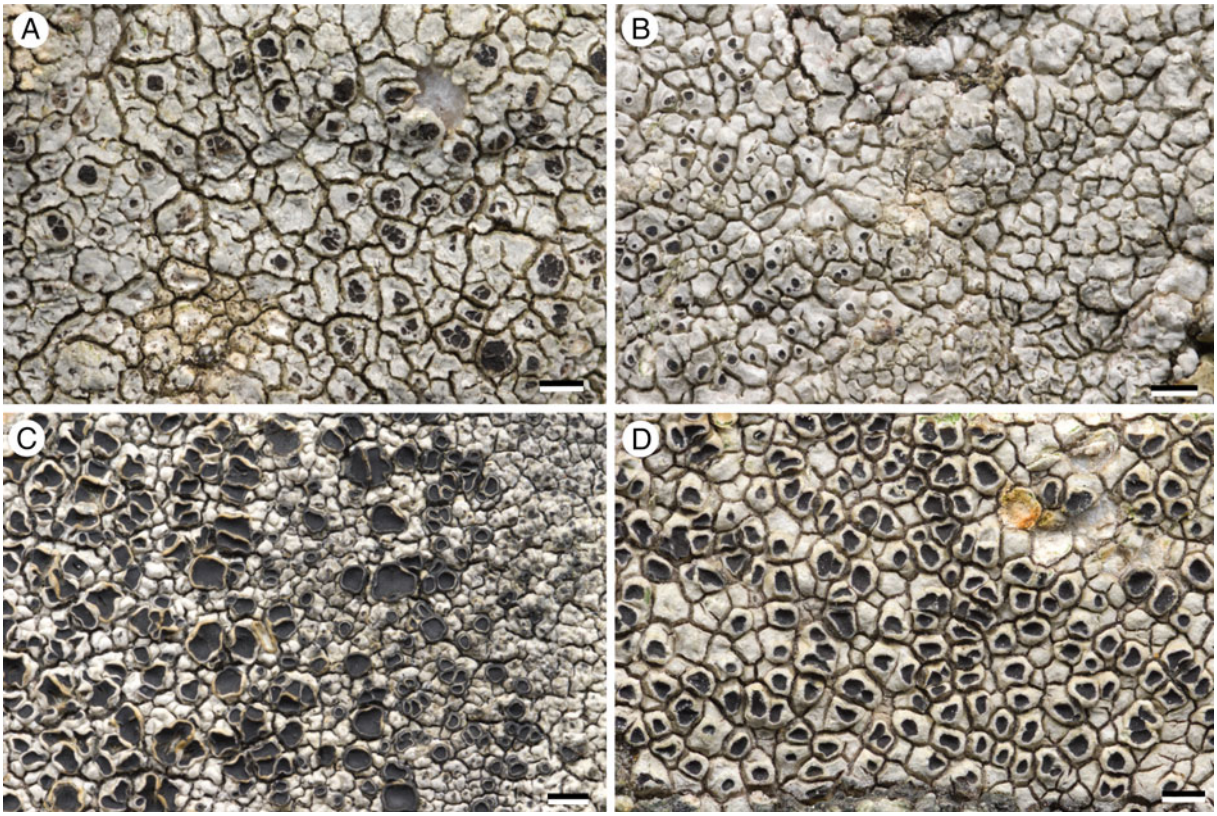

Figure 2. New genus: *Antidea brucei* and *Aspicilia cinerea.* A & B, *Antidea brucei* (A, *Knudsen* 15069; B, *Owe-Larsson* 9161—isotype). C & D, *Aspicilia cinerea* (A, *Wheeler* 6277; B, *Wheeler* 7214). Scales = 1 mm. In colour online.

