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Three new species of *Atla* from calcareous rocks (*Verrucariaceae*, lichenized Ascomycota)

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Abstract: Three new species of *Atla* are described from calcareous rocks in northern Finland based on morphology and ITS sequences. All new species have dark brown spores but have smaller perithecia and spores than previously known brown-spored species of *Atla*. *Atla tibelliorum* sp. nov. resembles *Sporodictyon arcticum*, but has a dark brown exciple and larger spores. *Atla oulankaensis* sp. nov. and *A. vitikainenii* sp. nov. differ from *A. alpina* in the smaller perithecia and spores. *Atla vitikainenii* has an involucrellum often slightly diverging from the exciple. *Atla oulankaensis* is similar to *A. vitikainenii*, differing in slightly narrower spores and in having some involucrella incurving under the exciple or even enveloping the exciple. An unidentified ITS sequence from Canada obtained from GenBank most probably belongs to *A. oulankaensis* and another unidentified sequence from the USA to *A. tibelliorum*. The new results strengthen the conclusion that the genera of *Atla* and *Sporodictyon* cannot be separated by morphology alone. A key to all known species of *Atla* and *Sporodictyon* is provided.

Key words: Canada, Finland, ITS, lichens, *Sporodictyon*, taxonomy, USA

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Introduction

Atla Savić & Tibell is a genus of lichens that has recently been segregated from *Polyblastia* A. Massal. based on molecular data (Savić & Tibell 2008). Morphologically the genus may be confused with *Sporodictyon* A. Massal., a genus resurrected in a molecular study of Savić & Tibell (2009). Both genera are characterized by large muriform spores (40–120 µm long), which may be pale or dark brown, large perithecia (0·3–1·2 mm) and a northern or alpine distribution. In *Sporodictyon* perithecia are usually thinly or thickly covered by thalline tissue, unlike those in most species of *Atla*. However, two species of *Atla* are characterized by perithecia with a thalline cover, which does not reach the ostiolum (Savić & Tibell 2009; Tibell & Tibell 2015). In some species of *Sporodictyon* cephalodia are frequent, whereas cephalodia have not previously been reported from *Atla*.

Only six species of *Atla* are currently known. Two of them, *A. wheldonii* (Travis) Savić & Tibell and *A. alpina* Savić & Tibell, are fairly widely distributed in Europe, although they mainly occur in mountain areas (Savić & Tibell 2008; Hafellner 2010). Two species (*A. palicei* Savić & Tibell and *A. praetermissa* Savić & Tibell) were described from Scandinavia by Savić & Tibell (2008). Recently, Tibell & Tibell (2015) described the new species *A. alaskana* S. Tibell & Tibell from Alaska and *A. recondita* S. Tibell & Tibell from Sweden. All the known species of *Atla* occur in calcareous habitats: *A. wheldonii* is restricted to calcareous soil, while the remaining five species are found on calcareous or calciferous rocks.

During field studies of lichens of calcareous rocks in Finland, the first author found some specimens which, based on morphology, represented *Atla* or *Sporodictyon*, but

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which did not conform to any known species. In this paper we describe three new species of *Atla* based on morphology and ITS sequences: *A. oulankaensis*, *A. tibelliorum* and *A. vitikainenii*.

Material and Methods

Fieldwork

Specimens of *Atla* and *Sporodictyon* were searched for during a large-scale field study of lichens of calcareous rocks and lime quarries in Finland. The sampling was most intensive in southern Finland, but only one species belonging to *Atla* or *Sporodictyon* was found: *A. wheldonii*, new to Finland from two neighbouring localities (Pykälä 2013). Field studies in the two largest areas of calcareous rocks in Finland, occurring in the northern part of the country, were more successful: Kilpisjärvi in the biogeographical province Enontekiön Lappi (EnL) and the Kuusamo-Salla area in the biogeographical province Koillismaa (Ks). Several dozen specimens of *Atla* and *Sporodictyon* were found, most of them belonging to *Atla alpina* and *Sporodictyon schaererianum* A. Massal. Five unidentified specimens were sequenced in this study. In addition, the status of one specimen representing *A. palicei* based on morphological characters (see Pykälä 2013) was examined with molecular data.

Morphology

Perithecia and thalli were hand-sectioned with a razor blade. The sections were examined and measured in water. Asci and ascospores were also studied in squash preparations of perithecia mounted in water. Additionally, involucrellum characters and exciple colour and width were studied by cutting perithecia into two pieces and studying the pieces using a dissecting microscope.