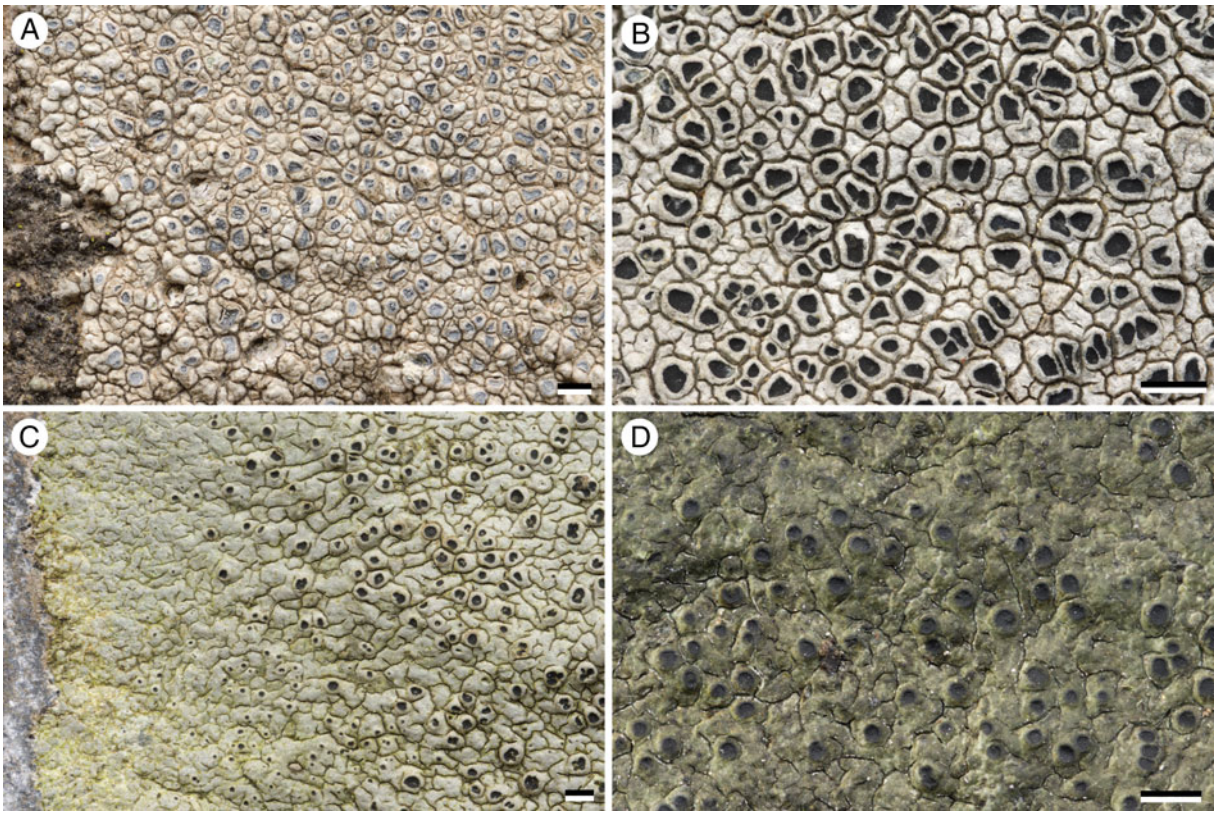

Figure 3. Newly described species. A & B, *Aspicilia indeterminata* (A, *Wheeler* 5460; B, *Wheeler* 7241—holotype). C & D, *Aspicilia suavis* (C, *Wheeler* 7226; D, *Wheeler* 7345—holotype). Scales = 1 mm. In colour online.

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1525 m, on Tertiary granite boulders, 2012, *Wheeler* 5460, 5464, 5470, 5471, 5472 (hb. Wheeler).

Aspicilia suavis T. B. Wheeler sp. nov.

MycoBank No.: MB 853847

Similar to *Aspicilia laevata* (Ach.) Arnold in its thin, greenish grey, smooth, weakly rimose to uncracked thallus, immersed apothecia, habitat near mountain streams in shaded locales, olive green epihymenium and production of stictic and norstictic acids, but differing in the slightly larger ascospores, submoniliform paraphyses, and multilocus sequence data.

Type: USA, Montana, Ravalli Co., Sapphire Mountains, Skalkaho-Rye Road near the summit, 48.985375°N, 113.859990°W, 2145 m, on granodiorite boulders in small stream, 16 September 2016, *Wheeler* 7345 (ASU).

(Fig. 3)

Hypothallus lacking, to thin and greyish. *Thallus* continuous, thin, smooth and uncracked, or becoming sub-rimose when older and thicker, non-determinate, 4–18 cm diam. *Surface* greenish grey to dark olive green, epruinose. *Areoles* continuous, 0.5–3 mm diam., 0.1–0.25 mm thick. *Upper cortex* pseudoparenchymatous, 20–35 µm thick. *Algal layer* continuous, 20–40 µm thick, algal cells chlorococcoid, mostly *c.* 10 µm diam. *Medulla* obscure, whitish.

Apothecia 1–3 per areole, aspicilioid, round, sunken but with a 100–130 µm thick raised thalline margin the same colour as the thallus or slightly darker, proper margin thick and darker than the thallus tissue, disc dark green to black, epruinose, 0.25–1.0 mm diam., eventually raised above the thallus. *Exciple* pseudoparenchymatous, cells 4–5 µm, dark grey to hyaline, up to 130 µm thick. *Epihymenium* 15–20 µm tall, olive blue-green. *Paraphyses* non-moniliform to submoniliform, 2–3 µm thick, top 1–2 cells rounded and expanded up to 3 µm, coherent even in KOH. *Hymenium* 100–130 µm tall, I+ blue. *Asci* 8-spored, *c.* 100 × 30 µm, *Aspicilia*-type. *Ascospores* simple, hyaline, (19–)21–24(–26) × 12–15 µm, broadly ellipsoid. *Hypothecium* hyaline, olive green in upper part, 80–125 µm tall, algal layer not continuous below hypothecium.

Pycnidia c. 175 × 100 µm, common, inconspicuous black ostiole. *Conidia* long, straight, (19–)21–23(–25) × 1–1.25 µm.

Spot tests and chemistry. Spot tests: K+ yellow diffusion, Pd+ red; stictic acid (major) and norstictic acid (trace) present in both specimens when analyzed by TLC.

Etymology. Named for the beautiful smooth greenish thalli and calm, idyllic streamside mountain settings where it is often found.

Ecology and distribution. Currently known only from Montana, where it has been collected from granodiorite and argillite boulders in the splash zone of mountain lakes and streams from 1700–2200 m altitude.

Notes. Aspicilia suavis is an indistinctive, thin, greenish grey *Aspicilia* with sunken discs that is found on splash zone siliceous boulders in montane and alpine habitats. In the type specimen the thallus is distinctly green, while in other specimens it is paler greenish grey. The discs are epruinose, and raised in smooth, steep-sided mounds. It is very close to *A. laevata* in general morphology, conidia shape and size, chemistry, and preference for shady streamside sites, but it has larger ascospores (19–26 µm vs 13–20 µm). However, molecular data place *A. laevata* in a poorly supported clade with *A. epiglypta* (Norrl. ex Nyl.) Hue, *A. subradians* (Nyl.) Hue, *A. indissimilis* (H. Magn.) Räsänen and others, and *A. suavis* in an unsupported 'pacifica group' clade. *Aspicilia aquatica* (Fr.) Körb. s. lat. can be similar and occurs in similar habitats, but it has moniliform paraphyses, smaller conidia and a paler yellowish thallus that lacks a thalline chemistry. Much of what has been identified in western North America as *A. aquatica* and *A. laevata* will most likely be referable to *A. suavis*.

Additional specimens examined. **USA:** *Montana*: Lake Co., Mud Lake, Mission Mountains, 47.615719°N, 113.994752°W, 1768 m, on argillite boulders along southern shore, 2016, *Wheeler* 7225 and 7226 (hb. Wheeler).

A second species of Aspilidea

The genus *Aspilidea* was introduced for the single species *A. myrinii* (Fr.) Hafellner (Hafellner & Türk 2001). However, the anomalous position of the species in *Aspicilia* was previously noted by Roux (1977), who included it with *Bellemerea* but did not make a formal new combination. Later, Clauzade & Roux (1984) acknowledged that *A. myrinii* was not congeneric with *Bellemerea* but did not suggest an alternative placement. *Aspilidea myrinii* has a superficial resemblance to the type species of *Bellemerea*, *B. alpina* (Sommerf.) Clauzade & Cl. Roux, in that both species have immersed apothecia with a pseudothalline margin and a thallus containing norstictic acid with an amyloid (I+ violet) medulla. However, they differ in important anatomical characteristics, most notably that the ascus of *Bellemerea* has a distinctive amyloid tube-like structure (*Porpidia*-type) and belongs in *Lecideaceae*, whereas the ascus of *Aspilidea* lacks the tube-like structure and belongs in *Megasporaceae*.

Hafellner & Türk (2001) separated *Aspilidea* from *Aspicilia* by the I+ pale purple medulla of the thallus, the euamyloid reaction of the hymenial jelly (hemiamyloid in *Aspicilia*), fine features of the ascus structure, conspicuous pycnidia with conidiophores of type II–III according to Vobis (1980), and different lichenicolous fungi.

In our analysis, *Aspilidea* is early diverging in the *Megasporaceae* and, as in Miadlikowska *et al.* (2014) but here with high support, is included in the family. The clade included previously sequenced collections from Europe as well as new specimens from Newfoundland, Quebec and Alaska that represent an additional species, for which the epithet '*subadunans*' is available.

Aspilidea subadunans (Vain.) T. B. Wheeler, J. W. McCarthy & Fryday comb. nov.

MycoBank No.: MB 853844

Lecanora myrinii var. *subadunans* Vain. [as '*myrini*'], *Meddeland. Soc. Fauna Fl. Fenn.* **6**, 169 (1881).—*Aspicilia subadunans* (Vain.) Räsänen, *Ann. Bot. Soc. Zool.-Bot. Fenn. 'Vanamo'* **12**(1), 78 (1939) *nomen non funga*.—*Aspicilia myrinii* var. *subadunans* (Vain.) Oxner [as '*myrini*'], in Kopaczevskaja *et al.*, *Opredelitel' Lishaĭnikov SSSR Vypusk* (*Handbook of the Lichens of the USSR*) (Leningrad) **1**, 191 (1971); nom. inval. (ICNafp Art. 41.5); type:

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'In rupe syenitica loco aprico ventoso in regione subalpina montis Päänuorunen in Lapponia Rossica.' (TUR!—holotype).

(Figs 4 & 5)

Hypothallus thin to thick, usually lacking, but in some specimens grey-black, occasionally visible between areoles and as a thin zone at the thallus margin. *Thallus* areolate, contiguous, separated by thin cracks, nondeterminate, up to 20 cm diam.; sometimes bimorphic with a thin primary thallus and a secondary thallus of ±dispersed convex areoles. *Areoles* cream-white to bluish grey, epruinose to faintly white pruinose, often shiny with a thin epinecral layer, irregular, even to irregularly ridged, 0.5–1.0 mm diam., 0.1–0.75 mm thick, 1–2 apothecia per areole. *Upper cortex* pseudoparenchymatous, 30–40 µm thick, epinecral layer thin, 3–7 µm thick, indistinct. *Algal layer* thin, discontinuous, irregular, 40–60 µm thick, algal cells chlorococcoid, 8–10 µm diam.

Apothecia 1–2 per areole, lecanorine, round, with thick outer thallus-coloured margin and a thinner inner darker ring coloured like the disc; immature disc initially sunken, soon becoming elevated and prominent with a narrowing base, margin smooth; mature disc smooth to slightly roughened, black, epruinose to blue-grey pruinose, 0.25–1.25 mm diam. *Exciple* pseudoparenchymatous, cells 4–6 µm, outer layer brownish, inner layer hyaline, 80–130 µm thick. *Hymenium* 80–120 µm, I+ blue; *epihymenium* 20–25 µm tall, dark brown to black, K+ brownish, N+ greenish. *Paraphyses* not branching, non-moniliform, thin, 1 µm thick, apices unexpanded, with pale brown tips. *Asci* 8-spored, 50–60 × 15–25 µm, *Aspicilia* type. *Ascospores* simple, hyaline, narrowly ellipsoid, (11.3–)*16.77* ± 2.50(–22.0) × (4.9–)*7.14* ± 1.19(–11.0) µm, l/w ratio (1.65–)*2.39* ± 0.42(–3.33); *n* = 103. *Hypothecium* hyaline, 80–100 µm, hyaline above, grading into greyish medulla below, algal layer not continuous below hypothecium.

Pycnidia c. 150 × 100 µm, rare to common, with a black, slightly elevated ostiole; *conidia* short bacilliform, (5–)5.5–6.5(–7) × 1–1.5 µm.

Spot tests and chemistry. Medulla K+ yellow to red crystals in section, I± pale brownish violet. TLC: norstictic acid.

Ecology and distribution. A northern species known from 100–1250 m altitude. In North America, it is known from Alaska in the west to Newfoundland in the east (Fig. 6). It has been collected from argillite, schist, phyllite, and quartzite.

To assess the distribution of this species and *A. myrinii* in North America, we examined all known collections of the latter species in North American herbaria available to us (*c.* 50). All were misidentified. They were revised as *A. subadunans*, *Aspicilia cinerea* s. lat. and *Aspicilia* spp., as well as *Bellemerea alpina*, *Lecidea lactea* Flöke ex. Schaer., *L. swartzioidea* Nyl. and, in one case, a heavily grazed *Rhizocarpon* species (Supplementary Material S2, available online). Thus, *A. myrinii* has not been correctly reported from North America. We also examined *A. myrinii* collections from Norway, Sweden and Finland, only one of which proved to be *A. subadunans* (UPS L-520804; Supplementary Material S2).