Spore size is indicated as a range with the arithmetic mean in bold. Minimum and maximum values are given in parentheses. The size of the perithecia is given in surface view.

DNA extraction and sequencing

Total genomic DNA was extracted from perithecia (1–3) of two to four year-old herbarium specimens. All samples were placed in 96-well microplates and sent to the Canadian Centre for DNA Barcoding (CCDB). CCDB's standard protocols (documentation available at http://ccdb.ca/resources.php) were used for extraction, PCR and sequencing. Primers ITS1-LM (Myllys *et al.* 1999) and ITS4 (Gardes & Bruns 1993) were used both for PCR and sequencing of the nuclear ribosomal ITS barcode region. The barcode sequences and their trace files along with all relevant collection data were uploaded to the Barcode of Life Data Systems (BOLD, http://www.boldsystems.org) database. The sequences are available in GenBank.

Phylogenetic analyses

We examined phylogenetic relationships of the new species using ITS sequence data. In our analysis we used our newly produced sequences, together with all *Atla* sequences and selected sequences of *Sporodictyon*, *Henrica* B. de Lesd., *Verrucaria muralis* Ach. and *V. rupestris* Schrad. obtained from GenBank. All these belong to the so-called "E clade" of the "*Polyblastia* group" as defined by Savić *et al.* (2008). Additionally we included sequences obtained from soil samples, which based on a BLAST search (Altschul *et al.* 1990) were closely related to *Atla* (Timling *et al.* 2014). *Thelidium umbilicatum* Th. Fr., *Polyblastia aurorae* Savić & Tibell and *P. borealis* Savić & Tibell were used as outgroups, based on the studies of Savić *et al.* (2008) and Thüs *et al.* (2015).

A total of 42 ITS sequences were aligned with MUSCLE v.3.8.31 (Edgar 2004) using EMBL-EBI's freely available web service (http://www.ebi.ac.uk/Tools/msa/muscle/). The aligned data set was subjected to maximum parsimony analysis as implemented in TNT v.1.1 (Goloboff *et al.* 2008). The analysis was performed using Traditional search with random addition of sequences, with 100 replicates and TBR branch-swapping algorithm. Ten trees were saved for each replicate. Gaps were treated as missing data. Node support was estimated using the bootstrapping method (Felsenstein 1985) with 1000 replicates.

Results and Discussion

Phylogeny

Seven new nuITS sequences were obtained in this study representing four species of *Atla* and one of *Sporodictyon schaererianum* (Table 1). Our ITS phylogeny largely agrees with the previous two-gene-loci analyses of Savić *et al.* (2008) and Savić & Tibell (2008), with one exception: in the strict consensus of 24 most parsimonious trees, the genus *Atla* is paraphyletic (but without support) (Fig. 1), while in the earlier analyses it appeared as a monophyletic sister group to *Sporodictyon*. An *Atla*-*Sporodictyon* clade is strongly supported, but the relationships between different *Atla* species remain unsupported.

One specimen representing a putative new species, *Atla oulankaensis*, groups with one unidentified ITS sequence collected from Banks Island, Canada (KF297239; Timling *et al.* 2014). The Canadian sequence differs from the Finnish one only by three gaps and most probably also represents *A. oulankaensis*. The sequence was obtained from a soil sample

TABLE 1. *Specimen information and GenBank accession numbers for taxa used in this study. New sequences are indicated by accession numbers in bold.*