Notes. Aspilidea subadunans is a distinctive species owing to its thick, white to cream-coloured thallus and prominent, thick-margined apothecia often with pruinose discs. It is similar to *A. myrinii* in morphology and chemistry, having a yellowish to greyish white thallus, small bacilliform conidia and producing norstictic acid, but it differs in the elevated apothecia with prominent, often pruinose discs with double margins and narrower ascospores (Figs 4 & 5, Table 3).

North American specimens have mostly been labelled as *Aspicilia arctica* Lynge ex Oxner, *A. cinerea* or *Aspilidea myrinii*. *Aspicilia arctica* and *A. cinerea* have long filiform conidia (15–23 µm) in contrast to the short bacilliform conidia (5–7 µm) of *A. subadunans*, as well as a hemiamyloid hymenium; *Aspilidea myrinii* has non-pruinose, black, angular or irregular, immersed to slightly sessile apothecia in contrast to the raised, thick-margined apothecia of *A. subadunans*. All three species differ from *A. subadunans* in having broadly ellipsoid ascospores.

When Räsänen (1939) raised Vainio's name to the rank of species, the exsiccatae specimen he cited was *Aspilidea myrinii* not *A. subadunans* but this does not invalidate the combination (ICNafp Art. 7.3). Räsänen (1939) also considered *Aspicilia cinerea* var. *sallensis* Räsänen to be a synonym of *Lecanora myrinii* var. *subadunans* Vain. However, the syntypes in H (H9503235, H9503236, H9503237) have been annotated as *A. myrinii* and our examination of these collections confirmed that they are referable to *A. myrinii* not *A. subadunans*. We designate here one of these syntypes (H5903235) as the lectotype, with the other two collections being isolectotypes (MycoBank No. MBT 10020079).

Selected additional specimens examined. See Supplementary Material S2 and map showing the distribution of *A. subadunans* in North America (Fig. 6).

New combinations in Lobothallia

Lobothallia was originally described as a subgenus of *Aspicilia* by Clauzade & Roux (1984) but was elevated to genus by Hafellner (1991). Although initially proposed for a small group of species with elongate marginal lobes, as has been shown with other recent additions to *Lobothallia* (Nordin *et al.* 2010; Kou *et al.* 2013; Roux *et al.* 2016), the extent of lobation is not an informative phylogenetic character for the genus. Based on our phylogeny, we here transfer two more species without extended marginal lobes to the genus.

Lobothallia determinata (H. Magn.) T. B. Wheeler comb. nov.

MycoBank No.: MB 822174

Lecanora determinata H. Magn., *Lichens from Central Asia* **1**, 96 (1940).—*Aspicilia determinata* (H. Magn.) N. S. Golubk., *Nov. Syst. Niz. Rast.* **9**, 236 (1972); type: China, Kansu [Gansu], Chia-yii-kuan, ad campum, Huang-tsao-ying, alt. 1580 m, 'on coarse-grained sandstone, HCl+ bubbling', 27.9.1930, *Birger Bohlin* Lich. No. 7 (S—holotype).

(Fig. 7A)

Lobothallia peltastictoides (Hasse) T. B. Wheeler comb. nov.

MycoBank No.: MB 822175

Lecanora peltastictoides Hasse., *Bryologist* **17**, 63 (1914).—*Aspicilia peltastictoides* (Hasse) K. Knudsen & Kocourk., *Mycotaxon* **124**, 354 (2013); type: USA, California, Palm Springs, on granite, 1901, *Hasse* 861 (FH—holotype).

(Fig. 7B)

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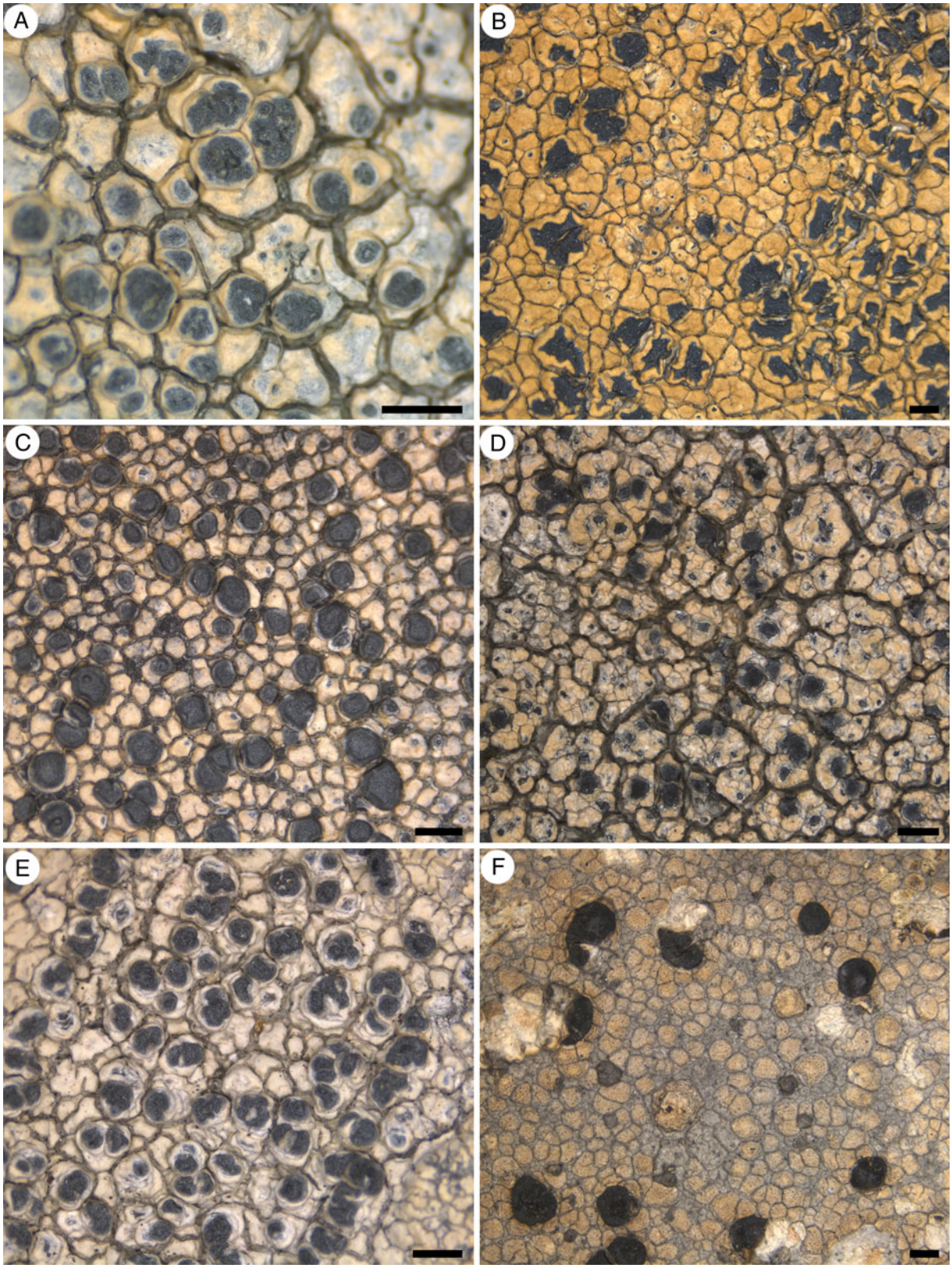