Species	Country	Voucher	GenBank accession number (ITS)
Atla alaskana	USA	*Savić* 5003 (UPS)	KP259842
A. alpina	Sweden	*Savić* 3919A (UPS)	EU697724
A. alpina	Sweden	*Savić* 3127 (UPS)	EU697725
A. alpina	Sweden	*Savić* 3129 (UPS)	EU697726
A. alpina	Sweden	*Savić* 3139b (UPS)	EU697720
A. oulankaensis	Finland	*Pykälä* 40105 (H)	**KT983413**
A. palicei	Sweden	*Palice* 7182 (UPS)	EU553499
A. palicei	Finland	*Pykälä* 45025 (H)	**KT983414**
A. praetermissa	Sweden	*Savić* 3285 (UPS)	EU697722
A. praetermissa	Norway	*Savić* 3283 (UPS)	EU697723
A. praetermissa	Sweden	*Savić* 3284 (UPS)	EU697721
A. recondita	Sweden	*Savić* 3304 (UPS)	FJ232936
A. recondita	Sweden	*Savić* 3305 (UPS)	FJ232935
A. recondita	Sweden	*Savić* 3263b (UPS)	FJ232937
A. tibelliorum	Finland	*Pykälä* 43330 (H)	**KT983415**
A. vitikainenii	Finland	*Pykälä* 40222 (H)	**KT983416**
A. vitikainenii	Finland	*Pykälä* 43378 (H)	**KT983417**
A. vitikainenii	Finland	*Pykälä* 43614 (H)	**KT983418**
A. wheldonii	Sweden	*Savić* 3070 (UPS)	EU553497
A. sp.	USA	no voucher	KC965258
A. sp.	USA	no voucher	KC966148
A. sp.	Canada	no voucher	KC965806
A. sp.	USA	no voucher	KC966268
A. sp.	USA	no voucher	KC965261
A. sp.	Canada	no voucher	KC966360
A. sp.	Canada	no voucher	KF297239
Henrica melaspora	Sweden	*Savić* 3307 (UPS)	FJ2329329
H. theleodes	Norway	*Savić* 3159 (UPS)	EU559733
Polyblastia aurorae	Sweden	*Tibell* 23601 (UPS)	JQ088062
P. borealis	Sweden	*Savić* 3151C (UPS)	JQ088073
Sporodictyon cruentum	Sweden	*Savić* 3031 (UPS)	EU553493
S. cruentum	Sweden	*Savić* 3400 (UPS)	EU697648
S. minutum	Sweden	*Savić* 3111 (UPS)	EU697660
S. minutum	Norway	*Savić* 3152 (UPS)	EU697677
S. schaererianum	Sweden	*Tibell* 23545 (UPS)	EU553504
S. schaererianum	Finland	*Pykälä* 36366 (H)	**KT983419**
S. terrestre	Sweden	*Tibell* 23067 (UPS)	EU559736
S. terrestre	Norway	*Savić* 3125 (UPS)	EU697668
Thelidium umbilicatum	Sweden	*Tibell* 23525 (UPS)	EU559737
Verrucaria muralis	France	*Gueidan* 578 (DUKE)	EU010261
V. muralis	Iceland	*Orange* 16916 (NMW)	FJ664876
V. rupestris	Estonia	*Suija* 652 (TU)	EU553501

(probably spores dispersed from the nearby rocks or stones) for which no lichen voucher is available.

The ITS phylogeny suggests a close, though unsupported, relationship between *A. oulankaensis* and *A. alaskana*, and comparison of ITS sequences revealed 97·6% sequence similarity between the two species. However, *A. oulankaensis* and *A. alaskana* are morphologically clearly different (see taxonomy below).

Two of the new *Atla* species discovered in this study (*A. vitikainenii*, represented by three sequences, and *A. tibelliorum*) group with the members of *Sporodictyon*, but this relationship receives no support. One sequence obtained from the soil sample from the USA forms a strongly supported clade with *A. tibelliorum*

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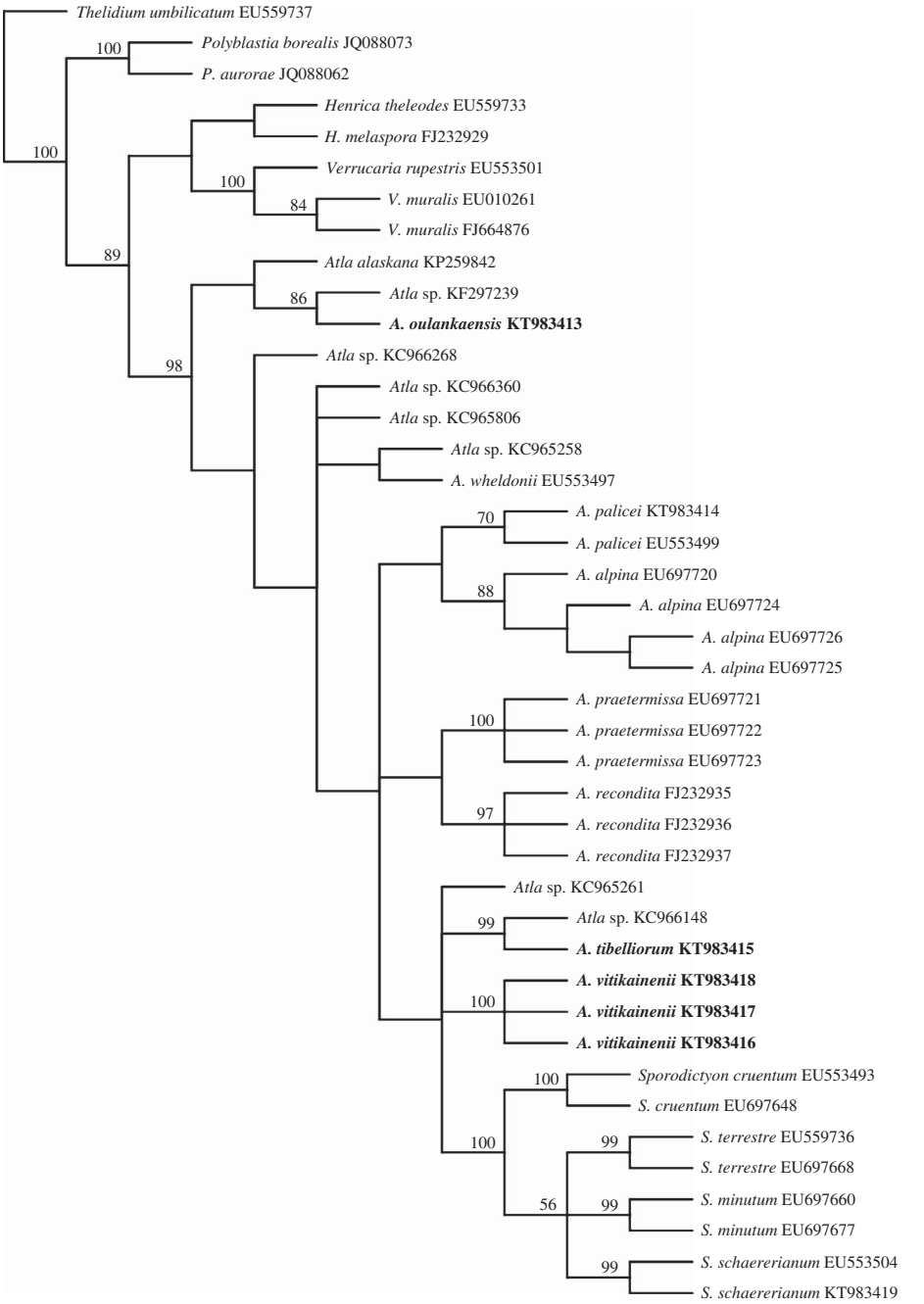

FIG. 1. Phylogeny of the genera *Atla* and *Sporodictyon*. Strict consensus based on ITS data set with bootstrap values (>50%) at nodes. New species described in this study are indicated in bold.

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and probably belongs to the same species. This suggests that the distribution of *A. tibelliorum* extends to North America.

In addition to the three new species, one specimen collected from Finland (and identified as *A. palicei* based on morphological characters; see Pykälä 2013) may represent yet another undescribed species. It groups with one GenBank sequence of *A. palicei* but this relationship receives only 70% bootstrap support. The two sequences differ by 3%, a value which has traditionally been used as a threshold for delimiting fungal species (Begerow *et al*. 2010). However, we could not find any clear morphological difference between the specimen and the description of *A. palicei* by Savić & Tibell (2008). The Finnish specimen has a slightly thinner involucrellum (70–90 µm thick) and a less developed non-areolate thallus. The specimen is for the time being included in *A. palicei*, pending more material.

Besides being distinguished from the other species of *Atla* by their ITS sequences, *A. oulankaensis*, *A. tibelliorum* and *A. vitikainenii* also show morphological differences with each other and with the previously known species of *Atla* and *Sporodictyon*. Thus, we are confident that they represent new species, although we have only one sequence available for each of *A. oulankaensis* and *A. tibelliorum*.

The main morphological differences between *Atla* and *Sporodictyon* have been the lack of cephalodia and usual absence of thalline cover of perithecia in *Atla*. Tibell & Tibell (2015) emphasized that thalline cover (if present) in *Atla* does not reach close to the ostiolum, unlike in *Sporodictyon* where it often (almost) reaches the ostiolum. However, *A. oulankaensis* and *A. tibelliorum* have cephalodia or cephalodia-like structures, and the perithecia of *A. tibelliorum* are thickly covered by the thallus up to the ostiolum. These results support the conclusion that *Atla* and *Sporodictyon* cannot always be separated by morphology alone.