Figure 4. Comparison of the thalli of *Aspilidea* species. A, C & E, *Aspilidea subadunans* (A, TUR–V-05894; C, *McCarthy* 4153; E, *McCarthy* 4352). B, D & F, *Aspilidea myrinii* (B, O–L-20820; D, *Tønsberg* 42336; F, O–L-175683). Scales = 1 mm. In colour online.

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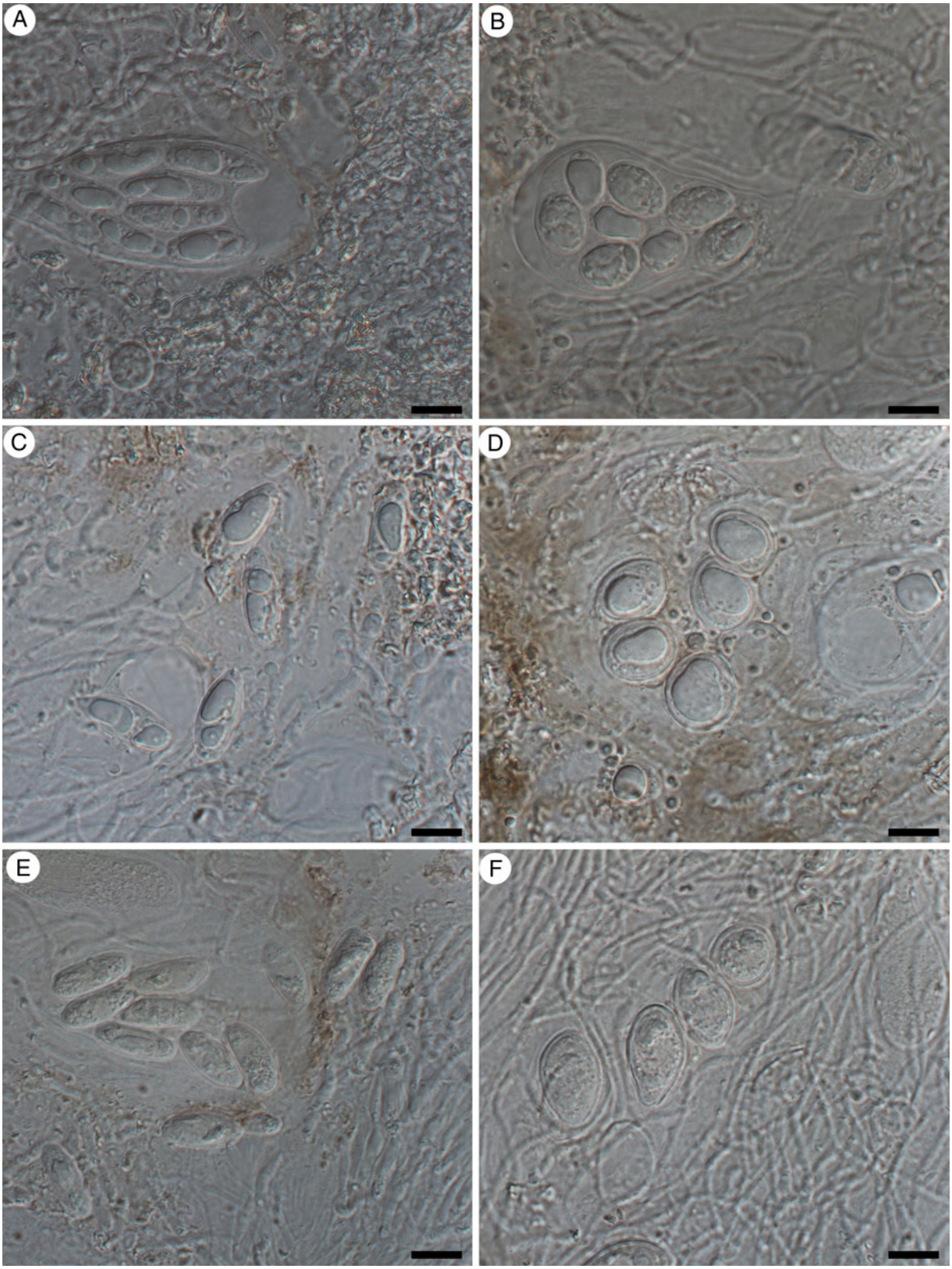

Figure 5. Comparison of the ascospores of *Aspilidea* species. A, C & E, *Aspilidea subadunans* (A, *McCarthy* 3195; C, *McCarthy* 4161; E, TUR–V-05894). B, D & F, *Aspilidea myrinii* (B, O–L-175683; D, O–L-190124; F, O–L-207353) Scales = 10 μm. In colour online.