Even though two of the new species, *A. tibelliorum* and *A. vitikainenii*, group with *Sporodictyon* in the ITS analysis, we have decided to include them in the genus *Atla* for the following reasons: members of *Sporodictyon* form a strongly supported group in the phylogeny and neither *A. tibellii* nor *A. vitikainenii* is included in this group. The strong support most probably stems from the characteristic ITS profile of all *Sporodictyon* sequences: these are *c*. 23–36 bases longer than ITS sequences of *Atla* due to indels. However, because *Atla* and *Sporodictyon* cannot be separated by morphology alone, we provide a key to all known species of *Atla* and *Sporodictyon*.

The new results underline the previously known fact that the genus *Atla* has a northern distribution. In Finland, all species of *Atla* are very rare and all of them (except *A. wheldonii*) occur only in northern Finland in areas with many other rare northern or even arctic species. Species described here as new were not found from Sweden or Norway in the study of Savić & Tibell (2008), which suggests that they are probably rare or absent in the other Nordic countries.

The soil samples studied from the North American Arctic (Timling *et al*. 2014) were surprisingly well represented by species of *Atla*. Four North American specimens used in the analysis may represent undescribed species of *Atla*. One of these groups is with *A. wheldonii* but this relationship receives no support. The result suggests that the genus *Atla* may be more species-rich in North America than previously thought. More studies on lichens of arctic areas are needed to discover the real species richness of the genus. These kinds of studies are urgently needed as *Atla* may prove to be among the most sensitive groups of lichens to global warming because of its northern distribution.

The Species

Atla oulankaensis Pykälä & Myllys sp. nov.

MycoBank No.: MB815133

Perithecia smaller than in *Atla alpina*, involucrellum to the exciple base level, appressed to the exciple, in some perithecia enveloping the exciple, spores (20–) 23–28(–32) µm wide.

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Type: Finland, Koillismaa, Kuusamo, Juuma, Oulanka National Park, gorge Jäkälävuoma, calciferous (dolomitic) schistose rock outcrop, on NW-facing wall, 208 m, 66° 15'N, 29°26'E, 16 August 2010, *Pykälä* 40105 (H—holotype); GenBank accession no. KT983413 (ITS).

(Fig. 2A)

Thallus grey to greenish grey, thin, *c.* 10–50 µm thick, continuous, rather frequently covered by cyanobacteria (*Nostoc*), some forming cephalodia or cephalodia-like structures, *Nostoc* cells 5–7 µm. *Photobiont* green, algal cells 5–8 µm.

Perithecia 0·30–0·38 mm diam., 1/4–immersed, young perithecia thinly covered by a thalline layer except at apex, thalline cover *c.* 8–15 µm thick, old perithecia without thalline cover; perithecial density *c.* 50–80 cm^{-2}. *Ostiole* pale to dark, depressed, 30–100 µm wide. *Involucrellum* to the exciple base level or incurving under the exciple, or enveloping the exciple, 38–76 µm thick, appressed to the exciple. *Exciple* 0·25–0·37 mm diam., wall medium brown to dark brown, *c.* 30–35 µm thick. *Periphysoids c.* 30–63 × 1–2 µm, branching to anastomosing. *Asci c.* 147–177 × 63–72 µm, 8-spored. *Ascospores* dark brown (a few mature or even overmature spores pale), muriform, (42–)51–**60**–69(–75) × (20–)23–**25**–28(–32) µm (*n* = 72), with (10–)12–16 transsepta reaching the periphery along one side of the spores in a median optical section, and with 4–6(–7) longisepta in the central part, spores often bent, old spores easily broken into two pieces.

Etymology. The species is named after the Oulanka National Park and surroundings, which is one of the lichenologically most valuable areas in Finland.

Habitat and distribution. The specimen is from a shady wall of a calciferous rock. The locality is a gorge famous for many rare and threatened lichens and plants. *Atla oulankaensis* is apparently a very rare and threatened species in Finland. The Canadian specimen from Banks Island was collected on bare soil with high pH (8·4) (Timling *et al.* 2014). It is possible that the main range of *A. oulankaensis* is in North America, reminiscent of the distribution pattern of *Peltigera retifoveata* Vitik., which occurs in the Oulanka area but is very rare elsewhere in Europe. Its main distribution lies in western North America (Goffinet 1992). In fact, Jäkälävuoma, the only Finnish locality of *A. oulankaensis*, is also the type locality for *P. retifoveata* (Vitikainen 1985).