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Figure 6. Known distribution of *Aspilidea subadunans* in North America. In colour online.

Sagedia mastrucata (Wahlenb.) A. Nordin, Savić & Tibell

The collection of *Sagedia mastrucata* that we sequenced did not cluster with sequences from other collections of this species that we downloaded from GenBank. Clearly either our collections (*Wheeler* 6430, 6434; hb. Wheeler) or those sequenced previously are incorrectly identified. The lectotype of *Lichen mastrucatus* Wahlenb. (Nordin *et al.* 2007) and the description given by Wahlenberg (1812) match our specimen collected from Varangerfjord in northern Norway, near the type locality of *Lichen mastrucatus*. It is probable, therefore, that previously sequenced specimens from Scandinavia and elsewhere identified as *S. mastrucata* are a different, presumably undescribed species. These are included in our phylogenetic tree (Fig. 1) as *S.* aff. *mastrucata*.

Lichenicolous fungus on Aspilidea subadunans

A lichenicolous fungus with large perithecia (*c.* 0.2–0.4 mm diam.) and simple ellipsoid ascospores ((8.7–)*12.0* ± 1.40(–15.1) × (4.9–)*6.6* ± 0.73(–9.1) µm, l/w ratio (1.24–)*1.84* ± 0.31(–2.94), $n = 68$) growing on several collections of *A. subadunans* was identified as *Sagediopsis aspiciliae* Nik-Hoffm. & Hafellner (Hoffmann & Hafellner 2000) (Fig. 8). This has been reported previously on *A. myrinii* in Europe but is reported here for the first time from North America.

Two species of *Sagediopsis* have been reported from *Aspilidea myrinii*: *S. aspiciliae* and *S. fissurisedens* Hafellner (Triebel 1993). *Sagediopsis fissurisedens* has larger perithecia (0.4–0.7 mm diam.) than *S. aspiciliae* and fusiform, 3-septate ascospores, 12–17 × 5–8 µm. We have not observed *S. fissurisedens* on any specimen of *A. subadunans*, or *S. aspiciliae* on any specimen of *A. myrinii* s. str. Given these observations and Hafellner's statement in Hafellner & Türk (2001) that the type specimen of *Lecanora myrinii* var. *subadunans* Vain. supported a different species of *Sagediopsis* to that reported from *A. myrinii* (Hafellner & Türk 2001), we suspect that previous reports of the occurrence of *S. aspiciliae* on *A. myrinii* are misidentifications of the host species and that the two species of *Sagediopsis* occur only on the two different species of *Aspilidea*. However, we note that the *Sagediopsis* sp. that occurs on the type species of *L. myrinii* var. *subadunans* has larger ascospores (14–18 × 8–11 µm, $\bar{x}$ *14.8* × *9.7* µm, l/w = 1.5, $n =$ 23) than are reported in the literature for *S. aspiciliae* and observed by us on other collections of this species.

Selected specimens examined. See Supplementary Material S2 (available online).

Discussion

This study is the largest comprehensive phylogenetic analysis of the family *Megasporaceae* so far performed. The family formed a well-supported monophyletic group composed of seven highly supported clades, corresponding to the genera *Aspilidea*, *Antidea*, *Lobothallia/Teuvoa*, *Circinaria/Megaspora/Aspiciliella/Atrostelia*, *Sagedia*, *Oxneriaria* and *Aspicilia* (Fig. 1: Roman

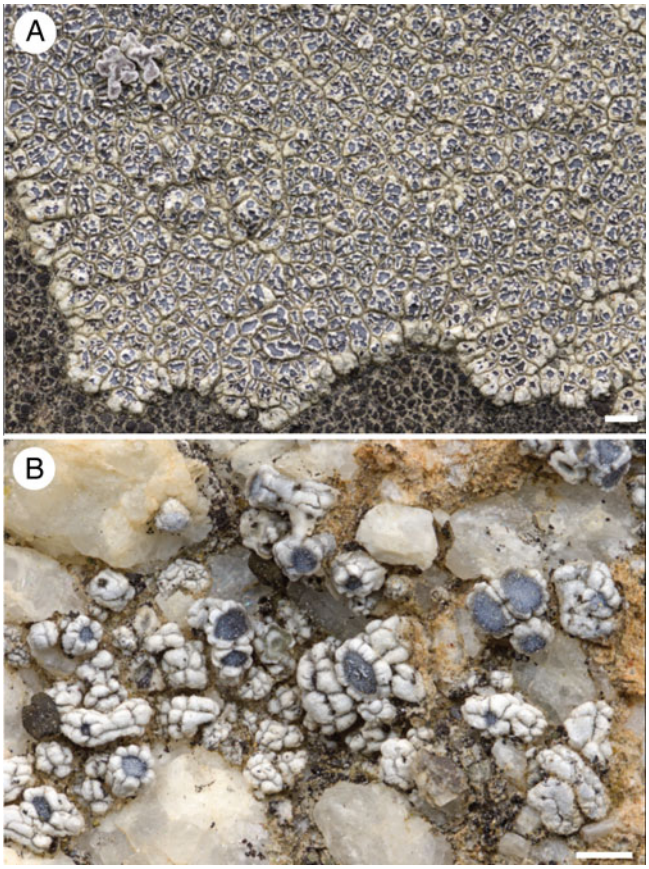

Figure 7. New combinations in *Lobothallia*. A, *L. determinata* (*Wheeler* 6017). B, *L. peltastictoides* (*Knudsen* 14420). Scales = 1 mm. In colour online.