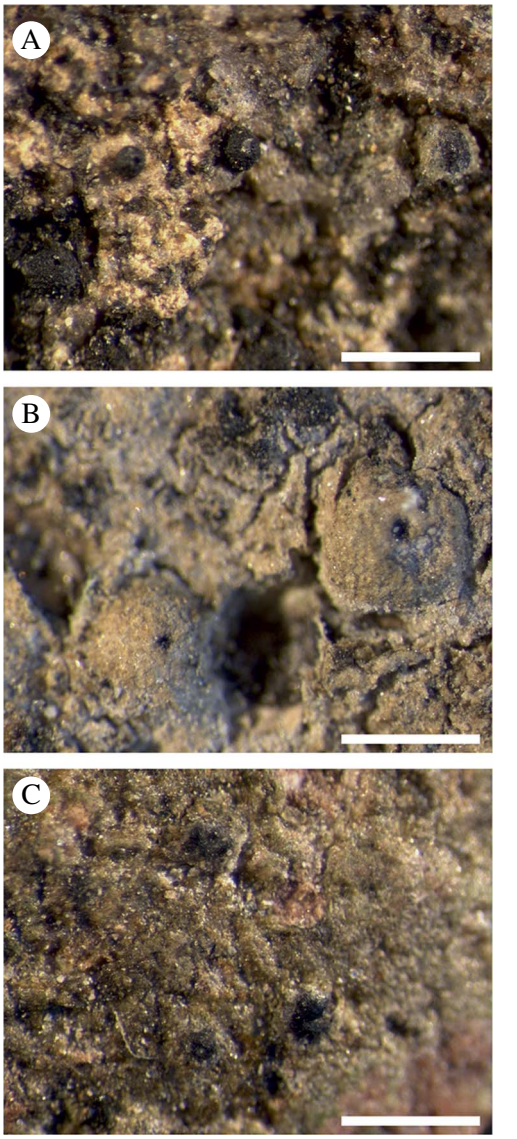

FIG. 2. A, *Atla oulankaensis* (holotype); B, *A. tibelliorum* (holotype); C, *A. vitikainenii* (holotype). Scales = 1 mm. In colour online.

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Notes. Based on ITS phylogeny, *A. oulankaensis* is closely related to *A. alaskana* but the two species clearly differ by their morphology and ecology. *Atla alaskana* has larger perithecia, pale spores and a thick thallus. It occurs on open calciferous rock (Tibell & Tibell 2015), whereas *A. oulankaensis* occurs on the shady NW-facing wall of a calciferous rock. Morphologically, *A. oulankaensis* is rather similar to *A. vitikainenii* and more material is needed to determine whether the species can be unambiguously identified on the basis of morphological characters. In *A. oulankaensis* the involucrellum is appressed to the exciple and often incurving under or even enveloping the exciple, while in *A. vitikainenii* the involucrellum is often slightly diverging from the exciple and not incurving under it. Spores of *A. oulankaensis* are on average narrower, but there is much overlap in the spore size. *Atla oulankaensis* may also be confused with *Sporodictyon cruentum* (Körb.) Körb., which has larger perithecia, a brown thallus and different habitat (siliceous rocks by water). The spores of *A. oulankaensis* may sometimes turn brown rather late and thus it may also be confused with species having pale spores. *Sporodictyon minutum* Savić & Tibell (Savić & Tibell 2009) has smaller spores and a thinner involucrellum.

Atla tibelliorum Pykälä & Myllys sp. nov.

MycoBank No.: MB815134

Similar to *Sporodictyon arcticum*, but exciple wall dark brown and spores larger (63–73 × 40–46 µm).

Type: Finland, Enontekiön Lappi, Enontekiö, Porojärvet, Toskalharji, Toskaljärvi N, fell, calcareous alpine grassland, on dolomite pebbles, 730 m, 69°12'N, 21°26'E, 2 August 2011, *Pykälä* 43330 (H—holotype); GenBank accession no. KT983415 (ITS).

(Fig. 2B)

Thallus pale ochraceous, rimose to areolate, *c*. 200–280 µm thick, areoles 0·4–1·0 mm wide, algal cells 6–11 µm, cortex *c*. 5–25 µm thick, epinecral layer 8–13 µm thick; few cephalodia or cephalodia-like structures (containing *Nostoc*) present.