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Table 3. Comparison of ascospore dimensions of *Aspilidea* species. Measurements are given as (lowest recorded–)$\bar{x}$ ± standard deviation(–highest recorded); *n* = number of spores measured

	Length (µm)	Width (µm)	l/w ratio	*n*
A. subadunans	(11.3–)***16.8*** ± 2.5(–22.0)	(4.9–)***7.1*** ± 1.2(–11.0)	(1.6–)***2.39*** ± 0.4(–3.3)	103
A. myrinii	(11.3–)***14.9*** ± 1.6(–18.9)	(7.9–)***11.0*** ± 1.5(–14.4)	(1.0–)***1.36*** ± 0.2(–1.8)	103

numerals I–VII). All clades were recovered as monophyletic and highly supported, with their relationships to each other also strongly supported, with the exception of the position of *Megaspora* and *Oxneriaria* as siblings to *Circinaria* and *Aspicilia* s. str., respectively. This analysis confirms the monophyly of the family, placing it with high support as sister to *Ochrolechiaceae*.

Systematic position of Aspilidea *and* Antidea

Our phylogeny shows that *Megasporaceae* is closely related to *Ochrolechiaceae* and that two genera, *Aspilidea* and *Antidea*, occupy a basal position in *Megasporaceae* close to *Ochrolechiaceae*. Although the two families have some similarities, they also differ in several respects.

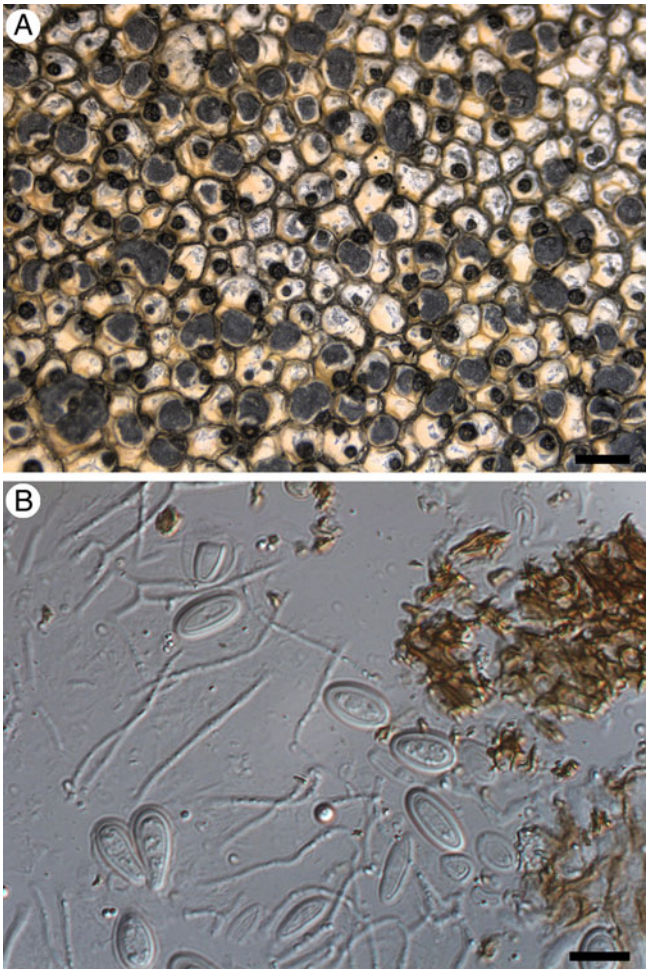

Figure 8. *Sagediopsis aspiciliae* (*McCarthy* 4423). A, thallus of *Aspilidea subadunans* with perithecia of *S. aspiciliae*. B, ascospores of *S. aspiciliae*. Scales: A = 1 mm; B = 10 µm. In colour online.

1) *Morphology*

The thalli of *Ochrolechiaceae* are pale creamy white in colour whereas those of *Megasporaceae* are predominantly pale to dark grey. *Antidea* has a grey thallus and resembles a species of *Megasporaceae* whereas *Aspilidea* has a pale cream-coloured thallus and more closely resembles *Ochrolechiaceae*.

Apothecia in *Ochrolechiaceae* are sessile to substipitate, discoid, lecanorine with a distinct, well-developed proper exciple, whereas those in *Megasporaceae* are immersed, sunken to sessile with a poorly developed exciple. The apothecia of *Antidea* and *Aspilidea* resemble those of *Megasporaceae*.

Ascospores in *Ochrolechiaceae* have thick walls and are large to very large (35–65(–300) × (18–)19–32(–100) µm in *Ochrolechia*) whereas those of *Megasporaceae* are thin-walled and smaller ((8–)15–25(–35) × 5–15(–26) um). The ascospores of *Aspilidea* and *Antidea* are thin-walled and within the range of *Megasporaceae*, and are much smaller than those of *Ochrolechiaceae*.

The epihymenium in *Ochrolechiaceae* is either hyaline or pale brown, whereas in *Megasporaceae* it is usually olivaceous (K+ brown, N+ green; Caesiocinerea-green). Consequently, the apothecial discs of *Ochrolechiaceae* are pale-coloured (yellow to pink to orange) whereas those of *Megasporaceae* are darkly pigmented (dark grey to black). Both *Antidea* and *Aspilidea* have an olivaceous epihymenium and dark-coloured apothecia.