Perithecia immersed in thalline warts, only exposed surrounding the ostiole, exposed part 0·10–0·15 mm wide, thalline cover of perithecia *c*. 50–150 µm thick; perithecial density *c*. 30 cm^{-2}. *Ostiole* inconspicuous, tiny, dark, depressed, *c*. 30–60 µm wide. *Involucrellum* to the exciple base level, 50–70 µm thick, sometimes thickened towards the base to 60–110 µm thick, appressed to the exciple, sometimes somewhat diffusely pigmented at base. *Exciple* 0·25–0·48 mm diam., wall dark brown. *Periphysoids* *c*. 55–93 × 1·0–1·5 µm, branching. *Asci* *c*. 147–177 × 63–72 µm, 8-spored. *Ascospores* dark brown, muriform, (57–)63–**68**–73(–80) × (38–)40–**43**–46(–52) µm (*n* = 30), with 10–15 transsepta reaching the periphery along one side of the spores in a median optical section, and with 5–7 longisepta in the central part.

Etymology. The species is named in honour of Sanja and Leif Tibell, the mother and father of the genus *Atla*, for their invaluable contribution to the taxonomy of the "polyblastioid" genera of lichens (*Polyblastia* s. lat.).

Habitat and distribution. The specimen is from a dolomite pebble on a fell in NW Finland. The species occurs on alpine grassland close to flat open dolomite rocks. Numerous rare lichens occur in the Toskalharji area, which is the largest area of calcareous rocks in Finland. Apparently *A. tibelliorum* is a very rare species in Finland. The North American soil sample including *A. tibelliorum* was collected from the dwarf shrub tundra in the Franklin Bluffs, Alaska (USA) from high pH soil (8·0) (Timling *et al*. 2014).

Notes. The species clearly differs morphologically from the other species of *Atla* by having the perithecia immersed in warts, and in the large brown spores. It is rather similar to *Sporodictyon arcticum* Savić & Tibell, which also has thickly thallus-covered perithecia, but that species has a pale exciple and smaller spores (see Savić & Tibell 2009). Based on morphology, *A. tibelliorum* and *S. arcticum* may be closely related. Unfortunately, no sequence of *S. arcticum* is available.

Atla vitikainenii Pykälä & Myllys sp. nov.

MycoBank No.: MB815132

Perithecia smaller than in *Atla alpina*, involucrellum mainly slightly diverging from the exciple, not incurving under the exciple, spores (25 −)26–30(−33) µm wide.

Type: Finland, Koillismaa, Salla, Oulanka National Park, W of Savikoski, cliff, dolomite rock outcrop, NE-facing wall, on pebbles, with *Verrucaria* cf. *inaspecta* Servít, 185 m, 66°25'N, 29°10'E, 17 August 2010, *Pykälä* 40222 (H—holotype); GenBank accession no. KT983416 (ITS).

(Fig. 2C)

Thallus thin, continuous or fleck-like, occasionally slightly rimose, grey, ochraceous, pale green or dark brown, *c.* 20–100 µm thick. *Photobiont* green alga, algal cells *c.* 5–7 µm.

Perithecia 0·25–0·46 mm diam., 1/4–1/2 (–3/4)-immersed, not leaving pits or leaving shallow pits, often thinly thallus-covered except for the apex; perithecial density *c.* 20–80 cm^{-2}. *Ostiole* dark, plane or depressed, 20–80 µm wide. *Involucrellum* extending to the exciple base level, 50–100 µm thick, appressed to the exciple or slightly diverging from the exciple. *Exciple* 0·25–0·38 mm diam., wall pale to dark brown, 25–34 µm thick. *Periphysoids c.* 44–54 × 1·5–2·5 µm, branching. One mature ascus seen 150 × 63 µm, 8-spored. *Ascospores* dark brown, muriform, (40–)54–**59**–64(–70) × (25–)26–**28**–30(–33) µm (*n* = 136), with (10–)12–16 (–18) transsepta reaching the periphery along one side of the spores in a median optical section, and with (3–)4–6 longisepta in the central part, spores often bent, old spores easily broken into two pieces.

Etymology. The species is named in honour of Orvo Vitikainen, who has contributed in many ways to our knowledge of the taxonomy, ecology and biogeography of Finnish lichens. The first author is much indebted to Orvo, who has generously helped in identifying lichens over many years and has provided encouragement during the process of becoming a professional lichenologist. Furthermore, Orvo has previously described a new species from calcareous habitats of Finland (*Peltigera retifoveata*).