Paraphyses in *Ochrolechiaceae* are thin, densely branching and anastomosing whereas in *Megasporaceae* they are thick, moniliform to submoniliform, unbranched to weakly branched, and not densely anastomosing. Both *Antidea* and *Aspilidea* have relatively narrow paraphyses but in *Antidea* they are submoniliform, suggesting a closer relationship to *Megasporaceae*. *Aspilidea* has non-moniliform paraphyses but in *Aspilidea myrinii* they are branched and anastomosing whereas those of *A. subadunans* are unbranched and not anastomosing.

Asci of *Ochrolechiaceae* have thick, multilayered, strongly amyloid walls, whereas *Megasporaceae* has thin-walled asci with a thin outer coat K/I+ blue, and K/I− wall and apical dome. The asci of *Aspilidea* and *Antidea* resemble those of *Megasporaceae*.

Aspilidea resembles *Ochrolechiaceae* in having a euamyloid (I+ blue) hymenium, whereas it is hemiamyloid (I+ orange-brown) in *Megasporaceae* and *Antidea*.

Many *Ochrolechia* species can have sterile vertical tissues dividing the hymenium. These are unknown in *Megasporaceae*, *Aspilidea* and *Antidea*.

Conidia in *Ochrolechiaceae* are elongate cylindrical to bacilliform (4–6 µm), whereas those in *Megasporaceae* are bacilliform to filiform long (5–40 µm). The conidia in both *Aspilidea* and *Antidea* are bacilliform (5–8 µm). Although there is some overlap in conidia size between *Ochrolechia* and *Antidea* and *Aspilidea*, other genera placed in *Megasporaceae* also have shorter conidia (e.g. *Lobothallia* and *Circinaria*).

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2) *Secondary metabolite chemistry*

Ochrolechiaceae usually produces orcinol depsides, depsidones, tridepsides or xanthones (gyrophoric, lecanoric, olivetoric, 5-*O*-methylhiascic, 4,5-di-*O*-methylhiascic, 4-*O*-demethylmicrophyllinic and hiascic acids, and lichexanthone), whereas *Megasporaceae* produce aspicilin and norstictic, connorstictic, hyposalazinic, hypostictic, stictic and substictic acids, or no substances. *Aspilidea* and *Antidea* both produce norstictic acid indicating a closer affinity with *Megasporaceae*.

3) *Ecology*

Megasporaceae is predominantly saxicolous whereas *Ochrolechiaceae* is also corticolous, lignicolous and terricolous. Both *Antidea and Aspilidea* are only saxicolous.

Given its grey thallus, euamyloid hymenium and submoniliform paraphyses, we consider the systematic position of *Antidea* to be firmly within *Megasporaceae*, but the position of *Aspilidea* is more ambivalent. The genus, apparently, occupies an intermediate position between the two families but we are reluctant to erect a new family for a single genus containing only two species without further evidence. Although some characters of *Aspilidea* suggest an affinity with *Ochrolechiaceae*, most point towards it being closer to *Megasporaceae* and so we include it in that family. However, we acknowledge that this may change when the systematics of *Pertusariales* are more fully explored.

Status of the genera

Two of the clades mentioned above are composed of more than one genus and it is worth considering the status of these genera. The two genera in the *Lobothallia* clade, *Lobothallia* and *Teuvoa*, share several morphological characters including short conidia and small ascospores. However, the recently described genus *Teuvoa* differs from *Lobothallia* by growing on lignin, and lacking thalline chemistry and a subhymenial algal layer. If *Teuvoa* is accepted at the genus level, then a case could be made for erecting additional genera to accommodate *L. determinata* and, perhaps, the *L. peltastictoides* group, resulting in the *Lobothallia* clade being split up into four genera. Alternatively, *Lobothallia* could be expanded to include *Teuvoa*, but here we take the conservative approach and retain *Lobothallia* and *Teuvoa* as distinct genera.

Similarly, the *Circinaria* clade also includes the genera *Megaspora, Aspiciliella* and *Atrostelia*, which could either be subdivided into separate genera or subsumed into *Circinaria,* but we again take the conservative approach and retain them as separate genera.

Given the arbitrary level at which genera are recognized, another approach would be to recognize the smaller clades inside *Circinaria* and *Lobothallia* as subgenera, or even to return them all to *Aspicilia* and recognize the individual clades I–VII as subgenera.

Conclusions

The phylogeny presented here represents a solid foundation for future research on *Megasporaceae*. The inter-family groups are well defined and supported, and the relationships among them, with the exception of *Oxneriaria* and *Megaspora*, are also well supported. However, worldwide, *Megasporaceae* comprises *c.* 300 species (Outline of Fungi 2024; Wijayawardene *et al.* 2022) but our phylogeny includes only 88 (i.e. *c.* 30%). The *Aspicilia/Oxneriaria* clade is particularly poorly represented, with only 50 out of an estimated global total of *c.* 200 being included and it is probable that the generic divisions proposed here will need adjustment as sampling improves. In addition, the intergeneric groups within *Aspicilia* and *Oxneriaria* are still poorly supported and unsettled, and further work involving different species and additional loci are required to elucidate these relationships.

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It gives us great pleasure to dedicate this paper to Teuvo Ahti, who has been a constant source of advice and information throughout our lichenological journeys. In particular, JMc expresses his sincere gratitude to Teuvo (Ted) for his generous mentorship, support and friendship over the years, and for his unwavering dedication to lichen research in Newfoundland and Labrador for more than 68 years. At the invitation of the Government of Newfoundland and Labrador, Teuvo first arrived in Newfoundland in the summer of 1956 as an undergraduate student studying the quality of Newfoundland caribou habitat, particularly the availability of reindeer lichens. His nine visits to Newfoundland reflect Teuvo's deep attachment to the people and land of the province. He has named two *Cladonia* species after the province, *Cladonia terrae-novae* Ahti (1960) and *Cladonia labradorica* Ahti & Brodo (1981).

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Competing Interests. The authors declare none.

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