Habitat and distribution. Four specimens are known (three sequenced specimens), three of them collected from dolomite pebbles and one from a dolomite boulder. The species occurs both in the Kilpisjärvi and Oulanka areas, the only two areas in northern Finland with a cluster of larger calcareous rocks. *Atla vitikainenii* is a northern species, probably mainly occurring in arctic areas and in northern mountains above the alpine tree line. The occurrences in the Oulanka area may be relictual. The Oulanka area has many northern/arctic-alpine lichens and plants considered to be relicts from colder climate periods.

Notes. Atla vitikainenii is fairly similar to *A. oulankaensis* (see *A. oulankaensis* for differences). *Sporodictyon cruentum* has larger perithecia, slightly smaller spores and a brown thallus. All three sequenced specimens of *A. vitikainenii* belong to the same haplotype, although they show considerable morphological differences in thallus colour and exciple wall colour.

Additional specimens examined. **Finland:** *Enontekiön Lappi*: Enontekiö, Porojärvet, Toskalharji, Toskaljärvi N, fell, dolomite scree, on dolomite pebbles, with *Thelidium fontigenum* A. Massal., 710 m, 69°11'N, 21°26'E, 2011, *Pykälä* 43378 (H); Enontekiö, Porojärvet, Toskalharji, 1·2 km NE of Toskaljärvi, fell, SW-slope, gentle E-slope, *Dryas* heath, on dolomite pebbles, 875 m, 69°12'N, 21°28'E, 2011, *Pykälä* 43614 (H). *Koillismaa*: Kuusamo, Oulanka National Park, Taivalköngäs, shore of Oulankajoki River, *Picea abies*- dominated herb-rich forest, NE-slope, dolomite boulder, on NE-facing wall, 171 m, 66°24'N, 29°11'E, 2011, *Pykälä* 44595 (H).

Key to the species of *Atla* and *Sporodictyon*

1 Spores pale when mature 2
Spores dark brown when mature 7

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2(1) Perithecia 0·45–0·75 mm, spores 51–65 × 23–32 µm 3
Perithecia 0·3–0·5 mm, spores 41–57 × 19–27 µm 4

3(2) Perithecia 0·45–0·7 mm, spores 51–65 × 23–30 µm, cephalodia frequent . . . . . **Sporodictyon terrestre**
Perithecia 0·60–0·75 mm, spores 53–62 × 27–32 µm, cephalodia absent . . . . . **Atla alaskana**

4(2) Involucrellum 70–110 µm thick, thallus blackish brown to black . . . . **Atla palicei**
Involucrellum 30–80 µm thick, thallus grey, green, pale brown or medium brown 5

5(4) Perithecia usually thalline covered, spores 47–57 × 22–27 µm . . . . . **Sporodictyon minutum**
Perithecia not thalline covered, spores 41–49 × 19–23 µm 6

6(5) Thallus grey to dark green, appearing fragmented, spores with 8–11 transverse walls and with 2–4 longitudinal walls . . . . . **Atla praetermissa**
Thallus ochraceous to olivaceous brown, continuous, spores with 9–15 transverse walls and with 3–4 longitudinal walls . . . . . **Atla recondita**

7(1) Involucrellum absent, on soil . . . . . **Atla wheldonii**
Involucrellum to the exciple base, on rock 8

8(7) Thallus thick, thalline cover of perithecia thick, complete or irregular 9
Thallus thin, thalline cover of perithecia absent or thin 11

9(8) Exciple dark brown, spores 57–83 × 39–52 µm . . . . . **Atla tibelliorum**
Exciple pale, spores 59–77 × 31–43 µm 10

10(9) Perithecia completely thalline covered, spores 63–77 × 36–43 µm . . . . . **Sporodictyon arcticum**
Thalline cover of perithecia usually irregular, more rarely completely thalline covered, spores 50–73 × 30–40 µm . . . . . **Sporodictyon schaererianum**

11(8) Perithecia 0·5–0·9 mm 12
Perithecia 0·25–0·50 mm 13

12(11) Perithecia 0·5–0·9 mm, without thalline cover, spores (55–)65–85 × (30–)32–50 µm . . . . . **Atla alpina**
Perithecia 0·5–0·7 mm, usually with thin irregular thalline cover, spores 50–65 × 24–32 µm . . . . . **Sporodictyon cruentum**

13(11) Involucrellum appressed to the exciple, some involucrella incurving under the exciple or enveloping the exciple, spores (20–)23–28(–32) µm wide . . . . . **Atla oulankaensis**
Involucrellum often slightly diverging from the exciple, not incurving under the exciple, spores (25–)26–30(–33) µm wide . . . . . **Atla vitikainenii**

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